AN ABSTRACT OF THE THESIS OF

David Randall Strehlow for the degree of ___Master of Science___

in the School of Oceanography presented on ___3 May 1982___

Title: The Relation of Tidal Height and Sediment Type to the Inter-
tidal Distribution of Marine Oligochaetes in Coos Bay, Oregon

Redacted for privacy

Abstract approved: _
_____
Dr. J.J. Gonor

The taxonomy of intertidal oligochaetes, and the relationships
between oligochaete species distributions, tidal height, and sediment
type, were studied in detail for a sand and mud flat in lower Coos
Bay, Oregon.

Eighteen species, representing four families, were identified.
Three species of Enchytraeidae (Marionina vaucheriae, Marionina
callianassae, and Marionina gonori) and one species of Tubificidae
(Aktedrilus oregonensis) are new to science. A preliminary description
of a new family, Psammotheriidae, based on Psammotherium hastatus n.g.,
n.sp. is given. Other species present were Marionina vancouverensis,
M. sjaelandica, M. subterranea, and M. achaeta (Enchytraeidae);
Aktedrilus locyi, Limnodriloides monothecus, L. victoriensis, L.
verrucosus, Tubificoides coatesae, and T. pseudogaster (Tubificidae);
and Paranais litoralis (Naididae). Individuals of Enchytraeus sp.
and Lumbricillus spp. (Enchytraeidae) were found but were not fully

mature, and therefore could not be identified to species. Nine of the eighteen species are known only from the northeast Pacific littoral zone, indicating the existence of a distinct regional oligochaete fauna. Earlier studies of the Enchytraeidae (Coates and Ellis 1981) and Tubificidae (Brinkhurst and Baker 1979) support this conclusion.

Distinct oligochaete species assemblages were closely associated with physical habitat types defined by tidal exposure and sediment type. The distributions of species were not correlated with each other or with physical habitat types, however.

Tide levels at which large changes in maximum continuous tidal exposure or submergence occur (critical tide levels) are strongly associated with the intertidal zonation of species. Sediment type is an important determinant of species composition, but is not closely associated with intertidal zonation.

The Relation of Tidal Height and Sediment
Type to the Intertidal Distribution of
Marine Oligochaetes in Coos Bay, Oregon

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of
Master of Science

Completed May 3, 1982

Commencement June 1982

APPROVED:

Redacted for privacy

Associate Professor of Oceanography in charge of major

Redacted for privacy

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Redacted for privacy

Dean of Graduate School

Date thesis is presented   May 3, 1982

Typed by Karen Dykes for   David Randall Strehlow

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General Introduction

The Oligochaeta are hermaphroditic, burrowing annelid worms found
in almost all soils and aquatic sediments worldwide. More than 5700
species belonging to 24 families are known (Reynolds and Cook 1976),
but only the Tubificidae and the Enchytraeidae are abundant in the
marine environment. There are about 200 marine species in these two
families together.

Most Enchytraeidae are terrestrial, but some species are aquatic.
Three of the 21 enchytraeid genera, Lumbricillus, Marionina, and Grania
are well represented in the marine environment, but Grania is the only
strictly marine genus. Almost all marine species in this family are
limited to the intertidal zone, with only Grania and some Lumbricillus
species found subtidally.

The Tubificidae are primarily freshwater, but most marine
oligochaete genera and species are included in this family, which is
distinctly divided at generic and subfamilial levels into marine and
freshwater forms. Tubificid genera as presently defined (see Holmquist
1978, 1979; Brinkhurst and Baker 1979; Baker and Brinkhurst 1981) gen-
erally contain either freshwater or marine species, but not both, and
most marine species belong to one subfamily, the Phallodrilinae.
Tubificids have been found in all marine benthic substrates from the
intertidal to the abyssal zone (Erséus 1980b).

Knowledge of the geographical distribution and biology of marine
oligochaetes has advanced considerably in recent years. Recent work

by Brinkhurst and Jamieson (1971), Giere (1975), Brinkhurst and Cook (1980), and Erséus (1980b) indicates that marine oligochaetes are a diverse, widespread group in the marine environment, and may be numerically very abundant, particularly in the littoral and sublittoral zones. The population biology of marine oligochaetes is poorly known, but the studies of Pfannkuche (1979, 1980) indicate that some tubificid species mature and reproduce only once, after their second year, and then die. Reproduction was found to occur mainly in the spring. Information from taxonomic studies (e.g. Nielsen and Christensen 1959, personal observations) indicates that fecundity is low with only one or a few mature eggs present in the coelom at a time.

Oligochaetes are important reworkers of soils and sediments in terrestrial and freshwater environments but are less important in marine sediments because marine species are small (Diaz 1980). The absence of large oligochaete species from marine habitats has been ascribed to competition from polychaetes (Diaz 1980), the dominant annelidan infaunal group of marine sediments. However the absence of large marine oligochaetes may be attributed more directly to the oligochaete reproductive strategy of direct development and few eggs. Marine oligochaetes are either interstitial or small burrowing forms. In this size range, lack of planktonic larvae and direct development are reproductive strategies generally employed by all taxonomic groups. Large oligochaete species in the marine environment would have the same reproductive strategy, but would be competing with similar sized infaunal polychaete species with high fecundity and planktonic larvae. High fecundity and good dispersal mechanisms may be required by large

infauna to maintain their populations despite high predation rates. Oligochaetes, without these features may be at a competitive disadvantage, and may be able to compete successfully only with the small macrofauna and meiofauna, where the oligochaete reproductive strategy is not disadvantageous.

The taxonomy of Pacific littoral oligochaete species was recently brought up to date by the studies of Cook (1974), Brinkhurst and Baker (1979), and Baker and Brinkhurst (1981) for the Tubificidae, and by Coates and Ellis (1981) for the Enchytraeidae. Knowledge of this fauna is still incomplete but it appears to be distinct from other regional faunas (Brinkhurst and Baker 1979, Coates and Ellis 1981). Only the studies of Cook (1974) on the tubificid fauna of the Bahia de San Quintin, Baja California, and Brinkhurst and Simmons (1968) provided quantitative abundance data for Pacific coast species. All other studies have been strictly taxonomic.

The present study describes the intertidal oligochaete fauna from a sedimentary beach in Coos Bay, Oregon, places it within the context of existing knowledge of Pacific coast marine oligochaete zoogeography, and provides quantitative information on the relationship between the distributions of species and physical factors.

Chapter One

The Systematics of Marine Intertidal

Oligochaetes from Coos Bay, Oregon, with

a Summary of the Zoogeography of West

Coast Species.

Introduction

Knowledge of the taxonomy and geographical distribution of marine oligochaetes of the Pacific coast of North America is increasing rapidly (Eisen 1904; Altman 1931, 1936; Brinkhurst and Simmons 1968; Tynen 1969; Cook 1974; Brinkhurst and Baker 1979; Coates 1980a, b, 1981; Erséus 1980; Baker and Brinkhurst 1981; Coates and Erséus 1980; Strehlow 1982). Of these papers only Strehlow (1982) includes species records for the section of coast between the strait of Juan de Fuca and San Francisco Bay. The purpose of this study is to partially fill this gap by describing the oligochaete fauna of an intertidal flat of sand and mud near the seaward end of Coos Bay, Oregon, and to complete the faunal description of this site begun by Strehlow (1982). A new oligochaete family will be described in a separate paper, along with a closely related species from the east coast of the United States. The physical description of the study site, and quantitative information on species distributions, will be discussed in detail in a separate paper.

Methods

All specimens were fixed in 10% formalin and stored in 70% isopropanol. Whole specimens stained in paracarmine and mounted in synthetic resin were used for all species identifications and descriptions. Observations were made under a light microscope using bright field, phase contrast, and differential interference contrast. The type series of new species described in this paper are on deposit in the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Taxonomy of the Species

Four families of marine oligochaetes were represented at the study site; the Enchytraeidae, the Tubificidae, the Naididae, and a previously undescribed family.

ENCHYTRAEIDAE

Marionina Michaelsen 1889

The revised generic definition of Marionina of Nielsen and Christensen (1959) was used in this study.

Marionina sjaelandica Nielsen and Christensen, 1961.

Marionina sjaelandica Nielsen and Christensen 1961, pp. 18-19, figs. 16-18.

Marionina sjaelandica. Coates and Ellis 1981, pp. 2137-2138, fig. 4.

Remarks: The Coos Bay specimens conform to the original description, except in features already noted by Coates and Ellis (1981). Specimens from both Coos Bay and British Columbia (Coates and Ellis 1981), possess a well developed glandular body on the ventral nerve cord of segment XIV of mature specimens; the presence of such a glandular body was not noted in the original description. The Coos Bay specimens are referred to M. sjaelandica because they are identical to the description of specimens, from British Columbia, referred to M. sjaelandica by Coates and Ellis (1981). M. sjaelandica has also been reported from Montery Bay, California (Steven Locy 1980, personal communication).

Habitat: In Coos Bay, patchy but abundant in upper intertidal (+1.5m to +2.0m) sand and slightly silty sand with Vaucheria spp. algal mat.

Marionina vancouverensis Coates, 1980.

Marionina vancouverensis Coates 1980, pp. 1307-1308, figs. 1-6.
Coates and Ellis 1981, p. 2135, fig. 4.

Remarks: The morphology of the Coos Bay specimens conforms to
the original description, and matches that of M. vancouverensis
specimens from British Columbia, loaned to me by Katherine Coates.

Habitat: Coarse to medium sand at the +2.0m level on Coos Bay
tide flats; abundant.

Marionina subterranea (Knöllner, 1935).

Michaelsena subterranea Knöllner, 1935, pp. 455-460, figs.
26-28.

Marionina subterranea (Knöllner). Nielsen and Christensen
1959, pp. 110-112, figs. 132-134. Lasserre 1966, p. 315.
Lasserre 1971a, pp. 451-452. Lasserre 1971b, p. 81, fig. 7.
Lasserre and Erséus 1976, p. 456.

Michaelsena glandulifera Jansson, 1961, pp. 81-88.
Nielsen and Christensen 1961, pp. 19-20.

Remarks: The two Coos Bay specimens available conform to the
original description of this species. M. subterranea was originally
described from Kiel Bay, but has since been reported from the Atlantic
coast of Europe, the Black and Mediterranean Seas, Massachusetts,
North Carolina, Bermuda, California, and Oregon.

Habitat: In Coos Bay, clean sand in the upper intertidal (+1.7m).

Marionina achaeta Lasserre, 1966.

Marionina achaeta Lasserre 1966, pp. 300-303, fig. 1.

Lasserre 1971a, p. 452. Lasserre 1971b, figs. 5B$_2$, C$_2$, D, 7.
Lasserre 1967, p. 282. 455.

Remarks: Two mature and two partially mature specimens were collected from Coos Bay. These specimens conform completely to the original description except for the presence of ventral septal gland lobes in IV and a seminal vesicle extending from segments IV through XII. These specimens are referred to M. achaeta because of their complete lack of setae and the morphology of their reproductive apparatus.

Habitat: Upper intertidal in sand (+2.0m).

Marionina vaucheriae n. sp.

Holotype: 00000 USNM, a whole mounted mature specimen.

Type Locality: Coos Bay, Oregon, USA. An intertidal flat in the lower estuary immediately south of the North Bend airport.

Paratypes: 00000 USNM, nn whole mounted mature specimens from the type locality.

Other material examined: About 30 mature specimens from the type locality were closely examined; more than 1000 additional specimens were found in the samples.

Description: Fixed specimens 1.7-2.8mm long, 21-25 segments. Three or four fairly distinct transverse rows of cutaneous glands per segment. Clitellum well developed over segments XII-½XIII. Setae straight, 30 μm long, with proximal hook; setal distributions 2-4 (5) per bundle anterior to clitellum, absent on segment XII, 2-3 per bundle posteriorly. Brain triangular with rounded posterior margin. Subesophageal ganglion very large. Septal glands present only on

septa 4/5 and 5/6 (fig. 1a); both pairs of glands united dorsally; ventral lobes absent. Granulate, nucleate lymphocytes abundant. Chloragogen present from V, dense from VI. Dorsal vessel arises in XII. Anteseptal part of nephridia large; postseptal part slender with efferent duct originating posteriorly. Seminal vesicles absent.

Reproductive structures laterally paired. One male duct is illustrated in figure 1b. Sperm funnels 40 μm long, 30-54 μm in diameter; highly glandular with an irregular outline; collar distinct, 10-13(19) μm in diameter. Vasa deferentia 150-170 μm long, 6 μm in diameter; coiled in XII. Penial bulbs 20-24 μm in diameter, spherical, and compact. Spermathecae (fig. 1a) 40-60 μm long; ampullae without diverticula, round to elongate depending upon state of contraction of specimen; each ampulla connected to esophagus by a short duct; sperm bundles coiled with ampullae; ectal ducts 19-25 μm long, 10-18 μm in diameter, covered with small gland cells; spermathecal pores in intersegmental furrow 4/5, slightly ventral to lateral setal line. One mature egg present in ovisac at a time.

Habitat: Vaucheria spp. algal mat between the +1.5m and +2.0m tidal levels, over silty sand.

Remarks: M. vaucheriae is very similar in appearance to M. vancouverensis Coates, 1980; the two species were separated because M. vaucheriae possesses only two pairs of septal glands, rather than three pairs as is the case for all other Marionina species.

Marionina callianassae n. sp.

Holotype: 00000 USNM, a whole mounted mature specimen.

Figure 1. <u>Marionina</u> <u>vaucheriae</u>. a: dorsal view segments V and VI;
BW, body wall; Ch, chloragogen cells; E, esophagus; SG, septal
glands; Sp, spermatheca. b: male duct; PB, penial bulb;
SF, sperm funnel; VD, vas deferens.

Figure 1
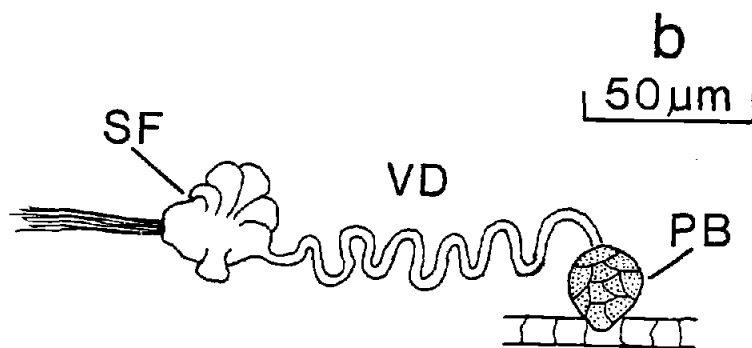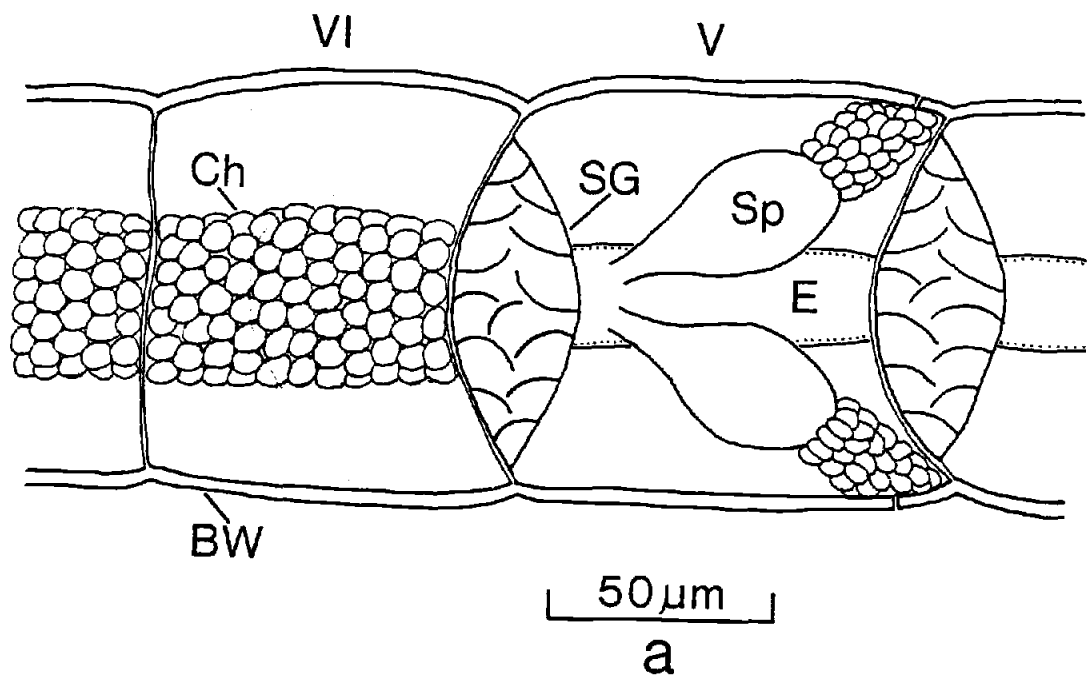
a

b

Type Locality: Coos Bay, Oregon, USA. An intertidal flat in the lower estuary immediately south of the North Bend Airport.

Paratypes: 00000 USNM, nn whole mounted mature specimens from the type locality.

Other material examined: Fifty-four mature specimens from the type locality.

Description: Fixed specimens 2.3-3.6mm long, 25-29 segments. Seven or eight transverse rows of cutaneous glands per segment. Clitellum well developed over segments XII-½XIII. Setae straight with proximal hook; 35 µm long; setal distribution (2)3,4(5) per bundle anterior to clitellum, absent on segment XII, (1)2,3(4) per bundle posteriorly. Three pairs septal glands (fig. 2a); glands on septa 4/5 and 5/6 united dorsally and usually without ventral lobes. Poorly developed ventral lobes are sometimes present on one or both sides in segment V. Septal glands in VI not united dorsally and possess large ventral lobes. Granulate, nucleate lymphocytes abundant. Choragogen present from VII. Dorsal vessel originates in posterior XIII. Anteseptal part of nephridia large; postseptal part slender, with efferent duct originating posteriorly. Seminal vesicles absent.

Gonads and reproductive structures laterally paired. One male duct is illustrated in figure 2b. Sperm funnels 70-90 (130) µm long, (4) 55-80 µm maximum diameter; glandular with an irregular outline; collar indistinct, 20-30 (39) µm in diameter. Vasa deferentia very long, 4-5 µm in diameter, highly coiled in XII. Penial bulbs 25-40 µm in diameter, spherical and compact. Spermathecae (figs. 2a, c) (72) 91-108 µm long. Ectal spermathecal ducts (15) 20-26 (39) µm

Figure 2. <u>Marionina</u> <u>callianassae</u>. Abbreviations as in figure 1.

a: dorsal view segments V and VI. b: spermatheca; AA, annulated

part of ampulla; AG, glandular part of ampulla; D, ectal duct;

SB, sperm bundle. c: male duct.

Figure 2
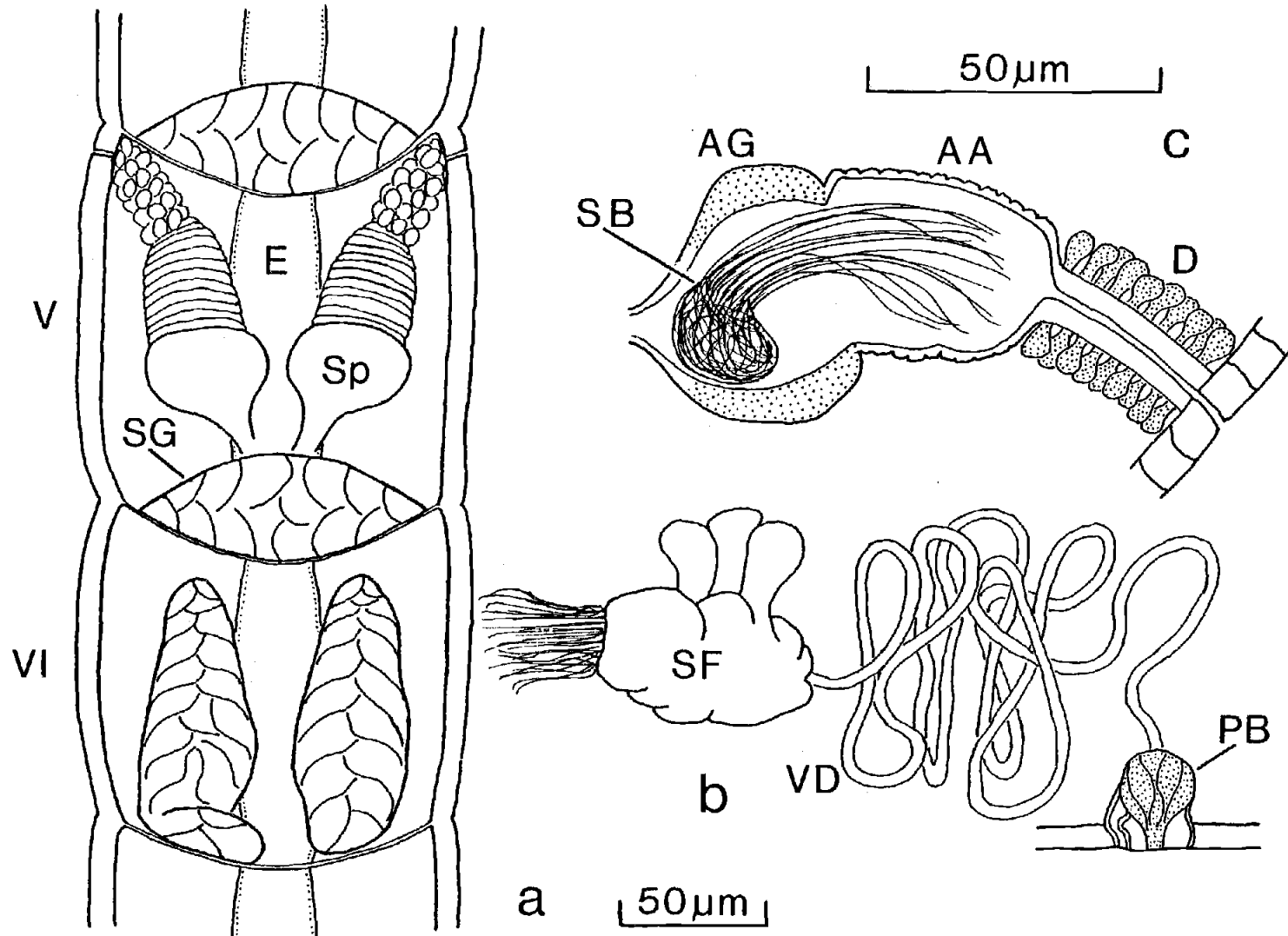
long, (10) 22 μm in diameter; ducts covered with gland cells. Sperma-
thecal ampullae 52-80 μm long; distal portion 29-40 μm long, 28-34 (60)
μm in diameter with very thin, annulated walls; proximal portion 35-36
μm long, 40-52 μm in diameter with 5 μm thick glandular walls; each
ampulla connected to the esophagus by a short duct; sperm oriented
along long axis of ampullae; spermathecal pores in intersegmental fur-
row 4/5, slightly ventral to lateral setal line. One mature egg
present in ovisac at a time.

Habitat: A *Callianassa californiensis* bed in sandy sediments
between the +0.6m and +1.5m tidal levels.

Marionina gonori n. sp.

Holotype: 00000 USNM, a whole mounted mature specimen.

Type Locality: Coos Bay, Oregon, USA. A tide flat in the lower
estuary immediately south of the North Bend airport.

Paratypes: 00000 USNM, nn whole mounted mature specimens from
the type locality.

Other material examined: About 30 mature and partly mature
specimens from the type locality closely examined. About 400
additional specimens were found in the samples.

Description: Fixed specimens (2.3) 2.9-3.6mm long, 25-29 seg-
ments. Clitellum moderately developed over segments XII-½XIII.
Setae straight to slightly curved, with proximal hook; setal dis-
tributions 2-4 setae per lateral bundle and (3)4,5(6) per ventral
bundle anterior to clitellum, absent on segment XII, (1,2)3,4(5) per
bundle in all segments posterior to clitellum. Paired septal glands
(fig. 3a) present on septa 4/5, 5/6, and 6/7; first two pairs united
dorsally, third pair separate dorsally; ventral lobes present in seg-

Figure 3. <u>Marionina</u> <u>gonori</u>. Abbreviations as in figure 1.

a: dorsal view segments V and VI. b: male duct.

Figure 3

a

50 μm

b
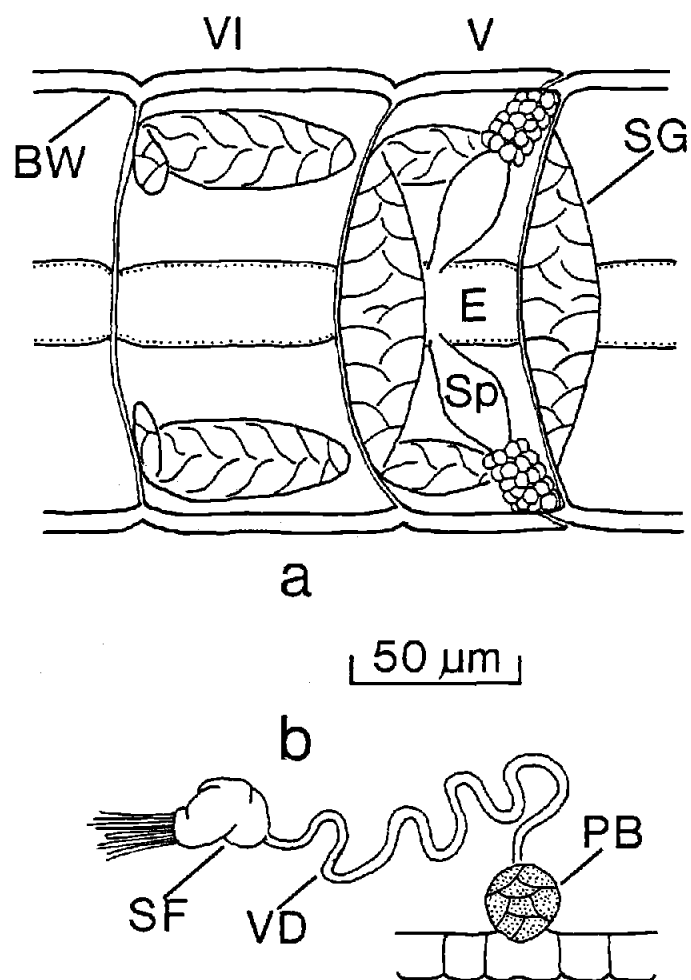
ments V and VI. Granulate nucleate lymphocytes abundant. Chlorogogen present from segment VI. Dorsal vessel arises in segment XII or XIII. Nephridia present from septum 7/8; anteseptal part large; postseptal part slender with efferent duct originating posteriorly. Seminal vesicles absent.

Gonads and reproductive structures laterally paired. One male duct is illustrated in figure 3b. Sperm funnels 20-25 μm long, 18-22 μm in diamter, highly glandular with an irregular outline; collar indistinct, about 10 μm in diameter. Vasa deferentia short, 4 μm in diameter, coiled in segment XII. Penial bulbs 18-21 μm in diameter, compact. Spermathecae (fig. 3a) 42-48 μm long; ampullae without diverticula ; ectal ducts 20-24 μm long, 17 μm in diameter, covered with small gland cells.

Habitat: _Vaucheria_ _spp_. algal mat over silty sand, between the +1.55m and +2.0m tidal levels.

Enchytraeus Henle 1837

The revised definition of Enchytraeus of Nielsen and Christensen (1959) was used in this study.

Enchytraeus sp.

Remarks: Specimens possessing paired peptonephridia were classified as _Enchytraeus_ sp. This species was found only at the highest tidal level sampled (+2.0m), indicating that it may be a supralittoral fringe species. None of the specimens were mature, therefore a species identification could not be made.

Lumbricillus Ørsted 1844

The revised definition of _Lumbricillus_ of Nielsen and Christensen

(1959) was used in this study.

Lumbricillus spp.

Remarks: Two, or possibly three, forms were placed in Lumbricillus because partially mature specimens possessed the lobed testes and seminal vesicles diagnostic of this genus (Nielsen and Christensen 1959). Since no mature specimens were collected, species identifications could not be made. Specimens ranged in length from about 6mm to about 20mm, with no clearly defined size classes which might represent separate species differing in size. Lumbricillus specimens were found rarely but consistently throughout the study site, but were only abundant in one sample from +2.0m (23 specimens) and one sample from +0.3m (24 specimens).

TUBIFICIDAE

Aktedrilus Knöllner 1935.

The expanded definition of Aktedrilus by Erséus (1980) was used in this study.

Aktedrilus locyi Erséus, 1980. Strehlow, 1982; Table 1.

Aktedrilus locyi Erséus 1980, p. 104; figs. 2E, 8, 12F, G.

Remarks: The Coos Bay specimens conform to the original description and match specimens of the original material loaned to me by Christer Erseus. A detailed comparison of Coos Bay and California material is given in Strehlow 1982.

Aktedrilus oregonensis Strehlow, 1982.

Aktedrilus oregonensis Strehlow 1982. pp. 000-nnn, figs. 1,2.

Remarks: A. oregonensis differs from other described species of

Aktedrilus in the structure of the posterior prostate and the possession of cuticular penis sheathes.

Habitat: In Coos Bay, silty sand in the mid to lower mid intertidal.

Limnodriloides Pierantoni 1903.

The revised definition of Limnodriloides by Cook (1974) was used in this study.

Limnodriloides monothecus Cook, 1974.

Limnodriloides monothecus Cook 1974, pp. 131-132, fig. 3. Brinkhurst and Baker 1979, p. 1564.

Remarks: The Coos Bay specimens conform in all respects to the original description. This species is now known from Baja, California, Oregon, and British Columbia.

Habitat: In Coos Bay, silty, mid-intertidal sediments.

Limnodriloides verrucosus Cook, 1974.

Limnodriloides verrucosus Cook 1974, pp. 132-134 fig. 4. Brinkhurst and Baker 1979, p. 1564.

Remarks: L. verrucosus from Coos Bay lack the intestinal diverticula present in the type specimens but otherwise conform to the original description. Specimens from California also lack diverticula (Brinkhurst 1980, personal communication).

Habitat: In Coos Bay, silty, lower intertidal sediments.

Limnodriloides victoriensis Brinkhurst and Baker, 1979.

Limnodriloides victoriensis Brinkhurst and Baker 1979, p. 1564, fig. 12.

Remarks: The Coos Bay specimens conform exactly to the original description.

Habitat: In Coos Bay, silty, mid and lower intertidal sediments.

Tubificoides Lastockin 1937.

The generic definition of Holmquist (1978) was used in this study.

Tubificoides pseudogaster (Dahl, 1960).

Complete synonymies for T. pseudogaster are given in Baker (1980).

Tubificoides pseudogaster. Baker 1980.

Remarks: The type specimens of T. pseudogaster were recently redescribed by Baker (1980). Several forms from the Pacific coast of Canada, were found to differ from the type specimens but were referred to T. pseudogaster by Brinkhurst and Baker (1979). The Coos Bay specimens differ from Baker's redescription of the types, in the shape of the penis sheathes. At present these Pacific coast forms are assigned to T. pseudogaster (Baker 1982, personal communication).

Habitat: Moderately silty, lower intertidal sediments in Coos Bay.

Tubificoides coatesae Brinkhurst and Baker, 1979.

Tubificoides coatesae Brinkhurst and Baker 1979, p. 1558, fig. 6, table 1.

Remarks: The Coos Bay specimens conform to the original description.

Habitat: In Coos Bay, silty, lower intertidal sediments.

NAIDIDAE

Paranais Czerniavsky 1880.

The revised definition of Paranais of Sperber (1948) is used in this study.

Paranais litoralis (Müller, 1784).

Complete synonymies for P. litoralis are given in Brinkhurst and Jamieson (1971).

Remarks: The Coos Bay specimens conform to the revised species description of Sperber (1948) with regard to somatic characteristics. All of the Coos Bay specimens were reproducing asexually by paratomy, but none showed sexual development. Therefore the structure of the reproductive ducts is not known.

Habitat: In Coos Bay, sandy to silty sediments at all tidal levels.

PSAMMOTHERIIDAE n. fam.

This family is placed within the Oligochaeta because it is hermaphroditic and the gonads are limited to two segments, with the testes anterior to the ovaries. The family is separated from other Oligochaete families, and defined, by the presence of both testes and male ducts in segment X only; the vas deferens does not penetrate septum 9/10 but opens directly through the wall of segment X; the ovaries are in segment XII, and the spermathecae are in segment VIII.

Psammotherium n. gen.

Male duct simple, without atrium or prostates. Glands, possibly analogous to the prostates of the Tubificidae, exit body separately near male pores; these glands extend free into the coelomic cavity. One pair of

giant penial setae present in segment X. Three pairs of spermathecae in segment VIII. Setae simple pointed, sigmoidal, and without nodulus; three setae per bundle in all segments. Esophagus with thick glandular walls; merges with intestine in segment IX; no pharyngeal glands or intestinal diverticula.

Psammotherium hastatus n. sp.

In this species the penial setae form into a tube for the distal third of their length and the tips of the setae are flared into a funnel shape. The spermathecae are round, with short ducts leading to the spermathecal pores.

Remarks: A complete description of this species will be published in a separate paper along with the description of a second very similar species from the Atlantic ocean off Delaware.

Discussion

The worldwide zoogeography of marine oligochaetes is not well established because of the scanty geographical records for many species (Brinkhurst and Baker 1979, Timm 1980). However, the available literature on the zoogeography of northeast Pacific littoral species can be summarized and the geographical distributions of species identified from Coos Bay can be compared to the rest of the regional fauna.

Marine oligochaete species known from the northeast Pacific littoral zone are listed in table 1. Of the forty-seven species listed, twenty-seven (57%) are known only from this coast. Of the non-endemic species, two are also known from northeastern Asia, five from the east coast of the USA, and four from Europe. Nine species are also known from both the eastern USA and Europe. Of the sixteen

species listed in table 1 found in Coos Bay, nine are endemic to the eastern Pacific littoral and four are known only from Coos Bay.

The North American marine tubificids were most recently reviewed by Brinkhurst and Baker (1979) and Baker and Brinkhurst (1981). Two species reported from the northeast Pacific littoral zone, Tubificoides pseudogaster and Tubificoides gabriellae, are species complexes (Brinkhurst and Baker 1979). The resolution of these species complexes will probably result in higher species richness and more endemic species for the northeast Pacific littoral fauna. Baker and Brinkhurst's (1981) revision of the genus Monopylephorus clarified the taxonomy and geographical distributions of several species. Three Monopylephorus species are now known from British Columbia, one of which is endemic. Monopylephorus was absent from the Coos Bay samples.

Coates and Ellis (1981) revised the taxonomy of the British Columbia intertidal enchytraeids and summarized the zoogeography of North American intertidal species. The northeast Pacific littoral enchytraeid fauna was found to have greater species richness and more endemic species than the northwest Atlantic littoral fauna. The description of three new species and the new record of Marionina achaeta in the present study reinforce their conclusions. The higher degree of endemism on the Pacific coast may be the result of the lack of information on the taxonomy and distribution of species from the Pacific coast of northeast Asia, however,

Despite the lack of geographical records and unresolved taxonomic problems, this work and other recent studies on the Pacific coast of North America indicate the existence of a distinct regional fauna for

Table 1. Marine oligochaete species known from the Pacific coast of North America (Northeast Pacific) with known geographical ranges indicated. C.B. Coos Bay; N.E.P.: Northeast Pacific only; N.E.P., A.P.: North Pacific coast of Asia and North America only; N.A.: East and West coasts of North America only; Pac., Eur.: North Pacific and Atlantic coast of Europe only; Pac., Atl.: Circumboreal.

	Coos Bay	N.E.P.	N.E.P., A.P.	N.A.	Pac., Eur.	Pac., Atl.
Enchytraeidae						
Enchytraeus albidus						+
E. kincaidi		+				
E. multiannulatus		+				
E. rupus		+				
Grania incerta		+				
G. paucispina		+				
Lumbricillus curtus		+				
L. tsimpseanus		+				
L. rupertensis		+				
L. pagenstecheri					+	
L. annulatus			+			
L. tuba						+
L. mirabilis			+			
L. qualicumensis		+				
L. lineatus						+
L. belli		+				
Marionina trevori		+				
M. charlottensis		+				
M. neroutsensis		+				
M. appendiculata					+	
M. sjaelandica	+				+	
M. subterranea	+					+
M. achaeta	+					+
M. vancouverensis	+		+			
M. vaucheriae	+		+			
M. callianassae	+		+			
M. gonori	+		+			
Tubificidae						
Aktedrilus locyi	+			+		
A. oregonensis	+		+			
Bacecuella sp.		+				
Limnodriloides winckelmanni					+	
L. monothecus	+			+		
L. verrucosus	+		+			
L. victoriensis	+		+			
Monopylephorus cuticulatus			+			
M. rubroniveus						+
M. parvus						+
Rhizodrilus pacificus			+			
Thalassodrilides belli			+			
Tubificoides gabriellae				+		
T. postcapillatus			+			
T. nerthoides					+	
T. apectinatus				+		
T. pseudogaster	+					+
T. coatesae	+		+			
Naididae						
Paranais litoralis	+					+
Psammotheriidae						
Psammotherium hastatus	+		+			

both enchytraeid and tubificid marine oligochaetes. Resolution of the _Tubificoides pseudogaster_ and _Tubificoides gabriellae_ species complexes will probably result in a North American Pacific regional oligochaete fauna even more distinct than it presently is.

Chapter Two

Aktedrilus locyi Erséus, 1980 and Aktedrilus oregonensis n. sp.

(Oligochaeta, Tubificidae) from Coos Bay, Oregon,

with Notes on Distribution with

Tidal Height and Sediment Type.

Introduction

Species of the tubificid genus <u>Aktedrilus</u> occur widely as a component of the marine littoral meiobenthos. Geographical records are, however, scanty (Erséus, 1980a). In this paper <u>Aktedrilus locyi</u> Erséus, 1980 is reported for the first time from the northwest coast of the United States and <u>Aktedrilus oregonensis</u> n. sp. is described.

Methods

Specimens used in this study were sorted from core samples (15 cm diameter, 20 cm deep), taken from sandy and muddy-sand intertidal areas in lower Coos Bay, Oregon, USA ($43^{o}25'N$, $124^{o}16'W$). Core samples were fixed in 10% buffered formalin, sieved on a 0.5 mm sieve and the retained fauna was stored in 70% isopropyl alcohol. Specimens were stained in paracarmine and mounted whole in synthetic resin. For a detailed discussion of the study site, the sampling design used, and the associated non-oligochaete fauna see Gonor, et al., (1979).

Taxonomy of <u>Aktedrilus</u>

<u>Aktedrilus locyi</u> Erséus, 1980.

<u>Aktedrilus locyi</u> Erséus, 1980; p. 104; Figures 2E, 8.

TYPE LOCALITY: Monterey Bay, California; very exposed high-energy beach; mid-tide level in medium to coarse sand.

MATERIAL EXAMINED: One mature and 2 partially mature specimens of the original material from the type locality (loaned by Dr. C. Erseus). Many mature specimens collected from Coos Bay, Oregon.

REMARKS: Body length, segment number, and atrial length for Coos Bay specimens fall outside the range given by Erseus (1980a); setal distribution and penes are similar in both populations (Table 2). After comparison with specimens of the original material, the Coos Bay specimens were classified as A. locyi on the basis of the form and arrangement of the reproductive structures, in spite of the observed differences.

The Coos Bay material was collected from a protected sandy beach in the lower estuary rather than an exposed, high-energy beach as at the type locality, but co-occurring tubificid species are marine forms (Strehlow, unpublished data).

Aktedrilus oregonensis n. sp.

HOLOTYPE: USNM 00000, whole mounted specimen.

TYPE LOCALITY: Coos Bay, Oregon, USA. Collected from the beach of an island in the lower estuary immediately south of the North Bend Airport, in silty sand between +0.6 and +1.1 m MLLW, rarely as low as 0 m or as high as +1.8 m.

PARATYPES: USNM 00000, whole mounted specimens from the type locality. The type series of A. oregonensis n. sp. is deposited in the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Table 2. _Aktedrilus locyi_. A comparison of Coos Bay specimens with the original description of California material (Erséus, 1980a).

Location	Body length (mm)	Number of segments	Setal length (μm)	Setal distribution	Atria	Penes
California	1.5-1.8	26-29	25	2-4 per bundle	65-85[a] x 11-16	14-17[b] x 12-18 x 6-8
Coos Bay	2.4-3.4	29-40	30	2-4 per bundle	75-105 x 10-15	14-20 x 7-20 x 5-8

a: length x diameter (μm).

b: length x diameter at tip x basal diameter (μm).

OTHER MATERIAL EXAMINED: whole mounted mature specimens from the type locality. Four whole mounted mature specimens from Powell River, B.C., Canada (49°52'N, 124°34'W) loaned by Mr. H.R. Baker.

DESCRIPTION: Fixed specimens 2.1-3.7 mm long, 28-35 segments; anterior end (segments 0-X) 0.65-0.88 mm long. Diameter of fixed, slightly compressed specimens 0.10-0.11 mm at segment V, 0.14-0.18 mm at XI, and 0.09-0.11 mm at XX. Clitellum well developed over segments ½X-XII. All setae bifid with upper tooth shorter and thinner than lower. Setae 30-35 µm long and about 1 µm in diameter; 2-4(5) setae per bundle throughout body. Ventral setae absent in XI. Male and spermathecal pores as in genus definition.

Pharyngeal glands present in IV-VI, small in VI.

The male ducts are paired. The left duct is illustrated (Fig. 4). Vas deferens: thin-walled, 5-6 µm in diameter and shorter than atrium. Atria: cylindrical, 80-110 µm long, 14-21 µm in diameter with an outer muscle layer about 0.6 µm thick, and an inner granulated and ciliated epithelium 5-8 µm thick. Each atrium terminates in a curved, strongly cuticularized penis 27-30 µm long with a 11-13 µm diameter base and a 4-6 µm diameter shaft. A large anterior prostate is attached to the ental end of each atrium near the attachment of the vas deferens. A large posterior prostate is broadly attached medio-dorsally to each penial sac and merges with the atrium at the base of the penis; a papilla extends ventrally from the posterior prostate along the inner wall of the penial sac.

Figure 4. <u>Aktedrilus oregonensis</u>. Lateral view of genital organs.
A, atrium; BW, body wall; F, funnel; P, penis; Pa, anterior
papilla; PA, anterior prostate; PP, posterior prostate; SpA,
spermathecal ampulla; SpD, spermathecal duct; VD, vas deferens;
X and XI, segments 10 and 11; ♂, male genital pore.

Figure 4
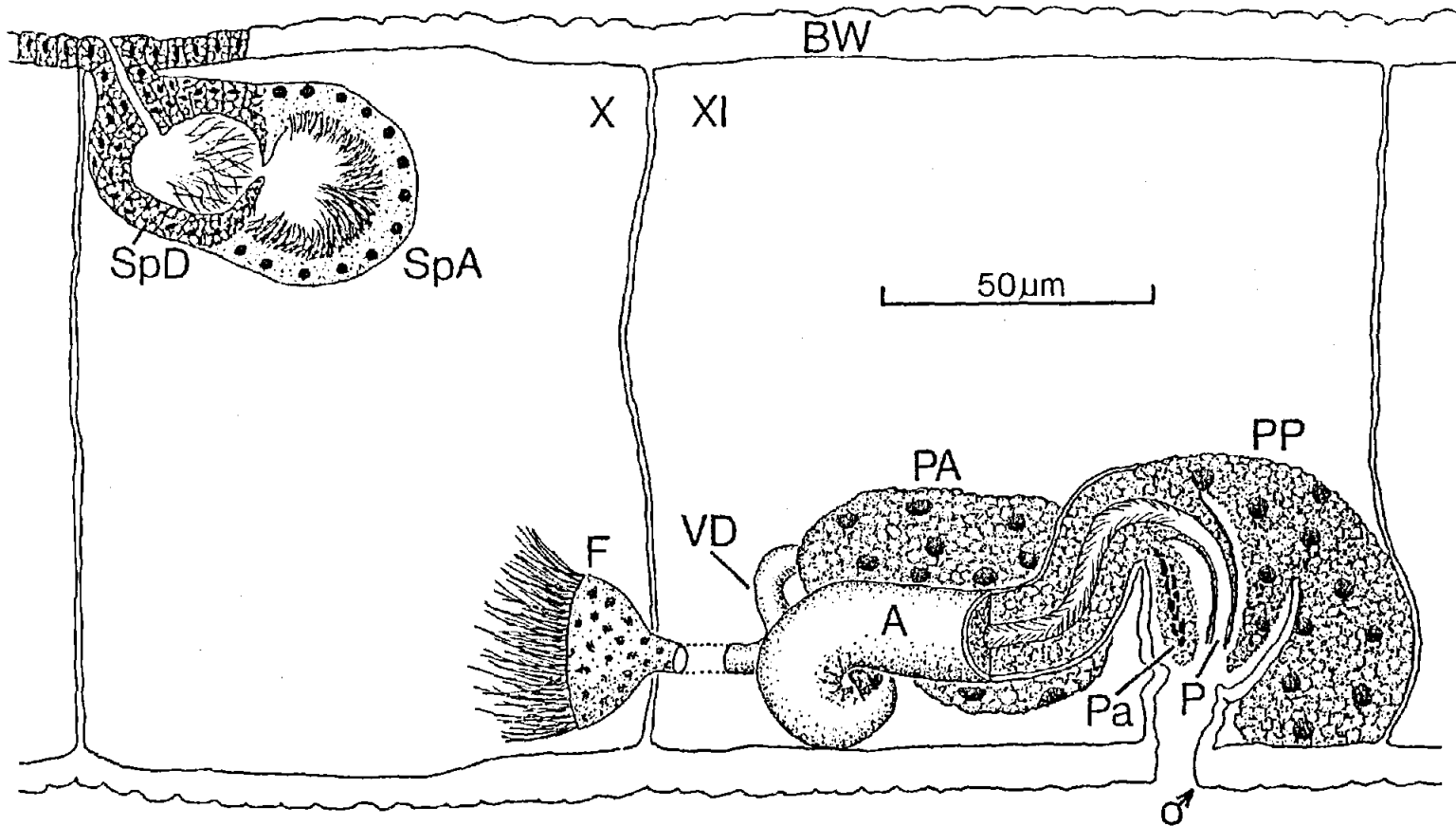
A second glandular papilla is attached ventrally to the ectal end of the atrium at its juncture with the penis and extends ventrally along the inner anterolateral wall of the penial sac; there is no direct connection between this papilla and the posterior prostate. Both papillae are attached throughout their length to the wall of the penial sac. The penial sac is roughly 20-25 µm wide and 55-65 µm deep.

The spermatheca is oblong, 50-65 µm long and 25-40 µm wide; the ampulla is 27-34 µm long. The lumen of the duct is nearly as voluminous as that of the ampulla and is surrounded by glandular cells. Spermatozoa are often found in the duct but are never embedded in the duct lining. Spermatozoa are embedded in the inner epithelial lining of the ampulla.

REMARKS: The organization of the male ducts in Aktedrilus oregonensis is very similar to the original description of A. brevis Erséus, 1980. Differences between the species are the existence, in A. brevis, of an anterior lobe of the posterior prostate external to the penial sac and larger penes. Total length of worm and setal numbers are greater for A. oregonensis than A. brevis but these characters are not regarded as taxonomically definitive (Erséus, 1980b). The spermathecae of these two species are different. A. brevis has a ductless saccate spermatheca with spermatozoa scattered throughout, whereas A. oregonensis possesses a spermatheca with a distinct duct and spermatozoa closely associated with, and embedded in the ampullar lining.

Erséus (1980a) notes that the spermatozoa in the spermatheca of _Aktedrilus_ _magnus_ Erséus, 1980 also appear to penetrate the ampullar lining. A similar situation occurs in the spermatheca of the polychaete _Spirorbis_ _spirorbis_ (L.) where it is thought to aid in sperm nutrition and storage (Daly and Golding, 1977).

None of the _A._ _oregonensis_ specimens from Powell River, B.C. had a voluminous spermathecal duct (Fig. 5). The paucity of specimens and geographical records makes it impossible to determine whether the observed difference in spermathecae is genetic, phenotypic, or related to reproductive state. In all other respects _A._ _oregonensis_ specimens from Powell River, B.C. conform to the description based on the material from the type locality.

Distribution Relative to Physical Factors

Aktedrilus spp. were found in 40 of the 59 samples examined. A total of 1,031 specimens of _A._ _locyi_ were identified from 34 samples and 147 _A._ _oregonensis_ were identified from 16 samples. The species co-occurred in 10 samples. _A._ _locyi_ was present in samples from the mid-to upper intertidal. _A._ _oregonensis_ was most abundant in a transition zone between a mid-intertidal zone with _A._ _locyi_ and _Marionina_ spp., and a lower intertidal zone with _Limnodriloides_ spp. and _Tubificoides_ spp.

Of the 21 oligochaete taxa found at the Coos Bay site, only the naidid _Paranais_ _litoralis_ (Müller, 1784) has a tidal height

Figure 5. <u>Aktedrilus</u> <u>oregonensis</u>. Lateral view of spermatheca of
a British Columbia specimen showing the narrow lumen of the
spermathecal duct. SpA, ampulla; SpD, duct.

Figure 5
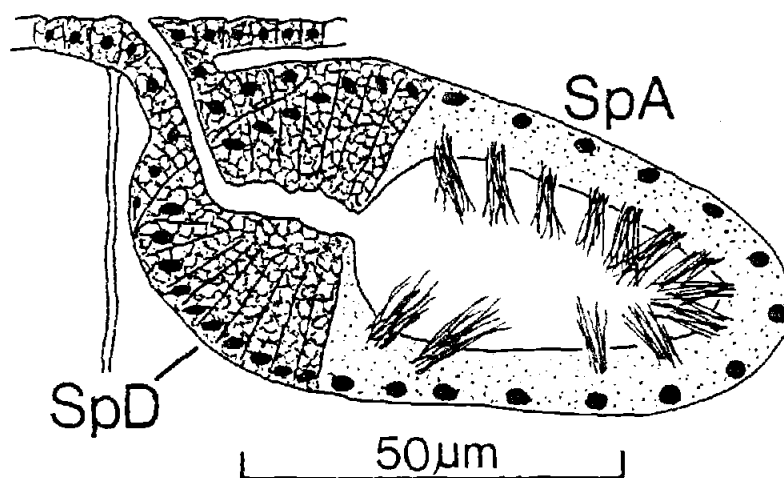
and sediment type distribution similar to <u>A</u>. <u>oregonensis</u>.

The two <u>Aktedrilus</u> spp. were found together in samples from an upper intertidal area of sand with 8% silt and a <u>Vaucheria</u> mat cover. This was the only area where <u>A</u>. <u>oregonensis</u> was found in the upper intertidal. In upper intertidal areas of clean, well-drained sand (≤ 2% silt) and no macrophyte cover, <u>A</u>. <u>locyi</u> was widespread and moderately abundant but <u>A</u>. <u>oregonensis</u> was absent. The difference in total number of the two <u>Aktedrilus</u> spp. collected at this site is probably due to the small number of samples taken in the narrow zone between the broad mid-intertidal sandflat and the steeper, lower-intertidal channel bank.

Acknowledgements

Chapter Three

The Relation of Tidal Height and
Sediment Type to the Intertidal
Distribution of Marine Oligochaetes
in Coos Bay, Oregon.

Introduction

For intertidal sedimentary environments, physical factors found to affect faunal distributions are salinity, temperature, oxygen availability, moisture, sediment granulometry, and organic matter content (Jansson 1962, 1967a, b, 1968; Lasserre 1969, 1971; McIntyre 1969; Fenchel 1969, 1978; Giere 1973, 1977). Because many of these factors are intercorrelated, elucidating their separate effects and interactions is difficult. Approaches used to attack this problem have ranged from laboratory studies with independently controlled factors (e.g. Jansson 1962, 1968; Giere 1980), to studies of the effects of suites of factors on faunal distributions, without attempting to completely understand their interactions (e.g. Cassie and Michael 1968, Hulings and Gray 1976). The latter approach does not elucidate causal relationships, but provides a framework for predicting the distributional patterns of organisms.

During a benthic faunal survey at an estuarine intertidal site, we found that 43% of the small macrofauna were oligochaetes (Gonor, et al. 1979, Strehlow in prep.). The abundance of oligochaetes in these samples provided the opportunity to investigate the physical factors governing the distribution of these species.

In this study the physical environment at the study site was divided into discrete habitat types and relationships between these types and independently derived species assemblages were examined. Tidal height and sediment type were the major gradients of physical habitat variation at the site. Simple factors such as oxygen, organic matter content, salinity, temperature, and moisture have

been shown to vary along these gradients (Sanders et al. 1962; Brafield 1964; Johnson 1965, 1967; Jansson 1967a, b, 1968; Enckell 1968; Fenchel 1969).

In addition to examining the effects of tidal height and sediment type on the distribution of the oligochaete fauna, the critical tide level hypothesis of Doty (1946) was examined. Doty (1946) proposed that critical tide levels were the limiting factors governing algal distributions in the rocky intertidal zone. Critical tide levels are levels at which the period of maximum exposure or submergence undergoes large increases; such large increases do not occur at other tide levels. Swinbanks and Murray (1981) concluded that critical tide levels influenced the zonation of benthic intertidal flora and fauna at a sedimentary study site in British Columbia, Canada. They did not, however, quantitatively examined the degree of association between species limits and critical tide levels, as this study does.

Study Site Description

The study site, an intertidal mud and sand flat in lower Coos Bay, Oregon USA ($43^o 24'$N, $124^o 17'$W) (Fig. 6), contained a mixture of habitat types typical of the seaward regions of Oregon estuaries. Two such major habitat types evident at the study site were sampled independently. The northeastern part of the site (S Fig. 1) was characterized by fast tidal currents, and a substrate consisting of clean medium to fine sand above ±0.6 m and sand with 5% to 13% silt below this level. The southwestern part of the site (M and ML Fig. 1), was protected from fast currents by a sandspit and its sediments

Figure 6. Topography of the study site and locations of sampling
areas: sandy area (S), muddy area (M), and lower muddy area
(ML). Tidal heights in meters above MLLW.

Figure 6
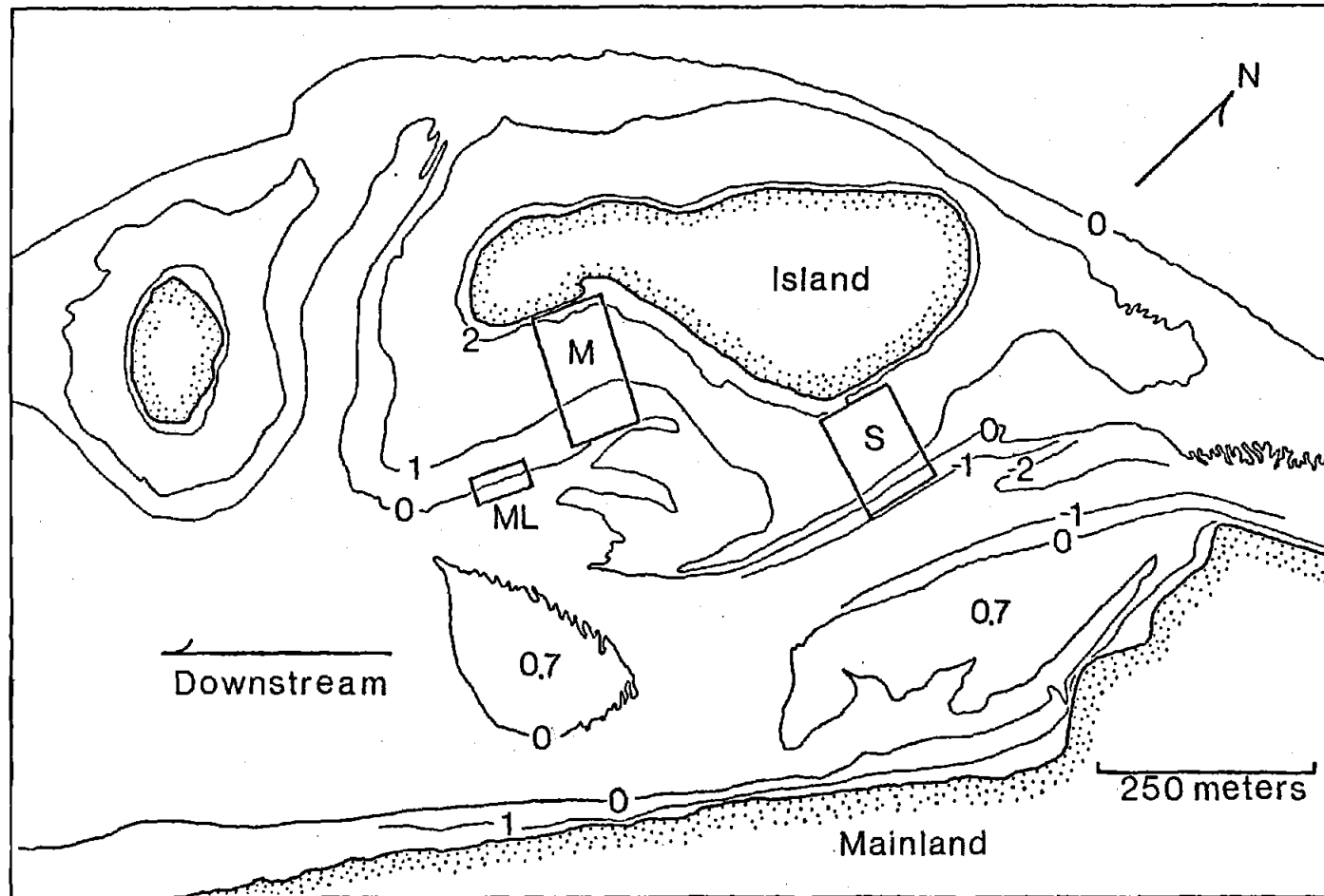
contained 4 to 6 times more silt and clay at all tidal heights than did the northeastern part of the site (area S). Upper and mid intertidal flats were broad throughout both parts of the site, with slopes of about one percent. At the sandier location, the lower part of the flat below +0.6 m tidal height was steeper, with a slope of about six percent. At the muddier location, below +0.9 m height the flat had a slope of two percent. The tidal range from mean lower low water (MLLW) to mean higher high water (MHHW) is 2.0 m at both portions of the study site.

The salinity regime at the study site, calculated from the data of Queen and Burt (1955), is typical of lower estuarine areas with a strong marine influence. Monthly average high tide surface salinities range from $18^{o}/oo$ to $23^{o}/oo$ from December through March, and from $28^{o}/oo$ to $32^{o}/oo$ during the remaining months. Monthly average low tide surface salinities are much more variable, ranging from winter lows of $9^{o}/oo$ to summer highs of $31^{o}/oo$.

The distributions of macrophytes and Callianassa californiensis at the study site (Gonor, et al. 1979) are described here because when they were present the physical appearance of the sediment was affected. Except for a bed of dense but patchy Zostera marina below +0.3 m, macrophytes were absent from the sandy area. Vegetation patterns in the muddy area were more complex. At the time of sampling the condition of a dense Vaucheria spp. mat between +1.5 m and +2.0 m varied with tidal height, being lush below about +1.8 m, and desiccated and cracked above this level. Patches of Enteromorpha spp. were found between +0.6 m and +1.5 m. An unvegetated zone extended

between +0.6 m and +0.3 m, the upper limit of a <u>Zostera</u> <u>marina</u> bed.
In the muddy area, <u>Zostera</u> was less dense and more evenly distributed
than in the sandy area.

The upper limit of <u>Callianassa</u> <u>californiensis</u> lay between +1.5 m
and +1.8 m throughout the study site. Its lower limit in the sandy
part of the study site was about +0.3 m, near the upper limit of the
<u>Zostera</u> bed, while in the muddy area <u>Callianassa</u> continued down into
the Zostera bed. <u>Callianassa</u> burrow densities appeared to be lower
in the muddy area relative to the sandy area. Where <u>Callianassa</u> is
abundant, sediments are heavily reworked by their continuous burrow-
ing activity.

Methods

Sampling procedures

The three sampling areas (S,M,ML) were stratified into 0.3 m
tidal height intervals by levelling with a transit from a benchmark
of known tidal height relative to MLLW. Straight lines separating
these strata were fit by sighting along range poles placed along the
tidal height contours located by surveying. Sampling points were
located randomly within strata, with approximately one sample for
every 400m^2 of area. All strata received at least two samples re-
gardless of area.

Faunal samples were taken on April 24-28, 1978 with a 15cm
diameter corer by pushing it 20cm into the sediment. Whole cores
were fixed in the field with 10% formalin, later washed on a 0.5mm
sieve, and the retained fauna stored in 70% isopropanol. Oligochaetes
were separated from the rest of the fauna, stained with paracarmine,

and mounted whole in synthetic resin for identification. The data
on the non-oligochaete fauna used in this study were taken from
Gonor, et al. (1979).

One surface sediment sample was taken from the center of each
stratum for analysis by the Oregon State University Soils Testing
Laboratory. Sediment granulometry was determined by dry sieving
after hydrogen peroxide treatment and deflocculation. Total organic
carbon was determined by wet oxidation with chromic acid (Walkley
and Black 1934), while total nitrogen was determined using micro-
Kjeldahl digestion (Bremner 1965).

Macrophyte distributions were determined by recording the
presence of macrophyte species in the samples and by field obser-
vations on June 22-24, 1978.

Predicted tidal heights for Empire, Oregon, 2 km downstream
from the study site, were used to calculate maximum continuous and
average percent tidal exposure and submergence at 6cm tidal height
intervals for the period between February 8 and April 24, 1978.
From these data the locations of critical tide levels were calculated
using the method of Swinbanks and Murray (1981).

Data analysis

Similarity of samples by species was analyzed using the index:

$$S_{ab} = \frac{\sum_{j=1}^{k} N_{aj} \, N_{bj}}{\left[\left(\sum_{j=1}^{k} N_{aj}^2\right)\left(\sum_{j=1}^{k} N_{bj}^2\right)\right]^{\frac{1}{2}}}$$

where k is the number of species in the collection, and N_{aj} and N_{bj} are the abundances of the jth species in samples a and b respectively. S_{ab} is the cosine of the angle between the sample vectors of a and b (Boyce 1969), and is insensitive to proportional size differences between samples. S_{ab} is also rather insensitive to changes in the relative abundance, between samples, of species other than the dominants. The range of S_{ab} is from 0 for no similarity to 1 for identity.

An analysis was performed to delimit groups of species with similar distributions. The same similarity index, S_{ab}, was used where k now refers to the number of samples in the collection, and N_{aj} and N_{bj} are the abundances of species a and b in sample j. In both analyses similarity values ≥ 0.750 were used to define groups of similar composition. Groupings were checked and finalized by visual inspection of the raw data matrix.

Sharp changes in the average abundance of species between contiguous strata, or between sampling areas at a given tidal height, were used to identify important environmental factors. The upper and lower limits of species distributions were considered special cases of changes in relative abundance. A change in the average abundance of a species in contiguous strata by a factor of four or more was considered to be significant. These changes were termed species breaks. Changes in relative abundance were accepted as more realistic and more informative than presence or absence data alone.

The average abundance of each species in each stratum was also used to test the relationship of species distributions to critical

tide levels. Association between environmental variables, and between habitat breaks and species breaks, was tested using the chi-square test of independence. The following criteria were applied to the data set to remove rare and scattered species occurrences:

1) All average abundances less than two were dropped;

2) For strata containing more than one sample, all average abundances for which one sample accounted for 100% of the total abundance of that species in a stratum, were dropped.

Association between sample classifications was measured using Rand's coefficient (Rand 1971, cited in Rohlf 1974). If two classifications are cross classified, Rand's coefficient equals:

$$R = \frac{\frac{1}{2} \sum\limits_i \sum\limits_j f_{ij} (f_{ij}-1) + \frac{1}{2} \sum\limits_i \sum\limits_j f_{ij} \left(\sum\limits_{k \neq i} \sum\limits_{\ell \neq j} f_{k\ell} \right)}{t(t-1)/2}$$

where i and j represent the rows and columns of the cross classification table, f_{ij} is the number of samples at location (i,j), $f_{k\ell}$ is the number of samples in location $(k,i) \neq (i,j)$, and t is the total number of samples classified. The coefficient R equals the number of samples classified the same in both classifications plus the number classified differently in both classifications, divided by the total number of sample pairs. Its range is from zero, for no association, to one for perfect association.

The degree to which the defined physical habitats could predict the species composition of samples was measured using the index of predictive ability (λ_B) of Goodman and Kruskal (1954, cited in Everitt 1977). The increase in the probability of correctly predicting the species composition of a sample when its habitat

classification is known, relative to when it is unknown, is calculated as:

$$\lambda_B = (P_1 - P_2)/P_1$$

P_1 is the probability of incorrectly predicting the species composition of a sample when its habitat classification is unknown and P_2 is the probability of incorrectly predicting the species composition of a sample when its habitat classification is known. The range of λ_B is from zero, for no predictive ability, to one for perfect predictability.

Results

Environmental variables

The physical variables used to characterize the study site were tidal height, duration of maximum continuous exposure and submergence, average percent of time of tidal exposure and submergence and sediment characteristics. These characteristics, sediment granulometry, total organic carbon, and total nitrogen data are given in Table 3.

Sediment analysis

The sediment type extremes found at the site were clean, moderately well sorted sand with little organic matter and very silty, very poorly sorted sediments containing much organic matter. The Pearson product moment correlations for the sediment grain size classes, total organic carbon, total nitrogen, median grain size, and sorting are given in Table 4. The seven granulometric classes separated into three groups: coarse and medium sand, fine sand, and very fine sand through clay. Correlations within the coarse to

Table 3. Sediment composition of sampling areas at the study site.

(m) Tidal height	grain size (um)							Organic carbon(%)	Total organic nitrogen(%)	Median Grain Size(m)	Sorting (Ø)
	500-1000	250-500	100-250	50-100	20-50	2-20	<2				
Area S											
+1.68	8.2	38.9	47.2	1.7	0.2	2.8	1.1	0.19	0.02	.233	0.83
+1.37	11.5	40.8	45.7	0.8	0.1	0.9	0.2	0.25	0.01	261	0.79
+1.07	7.1	39.1	50.6	0.9	0.1	1.3	0.9	0.31	0.01	233	0.80
+0.76	5.4	30.3	57.4	1.8	0.9	2.1	2.0	0.44	<0.005	203	0.75
+0.46	6.0	26.5	53.6	5.0	2.5	3.2	3.2	0.94	0.04	203	0.80
+0.15	8.5	28.3	48.4	5.0	2.4	3.9	3.5	1.50	0.05	203	0.85
-0.15	1.5	12.6	56.7	10.0	5.6	7.1	6.5	1.62	0.07	168	1.28
Area M											
+1.98	11.7	36.3	38.7	1.6	3.6	4.3	3.7	0.59	0.08	237	0.90
+1.68	7.8	34.2	44.3	1.7	2.8	4.8	4.4	1.01	0.03	218	0.85
+1.37	8.4	33.2	42.0	2.2	4.7	4.9	4.6	1.24	0.04	218	1.00
+1.07	5.1	23.1	47.5	4.5	7.2	3.9	8.7	2.42	0.09	180	1.53
+0.76	3.3	14.3	44.0	7.5	11.2	10.4	9.4	3.25	0.10	151	2.25
+0.46	0.9	4.3	32.8	15.8	16.9	15.8	13.4	4.73	0.15	174	3.00
Area ML											
+0.46	1.5	15.8	44.1	10.9	12.0	8.6	7.1	2.78	0.09	151	1.55
+0.15	0.9	14.7	40.0	9.6	12.7	11.4	10.7	3.19	0.10	134	2.90

Table 4. Sediment correlation matrix

	500-1000	250-500	100-250	50-100	20-50	2-20	<2	TOC (%)	TON (%)	Md
Grain Size Classes (μm)										
250-500	0.79									
100-250	-0.63	-0.39								
50-100	-0.71	-0.91	-0.06							
20-50	-0.66	-0.88	-0.03	0.92						
2-20	-0.67	-0.86	-0.03	0.89	0.95					
<2	-0.69	-0.90	0.06	0.88	0.97	0.93				
TOC(%)	-0.61	-0.85	-0.02	0.84	0.96	0.91	0.94			
TON(%)	-0.64	-0.85	-0.63	0.85	0.93	0.90	0.94	0.92		
Md	0.89	0.96	0.39	-0.95	-0.93	-0.93	-0.93	-0.95	-0.86	
ø	-0.75	-0.83	-0.60	0.82	0.93	0.93	0.93	0.93	0.86	-0.90

TOC: total organic matter

TON: total organic nitrogen

Md: median grain size (μm)

ø: graphic phi deviation (sorting)

medium sand group, and very fine sand through clay (fines) group ranged from 0.86 to 0.95; between group correlations ranged from -0.75 to -0.92. Fine sand was not correlated with either group. Correlations of total organic carbon, total nitrogen, median grain size, and sorting are all very high, with absolute values between 0.86 and 0.95. Since the proportion of fines was shown to be correlated with the other sediment parameters measured, it was used to separate the sediments into five groups: 2-7% fines, 13-16% fines, 24-29% fines, 38-44% fines, and 62% fines.

Carbon-nitrogen ratios ranged from 12 to 16, and were independent of overall sediment type, indicating that the food quality of the organic matter present was fairly constant regardless of the total amount of organic matter present.

Only the intermediate sediment types, 13-16% fines and 24-29% fines, were found in both the sandy and muddy areas and were found higher in the muddy area than in the sandy area.

Tidal exposure and submergence

The sampling areas were divided by tidal height using both predicted critical tide levels and information from field observations. Predicted critical tide levels were +2.0 m, +1.5 m, +0.4 m, and 0.0 m. The first two correspond to levels at which maximum continuous exposure increased from 13 to 48 days, and from 0 to 2 days, respectively, while the latter two correspond to maximum continuous submergence increased from 0 to 2 days, and 17 to 46 days.

An abrupt change in the appearance of the sediment surface, apparently caused by recent tidal exposure, was noted at about +1.8 m

in area M. The algal mat and surface sediments above this level were dried and cracked, whereas below this level the mat was lush and the surface sediment moist. This level was not predicted to be a critical tide level by tidal data of the previous three months.

A similar change in sediment appearance was noted in S but was not associated with a single tidal level. It ran diagonally from about +1.5 m at the north edge of S to +1.8 m at the south edge, and was associated with the lower limit of Mya arenaria and the upper limit of Callianassa californiensis. Factors other than tidal exposure alone may have been affecting desiccation in this zone. Thum (1972) found that groundwater drainage patterns at a similar site in Yaquina Bay, Oregon affected desiccation in the upper intertidal zone.

Only predicted critical tide levels were used to test the critical tide level hypothesis. A complete physical habitat map of the sampling areas was constructed by using sediment type, predicted critical tide levels, and field observations (Figure 7). The characteristics of the mapped habitats are given in Table 5.

The fauna

Oligochaete species found at the study site are listed in Table 6, and species abundance data in Table 7. These species fell into two distinct size classes; those less than about four millimeters long and those greater than ten millimeters long, referred to as meiofauna and macrofauna respectively. Meiofaunal species were strongly associated with upper intertidal strata and macrofaunal species with lower intertidal strata. There was a sharp break between the two species groups at approximately +0.6 m in S and +1.5 m

Figure 7. Sampling areas mapped using three sets of attributes: physical habitat type
(capital letters), oligochaete species composition (Arabic numerals), and non-
oligochaete species composition (Roman numerals). Areas classified identically
by the three are enclosed by solid lines only. Where the classifications differ
solid lines delimit habitat types, evenly dashed lines delimit areas of homogeneous
oligochaete species composition, and short-long dashed lines delimit areas of
homogeneous non-oligochaete species composition. The characters defining the
classes are given in Tables 3, 6, and 9.

a: sediment type breaks.

b: critical tide levels.

Tidal heights in meters above MLLW.

Figure 7

Area ML

Area M

Area S
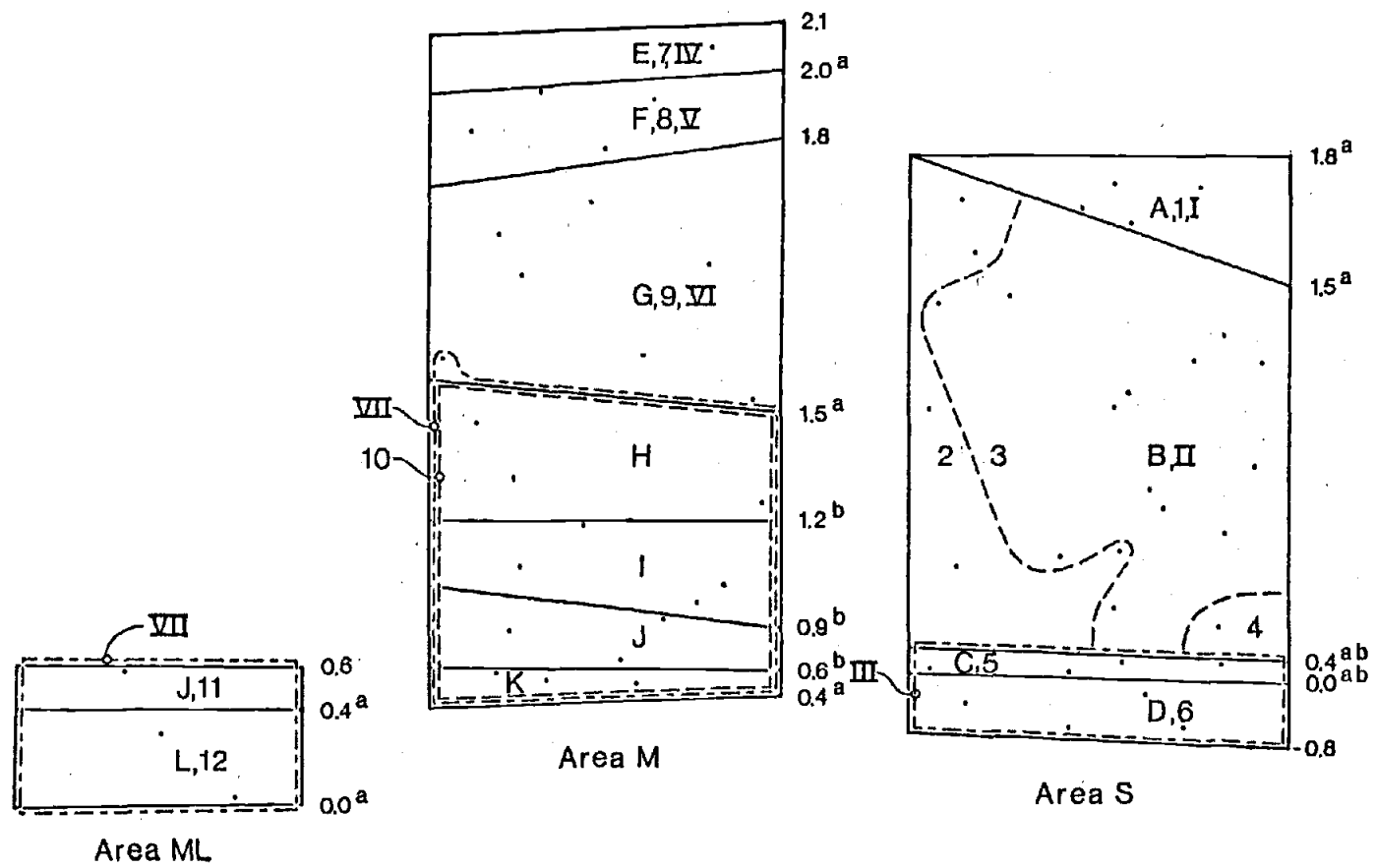
Table 5. Description of physical habitat types mapped in Figure 7.
Fines: percent sediment ≤ 100 μm.

Group

A   Callianassa and Vaucheria mat absent; 2-7% fines; 3-7 days
     maximum continuous exposure.

B   Dense Callianassa; no algal mat; 2-7% fines; exposed and
     submerged twice a day.

C   Rare Callianassa; patchy Zostera; 13-16% fines; 5-11 days
     maximum continuous submergence.

D   No Callianassa; Zostera; 24-29% fines; 46-127 days maximum
     continuous submergence.

E   Callianassa and Vaucheria mat absent; 13-16% fines; 25 days
     maximum continuous exposure.

F   No Callianassa; dried out Vaucheria mat and surface sediments;
     13-16% fines; 9-13 days maximum continuous exposure.

G   No Callianassa; lush Vaucheria mat; 13-16% fines; 2-7 days
     maximum continuous exposure.

H   Callianassa; no Vaucheria mat; 13-16% fines; exposed and
     submerged twice a day.

I   Callianassa; no Vaucheria mat; 24-29% fines; exposed and
     submerged twice a day.

J   Callianassa; no Vaucheria mat; 38-44% fines; exposed and
     submerged twice a day.

K   Callianassa; no Vaucheria mat; 62% fines; exposed and
     submerged twice a day.

L   Callianassa; Zostera; 38-44% fines; 5-18 days maximum
     continuous submergence.

Table 6. Oligochaete species found in this study.
Species less than 4 mm long: meiofauna.
Species greater than 10 mm long: macrofauna.

size class

Enchytraeidae

Marionina vancouverensis Coates, 1980	meiofauna
M. sjaelandica Nielsen and Christensen, 1961	meiofauna
M. subterranea (Knöllner, 1935)	meiofauna
M. achaeta Lasserre, 1966	meiofauna
M. vaucherii Strehlow, m.s.	meiofauna
M. callianassae Strehlow, m.s.	meiofauna
M. gonori Strehlow, m.s.	meiofauna
Enchytraeus sp.	macrofauna
Lumbricillus spp.	meiofauna, macrofauna

Tubificidae

Aktedrilus locyi Erséus, 1980	meiofauna
A. oregonensis Strehlow, 1982	meiofauna
Limnodriloides monothecus Cook, 1974	macrofauna
L. verrucosus Cook, 1974	macrofauna
L. victoriensis Brinkhurst and Baker, 1979	macrofauna
Tubificoides pseudogaster (Dahl, 1960)	macrofauna
T. coatesae Brinkhurst and Baker, 1979	macrofauna

Naididae

Paranais litoralis (Müller, 1784)	meiofauna

Undescribed family

Oligochaeta sp.	meiofauna

Table 7. Average number of oligochaete specimens per sample (177 cm^2) for strata.

(   ): Values not used, following criteria one and two in methods section.

Tidal Height (m)	Oligochaeta sp.	Aktedrilus locyi	Aktedrilus oregonensis	Marionina callianassae	Marionina siaelandica	Marionina vaucheri	Marionina gonori	Paranais litoralis	Marionina subterranea	Marionina achaeta	Marionina vancouverensis	Lumbricillus spp.	Enchytraeus sp.	Tubificoides pseudogaster	Tubificoides coatesae	Limnodriloides victoriensis	Limnodriloides verrucosus	Limnodriloides monothecus
Area S																		
+1.83	7.3	6.8			29.3			(0.7)	(0.3)			(1.2)					(0.9)	
+1.52	8.7	23.0		2.9	(0.8)			2.6				(0.3)			(0.3)		(0.4)	
+1.22	10.2	18.2	2.3	4.5				(0.2)				(0.2)			(0.2)			
+0.91	5.5	19.0	29.5	(0.5)				(4.0)				(1.0)				(0.5)		
+0.30				(0.5)				14.5						23.0	35.5	15.0		
0.00			(1.0)	(0.5)	(0.5)			15.0						15.5	85.5	55.5	(0.5)	
-0.30		(6.0)			(1.5)			(0.5)						2.5	207.5	16.6	10.5	
-0.61	(0.5)							(0.5)						6.0	158.0	(1.5)	5.0	
Area M																		
+2.13		20.0			5.0	77.0	103.0	(1.0)		4.0	914.0	34.0	21.0					
+2.04		15.0		(1.0)	2.3	62.8	14.3	(1.5)			(0.3)	(0.3)					(0.3)	(0.5)
+1.83		77.7	5.7	(0.3)	42.1	151.7	30.9	55.0	(0.1)		(1.0)	(0.3)			(0.7)	2.7	2.4	
+1.52			(0.3)	(1.0)	(0.3)			11.0						(1.0)		175.7	(1.0)	14.3
+1.22								(0.3)				(0.3)				54.5	(1.0)	(0.8)
+0.91			(1.3)		(1.0)	(2.7)	(1.7)					(1.0)			2.0	13.3	2.3	
+0.61	(0.3)		(0.3)															
+0.30								(1.0)						(0.3)		49.0	4.9	(1.0)
Area ML																		
+0.61			26.0		6.0	10.0		5.0				24.0			13.0	22.0	26.0	
+0.30						(0.5)		(0.5)										
0.00														(1.5)	383.5	143.5	718.5	(1.0)

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in M. Average abundance and species richness are highest   in
upper and lower strata, and lowest in mid intertidal strata. The
spatial distribution of sample groups based on oligochaete species
composition is given in Figure 7, and the species composition of
the groups in Table 8.

Dominant species of small non-oligochaete macrofauna are
listed in Table 9 and species abundance data in Table 10. Tidal
levels above +0.6 m in S and +1.5 m in M were dominated by bur-
rowing species, and lower tide levels by tube dwelling and surface
deposit feeding species. The spatial distribution of sample groups
based on non-oligochaete species composition is given in Figure 7,
and the species composition of the groups in Table 11.

Similarity classifications of samples

Twelve distinct sample groups, each of uniform oligochaete
species composition, were revealed by the similarity and matrix re-
arrangement procedures (Fig. 7). Seven sample groups, of uniform
non-oligochaete species composition, (Fig. 7) were revealed by the
same procedures. These seven groups were also distinct from each
other with respect to faunal composition, but probably would have
been more sharply differentiated if all taxa involved had been
classified to the species level. Sample clusters based on both the
oligochaete and non-oligochaete taxa are highly similar, with a
Rand's association coefficient of 0.914 between the two classifi-
cations.

Table 8. Numerically dominant species in sample groups clustered
          by oligochaete species composition as mapped in Figure 7.
          Species listed in order of decreasing abundance.

Group

1   Marionina sjaelandica, Lumbricillus spp. (85.9%)[a] (5)[b].

2   Oligochaeta sp., Aktedrilus locyi (82.2%) (5).

3   Aktedrilus locyi (74.5%) (8).

4   Aktedrilus oregonensis, A. locyi, Paranais litoralis (90.7%)
     (3).

5   Tubificoides coatesae, Limnodriloides victoriensis, Tubifi-
     coides pseudogaster, Paranais litoralis (98.9%) (4).

6   Tubificoides coatesae, Limnodriloides victoriensis, Limno-
     driloides verrucosus, Tubificoides pseudogaster (97.8%) (4).

7   Marionina vancouverensis, Marionina gonori, Marionina
     vaucherii, Lumbricillus spp., Enchytraeus sp. (99.5%) (2).

8   Marionina vaucherii, Aktedrilus locyi, Marionina gonori
     (94.9%) (7).

9   Marionina vaucherii, Aktedrilus locyi, Paranais litoralis,
     Marionina sjaelandica, Marionina gonori, Aktedrilus
     oregonensis (97.8%) (7).

10   Limnodriloides victoriensis (86.7%) (9)

11   Aktedrilus oregonensis, Limnodriloides verrucosus, Lumbri-
     cillus spp., Limnodriloides victoriensis, Tubificoides
     coatesae (84.1%) (3).

12   Limnodriloides verrucosus, Tubificoides coatesae, Limno-
     driloides victoriensis (99.7%) (4).

     a: Percent of the total number of specimens belonging to
         the dominant species.
     b. The number of species present in addition to the
         dominant species.

Table 9. Numerically dominant non-oligochaete species used in this
          study and their habits.

Amphipods

   Corophium brevis   tubiculous, surface deposit feeder
   Eohaustorius estuarius   burrowing, fine detritus feeder
   Paraphoxus spinosus   burrowing, fine detritus feeder

Cumacea

   Cumella vulgaris   burrowing, fine detritus feeder
   Hemileucon sp.   burrowing, fine detritus feeder

Tanaidacea

   Leptochelia dubia   tubiculous, surface deposit feeder

Insecta

   Ceratopogonidae larvae   living in algal mat
    and pupae
   Dolicopodidae larvae   living in algal mat
   Ephydridae larvae   living in algal mat
   Ephydridae pupae   living in algal mat

Polychaeta

   Paraonidae sp.   motile surface deposit feeder
   Phyllodocidae spp.   motile carnivores
   Spionidae spp.   tubiculous surface deposit feeder

Phoronida

   Phoronida sp.   tubiculous filter feeder

Turbellaria

   Turbellaria spp.   interstitial ciliary glider,
                             predators and herbivores

Table 10. Average number of non-oligochaete specimens per sample (177 cm^2) for strata.
( ): Values not used, following criteria one and two in methods section.

Tidal Height (m)	Hemileucon sp.	Phoronida sp.	Paraphoxus spinosus	Corophium brevis	Turbellaria spp.	Eohaustorius estuarius	Paraonidae sp.	Phyllodocidae spp.	Camella vulgaris	Leptochelia dubia	Spionidae spp.	Ceratopogonidae larvae and pupae	Dolicopodidae larvae	Ephydridae larvae	Ephydridae pupae
Area S															
+1.83					11.7	33.0	15.3	4.8	(0.2)		(0.2)	4.7			
+1.52					2.0	3.4	114.8	12.2			(1.0)				
+1.22					3.8	10.5	106.5	13.0			(1.5)				
+0.91					(1.5)	17.5	(1.0)	5.5	(0.5)		7.0				
+0.61			(0.50)			9.5	4.5	(1.5)		8.0	32.0				
+0.30			(1.0)		(1.5)		3.0	(0.5)	(1.5)	2.0	42.0				
0.00	(1.0)			(2.5)			(0.5)		14.5	(1.0)	53.0				
-0.30							(1.0)	(0.5)	9.0	5.5	29.5				
-0.61							(1.0)	(0.5)				(0.5)			
Area M															
+2.13											2.0	9.0	3.0	12.0	
+2.04										(0.3)	(1.5)	36.0	6.8	60.5	41.0
+1.83					(0.4)		(0.1)	3.7	2.4	(0.9)	232.6	31.0	3.0	(1.0)	43.0
+1.52			(0.3)	3.0			(0.7)	12.7	9.3	177.0	147.0	(1.0)			
+1.22			(1.0)	27.8				6.0	30.0	465.0	436.5				(0.3)
+0.91	2.0	48.3	13.0	13.3	(0.7)			12.0	17.7	528.0	514.0				
+0.61	5.3		14.7	(0.3)	(0.3)			(1.3)	17.3	319.0	175.3				
+0.30															
Area ML															
+0.61			(1.0)	25.0	6.0			2.0	24.0	7.0	123.0				
+0.30	3.5	157.5	6.5	4.0					68.5	16.5	45.0				
0.00															

Table 11. Numerically dominant species in sample groups clustered
by non-oligochaete species composition as mapped in
Figure 7. Species listed in order of decreasing abundance.

Group

I   Eohaustorius estuarius, Turbellaria spp., Phyllodocidae spp.
$(98.8\%)^a$ $(3)^b$.

II   Paraonidae sp., Phyllococidae spp., Eohaustorius estuarius
(94.0%) (4).

III Spionidae spp., Leptochelia dubia (76.7%) (8).

IV   Ephydridae larvae, Ceratopogonidae larvae and pupae,
Dolicopodidae larvae (92.3%) (1).

V   Ephydridae larvae, Ephydridae pupae, Ceratopogonidae larvae
and pupae, Dolicopodidae larvae (98.8%) (2).

VI   Spionidae spp., Ceratopogonidae larvae and pupae (82.4%)
(8).

VII Spionidae spp., Leptochelia dubia, Cumella vulgaris,
Phyllodocidae spp., (98.7%) (5).

a: Percent of the number of specimens of the species
listed to the total number of specimens from all
species used in the analysis.

b: The number of speices present in addition to the
dominant species, for those species used in the
analysis.

Recurrent species groups

The analysis of similarity of species distribution by sample composition indicated that both oligochaete and non-oligochaete recurrent species groups were rare at the study site (Fig. 8). A few high similarities were found, but the only distinct recurrent oligochaetes species group was the _Marionina vaucherii_ and _Marionina gonori_ pair. Both species were distributed almost exlusively in the _Vaucheria spp._ algal mat. The other cases of high correlations resulted from the coincidence of the narrow distribution of a rare species with an area of high abundance of a common species. The high number of species pairs with zero similarity indicates that the distributions of most species did not overlap spatially, reflecting environmental heterogenity of the study site.

Faunal classifications versus physical habitat classifications

For both the oligochaete and the non-oligochaete species, classification of samples by species composition and by physical variables resulted in the same general sample groupings (Fig. 7). A comparison of the two classification strategies using the oligochaete fauna alone showed that the faunal and physical variables grouped samples identically in the upper and the lower intertidal, but differently in the mid intertidal. In area S the mid intertidal was divided more finely by species composition than by the physical variables, but the observed species groups were separated in the horizontal and so could not be resolved by the use of critical tide levels. Sediment samples were not taken on a scale fine enough to show horizontal variation in sediment types within strata. In area

Figure 8. Frequency histogram of the similarity coefficients of

spatial distributions for all oligochaete species pairs

(a), and non-oligochaete species pairs (b).

Figure 8
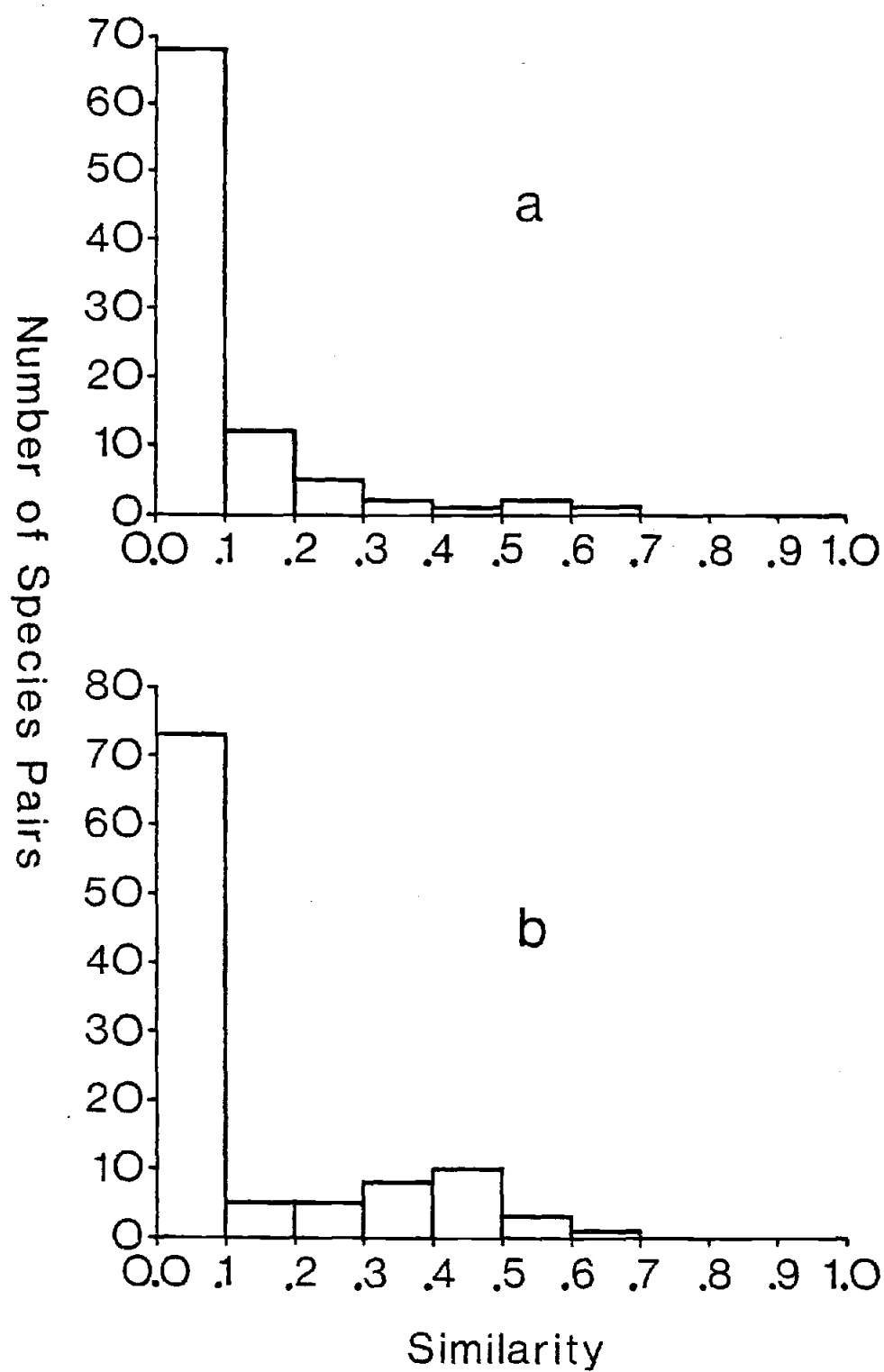
M, the mid-intertidal was divided less finely by species than by the physical variables. There was much variability in density but species composition was fairly constant. The only measured physical factor that changed in mid M was general sediment type, with percent fines increasing from 14.3% to 46.1%. This zone was characterized by a single dominant oligochaete species, Limnodriloides victoriensis. Above 14% fines, general sediment type and its associated factors did not affect the most abundant oligochaete species in this zone.

The degree to which the similarity classification depended on the physical habitat classification was estimated with Goodman and Kruskal's λ_B coefficient. Knowledge of the physical habitat classification improved the probability of correctly classifying a given sample by 87% over the probability when only the number of samples defined by each species spatial assemblage was known. The value of λ_B was 0.95 for the dependence of the non-oligochaete sample classification on the physical habitat classification. The non-oligochaete and habitat classifications were identical in upper and mid S, but in lower S the classification based on species composition resulted in one sample group, while the habitat classification resulted in two samples groups. All samples from upper M except one were grouped identically by both the fauna and the physical variables. The remaining sample from upper M showed a high similarity to the mid M samples and was grouped with them. All samples in mid and lower M and ML were classified into a single group.

Sediment type and critical tide levels

The vertical distribution of species breaks, sediment type

breaks, and critical tide levels were tested for independence,

separately for oligochaete and non-oligochaete species. All tests

were made against a $\chi^{2(0.99)}_{(1)}$=6.63. The null hypothesis of independ-

ence was not rejected for the comparison of sediment type breaks and

critical tide levels (χ^2=0.79). The null hypothesis also was not re-

jected for the comparison of species breaks and sediment type breaks

(χ^2=0.81 for the oligochaetes, and 0.97 for the non-oligochaetes).

Species breaks and critical tide levels showed a significant degree

of association (χ^2=9.65 for the oligochaetes, and 8.98 for the non-

oligochaetes).

Discussion

Physical habitat types

Physical habitat types at the study site were defined on the

basis of percent fine sediments ($\leq$ 100 m diameter) and length of

maximum continuous tidal exposure or submergence. The high positive

and negative correlations between all sediment grain size variables

except fine sand indicate that percent fines describes overall sedi-

ment character well and is a good indicator of other physio-chemical

conditions.

Available pore space determines which locomotory types live in

a given sediment (Wieser 1959, Jansson 1967a, Fenchel 1969), and is

related to both median grain size and sorting. Since both variables

are highly correlated with percent fines, the latter can be considered

representative of available pore space. Permeability, sediment

sorting, and oxygen are consistently correlated in tidal marine,

atidal brackish, and freshwater beaches in Europe (Jansson 1967a, b; Enckell 1968; Brafield 1964; Fenchel 1969), implying a fundamental relationship among these factors. Since sediment sorting and percent fines are highly correlated, percent fines may also be a good indicator of sediment permeability and oxygen concentration. Other factors correlated with sediment grain size are bacterial biomass (Dale 1974) and detritial food particle abundance and diversity (Whitlatch 1981).

Classification of the sampling areas by both sediment and tidal height delimited discrete physical habitats. The distributions of macrophytes and *Callianassa californiensis* were confounded with the defined habitat types and were therefore not used in mapping habitat distributions.

Classifications of samples by species composition

Separate analyses of sample classifications based on oligochaete and non-oligochaete species served as a check on the consistency of the methods used. The high value of Rand's association coefficient indicates that the sample groups, independently derived using both sets of species, are very similar. This implies that the two sample classifications resulted from the same physical cause and were not artifacts of the statistical analyses.

Species assemblages versus physical habitat types

Each sample group derived from the similarity classification is characterized by a unique assemblage of dominant species. When degree of dependence of species assemblages on physical habitat types was examined for the oligochaete and non-oligochaete fauna separately,

high values of Goodman and Kruskal's λ_B were obtained in both cases. The physical habitat types used were good predictors of the dominant species in a given area. Sediment type and maximum tidal exposure and submergence periods are important physical factors affecting faunal distributions at this site. The rarity of recurrent species groups among the oligochaetes and the non-oligochaetes indicates that the defined physical habitats were not good indicators of factors limiting individual species distributions. In general, species at the study site were distributed independently of one another, indicating that each species was responding in a unique way to its environment.

Critical tide levels

There is agreement that factors associated with tidal height have an effect on species distribution, but whether tidal height effects alone can result in sharply defined intertidal floral and faunal zones is disputed (compare Doty 1946 and Underwood 1978).

Tidal exposure and submergence have been quantified in two ways: average percent exposure and submergence, and maximum continuous exposure and submergence. Colman (1933) discussed both methods in relating faunal zonation on a rocky shore to tidal exposure, but did not distinguish between the two concepts. Doty (1946) noted the conceptual difference and proposed that maximum continuous exposure and submergence would be the more important determinant of species vertical boundaries.

Null hypotheses derived from critical tide level concepts based

on average percent exposure and maximum continuous exposure curves differ. When percent exposure and submergence times' are used, no discontinuities in the exposure curve are evident, giving rise to the null hypothesis that species boundaries are independently distributed along the tidal height gradient (Underwood 1978). When maximum continuous exposure and submergence curves are constructed, sharp changes are evident at a few tidal heights (predicted critical tide levels), resulting in the prediction that these tidal heights will be associated with the limits of species distributions (Swinbanks and Murray 1981).

The critical tide level hypothesis was modified in this study, by using abrupt changes in species abundances along the tidal height gradient rather than observed vertical limits only. Proportional rather than absolute change in abundance was used because of the large range of species abundances found in the samples. Because it is impossible to distinguish between zero abundance in a sample due to absence of a species from an area and absence due to sampling error when the species is rare, in this study upper and lower species limits were treated as abundance changes rather than abundance discontinuities. Since a proportional factor always treats presence versus absence as a discontinuity, an absolute abundance of less than two specimens per sample was used to form an abundance class encompassing both rarity and absence of species. Occasionally single samples contained very high numbers of a species, but the same species was absent in the surrounding samples. The cause of this type of patchiness was not resolvable at the sampling scale

used. For this reason, if all of the specimens of a species from an assemblage were from a single sample, the species was put in the rare to absent category for the stratum.

Critical tide levels for the three months preceeding sampling were calculated from predicted rather than observed tidal data, making it impossible to evaluate any error resulting from using predicted tidal heights. The precision of the estimates of the tidal heights at which faunal breaks occurred varied inversely with stratal area, and therefore with tidal height at the study site. The equation for the mean tidal height interval between samples in stratum i for randomly placed samples is:

$$\bar{h}_i = 1/(K \cdot A_i)$$

where K is the number of samples allocated per unit area and A_i is the area of stratum i. The value of $\bar{h}_i$ ranged from 4cm in the upper intertidal to 10-15cm in the lower intertidal. This range was small enough to permit accurate estimates of the true elevations of faunal breaks.

Faunal breaks and critical tide levels were found to be associated. Exposure and submergence at critical tide levels either directly caused the observed zonation or the levels themselves are correlated with other actual operating factors. Breaks in sediment type were associated with both critical tide levels in lower S. The upper limit of the Zostera marina bed was not associated with a critical tide level. Breaks in sediment type were not associated with critical tide levels in areas M or ML. The +2.0 m and +1.5 m critical tide levels in area M were associated with the upper and

lower limits of the <u>Vaucheria</u> <u>spp.</u> algal mat, however. Factors associated with critical tide levels, rather than critical tide levels directly, appear to govern the pattern of vertical zonation of the oligochaete fauna in Coos Bay.

The non-oligochaete fauna examined also show a high association between critical tide levels and faunal breaks, indicating that the relationship is fairly constant for small macrofauna of various habits.

Effect of sediment type and vegetation

Wieser (1959), Jansson (1967a), and Fenchel (1969, 1978) concluded that there was a relationship between sediment pore space and community structure. These workers found that a true interstitial fauna would not be found below a critical grain size in well sorted sediments. Clearly, grain size cannot account for the observed distribution of meiofaunal and macrofaunal species at the study site. No discontinuities in median grain size, sorting, or percent fines (Table 3) correspond to the sharp boundaries separating the distributions of meiofauna and macrofauna in area M. Factors other than sediment granulometry appear to be responsible for the observed divisions. The limit of the meiofauna was associated with the lower limit of the <u>Vaucheria</u> <u>spp.</u> algal mat (+1.5 m). Fenchel (1969) and Nicholls, et al. (1981) found that the fauna in areas covered by algal mats was largely limited to the mat and depauperate in the anoxic sediment beneath it. The meiofauna in area M were probably in the <u>Vaucheria</u> mat, and the lower limit of the mat probably determined the boundary between strata dominated

by meiofaunal species and strata dominated by macrofaunal species.
The boundary between the meiofauna and the macrofauna was between
+0.4 m and +0.7 m tidal height in area S. This boundary is associated with the change from sediments with 2-7% fines to sediments with
13-16% fines. In this region _Callianassa_ _californiensis_ density declined sharply but did not drop to zero. The loose, reworked sand
characteristic of the _Callianassa_ zone was replaced by firmer sediment with a very thin surface layer of silt. Macrofaunal species
were abundant in area M but not in area S above +0.6 m, and may be
excluded from S above this level by the burrowing activity of
Callianassa. Tidal exposure may play a direct role in limiting some
of the enchytraeid species to the upper intertidal, but sediment
type was almost certainly the limiting factor for _Aktedrilus_ _locyi_,
_A_. _oregonensis_, and _Paranais_ _litoralis_. These species were probably
also indirectly limited by the effect of tidal exposure on the algal
mat. Macrofaunal species may have been limited to lower intertidal
areas by the presence of the algal mat in M and the burrowing of
Callianassa in S.

General Conclusions

1) The enchytraeids *Marionina vaucheriae*, *M. callianassae*, and *M. gonori*, and the tubificid *Aktedrilus oregonensis* were described, and a preliminary description of Psammotheriidae n. fam., based on *Psammotherium hastatus* n. gen., n. sp., is given. *Marionina achaeta*, previously known from the littoral zone of both coasts of the north Atlantic, was described from Coos Bay.

2) The littoral oligochaete fauna of the northeastern Pacific is distinct from other regional faunas, with 27 endemic species out of 47 species recorded from the taxonomic literature. Nine of the 18 species found in Coos Bay are endemic to the northeastern Pacific, supporting the zoogeographic information available in the literature.

3) Discrete physical habitats, based on tidal exposure and sediment type, were found at the study site.

4) Distinct species assemblages, were found at the study site.

5) The spatial distribution of physical habitat types was strongly associated with the spatial distribution of species assemblages.

6) Recurrent species groups were rare, indicating that each species was responding independently to its environment.

7) Critical tide levels were strongly associated with the intertidal zonation of species.

8) Changes in sediment type were not associated with the intertidal zonation of species.

9) Algal mats and sediment disturbance appeared to affect the distribution of macrofaunal and meiofaunal species.

10) The results of the analyses are independent of the group of species analyzed, indicating that the observed spatial patterns are determined by factors associated with tidal exposure and sediment type, and are independent of species' lifestyle.

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