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CLASSIFICATION OF BENTHIC INVERTEBRATES INTO INFAUNAL TROPHIC INDEX FEEDING GROUPS

The purpose of the Infaunal Trophic Index is to describe the feeding behavior of soft bottom benthic communities in terms of a single understandable number. These animals fall into four groups; they are either suspension or deposit feeders that feed above, on, or below the mud surface. Although this idea has been under development for several years, it was first published in the 1978 Annual Report (Word 1978). Since then modifications have been made that extended the scope of the Index's usefulness beyond the stated depth range of 20 to 200 meters. Now, by increasing the number of taxa from 46 to 53, the Index effectively describes invertebrate community feeding structures to a depth of about 800 m. It now is probably useful in many other parts of the world.

Since the Index was first devised, it has been applied to more than 2000 benthic samples taken in the coastal waters of southern California. Some of these were plotted and contoured in the 60 m control survey and the Bascom survey that were published in the 1978 report. The results are so reliable, it is now possible to make accurate forecasts of what the Index will be at points several kilometers from existing stations. We feel this method of ecological mapping is very effective in describing the coastal shelf of southern California and it will find similar usefulness elsewhere.

Our first priority was to extend the Index' usefulness to deeper water so we could determine the effects of the large local outfalls on the benthic animals well down the slope where it was evident that some waste particles were being deposited. 63 repeat and additional samples were taken at depths of 200 to 800 m and subjected to detailed study. The result was the expansion of the Infaunal Trophic Index taxa to the list present here. The results of the deepwater expansion are reported in the following paper.

A number of scientists have asked how the animals (taxa) chosen for the Index were selected and grouped into the four feeding classes. This paper is a description of the research, observations, and thought processes that went into the classification.

PROCEDURES FOR CLASSIFICATION INTO TROPHIC GROUPS

Selection of Dominant Species

Benthic invertebrate species were selected on the basis of abundance in a sample. The species accounting for the most abundant 60 percent in each sample were included. The most numerous species or taxa were selected from all of the samples, and their abundance tabulated in all of the samples. At 63 deep water stations, the species selected from each grab sample accounted for 75 percent of the total number in a sample after being tabulated. The comprehensive list of taxa is given in Table 1; names of species or taxa added as a result of this new depth range are preceded by a dot or asterisk. An asterisk preceding the taxon name indicates that the previous list contained a lower level of the current taxonomic classification.

It is important to note the distinctions between detrital and deposit feeding behavior as defined by the author. These definitions may differ from those contained in some of the literature. Detrital feeding animals use particulate organic material as a food source (either whole or portions of live or dead plants or animals and their waste products). Deposit feeding taxa are dependent upon the less identifiable organic debris attached to or deposited within the interstices of the sediment grains. The deposit feeding taxa contain abundant quantities of sediment grains or identifiable plant debris in their digestive cavities; the detrital feeding taxa generally lack these materials.

Determination of Feeding Habits

It is widely recognized that all invertebrates can feed in a variety of ways and that a species may switch from one feeding technique to another. There are, however, operative environmental conditions which favor each method; and one of these becomes the most advantageous for each species. The taxa may become dominant when that manner of feeding is environmentally favored.

Several observations are crucial to the determination of prevailing feeding habits; each contributes only a fragment to the necessary picture of an animal's feeding behavior. Defining the feeding habit of benthic invertebrates requires information from the physical, chemical, and biological sciences. Strengths of bottom currents, settling rates of particulates, and influence on

Table 1. Fifty-three invertebrate taxa divided into four categories of Infaunal Trophic Index Feeding Strategies.

GROUP I
Suspended Detritus Feeders

Passive

- ● Maldanidae (Po)
- ● Onuphidae (Po)
- ● Ampharetidae (Po)
- ● Terebellidae (Po)

Normal

- ● *Owenia* (Po)
- ● Sabellidae (Po)
- ● Serpulidae (Po)
- ● *Amphipholis* (E)
- *Amphiodia* (E)
- *Phoronis* (Ph)
- ● Caprellida (A)
- *Ampelisca I (A)*

Active

- ● *Nemocardium* (Pe)
- ● *Crenella* (Pe)
- *Ampelisca II* (A)
- ● *Byblis* (A)
- Phoxocephalidae (A)
- ● *Cucumaria* (E)
- *Sthenelanella* (Pe)

GROUP II
Surface Detritus Feeders

Stationary

- ● Spionidae (Po)
- ● Magelonidae (Po)
- Cirratulidae (Po)
- ● *Myriochele* (Po)
- *Axinopsida* (Pe)
- *Mysella* (Pe)
- ● *Calyptogena* (Pe)
- *Photis* (A)

Mobile

- ● Orbiniidae (Po)
- Capitellidae (Po)
  - *Mediomastus*
  - *Decamastus*
- ● *Nephtys* (Po)
- ● *Glycera* (Po)
- ● *Goniada* (Po)
- ● Tanaids (A)
- Ostracoda (A)
  - *Euphilomedes*
- ● Cumacea (A)

Specialized

- ● *Cistena californiensis* (Po)

GROUP III
Surface Deposit Feeders

Stationary

- *Parvilucina tenuisculpta* (Pe)
- *Macoma carlottensis* (Pe)
- ● *Nuculana* (Pe)
- ● *Nucula* (Pe)
- ● *Yoldia* (Pe)

Mobile

- ● *Travisia* (Po)
- ● *Nereis* (Po)
- ● *Bittium* (G)
- ● *Mitrella permodesta* (G)
- ● *Nassarius* (G)

GROUP IV
Sub-Surface Deposit Feeders

- *Capitella capitata* (Po)
- *Armandia bioculata* (Po)
- ● *Ophelina acuminata* (Po)
- Oligochaeta (An)
- *Solemya* (Pe)
- Stenothoidae (A)
- Dorveilleidae (Po)

(A) = Arthropoda
(AN) = Annelid
(E) = Echinodermata
(G) = Gastropoda
(Pe) = Pelecypoda
(PH) = Phoronid
(Po) = Polychaeta

● Indicates new taxa added to lists previously published.

these parameters by the organisms determine the quantities of particulates available to the animals. Chemical measurements (BOD, COD, volatile solids) help verify the quantity of these particulates that remain available to the organisms and their biological utilization. The types of particulates eaten, how they were collected, where they were obtained, and the relative amounts of energy required to accumulate them are important biological considerations.

Table 2 gives a list of biological and environmental characteristics that are used to determine feeding habits. The combined information from these observations provides a reasonably accurate assessment of the prevailing feeding habit used by benthic invertebrates in the specific locations where each of the taxa are dominant. The description of feeding habits must be consistent with all of these observations. Conflicting pieces of information sometimes emerge, although generally these can be reconciled and a consistent description of an organism's feeding habits can be developed. The discussion that follows exemplifies two common sources of controversy and the process of resolution.

Table 2. Guide to determining feeding characteristics.

BIOLOGICAL

A. Possible feeding techniques available to the animal are determined by:

1) assessment of morphological characteristics.
2) observations on feeding behavior made under both laboratory and field conditions are collected (these records are often sparse or incomplete).
3) noting the presence or absence of sediment grains in the animals' stomach contents. These may be indicative of patterns of either deposit or detrital feeding.

B. The type of habitat is determined by:

1) the level within the sediments and the vertical stratification
2) by the existence of tubes, burrows, etc.

C. The level of energy is determined (qualitatively) by estimating the energy required to sustain the animals' feeding strategy.

D. The animal's position in its community is compared with other dominant species feeding behaviors at the location.

ENVIRONMENTAL

A. Quantitative measurements are made to determine the amounts and quality of organic material available to the animal in its benthic habitat. These measurements include biological oxygen demand (BOD_5), chemical oxygen demand (COD), and volatile solids of substrate samples.

B. Current strengths and their possible consequences to individual species are estimated.

Presence of sediment in stomach contents does not always indicate deposit feeding.

Cistena californiensis (*Pectinaria californiensis*) is an example of one type of detritus feeding polychaete that includes sediments in its stomach contents. (A complete example of this animal's feeding habit is presented in the discussion of Group II strategies and taxa). Other examples are polychaetes in the family Sabellariidae that require sediments in the building of their tubes but depend upon suspended detrital materials for their food.

Various members of the phyla Sipuncula often contain sediment in their stomach contents but they are considered to be surface detritus feeders. In this case, I believe that the sediments serve as a means for crushing the hard exoskeletons of diatoms and crustaceans that also appear in the stomach contents. The lack of crushing jaws creates a dependence upon the crushing power of peristaltic contractions against the hard mineral grains. Description of the feeding habits of several Sipuncula have been made by Hyman (1959), who indicated that diatoms are their major food. In addition, Hyman noted that Sipuncula contain large quantities of sediment in their stomachs. These observatons are consistent with the above hypothesis.

These examples serve as a caution to interpretation of deposit feeding based solely upon the presence of sediments in stomach contents. Identification of deposit feeding or detrital feeding requires a description of feeding behavior that is consistent with all the observations; none are sufficient by themselves.

Behavioral observations made under laboratory conditions may differ from those made in the field.

The presence of modified feeding appendages and observations of how they are used under conditions that closely parallel natural bottom currents is required before a detrital feeder can be classified as suspended or surface feeding and before a deposit feeder can be described as surface or sub-surface feeding. Scientific literature contains many useful descriptions of the feeding ecology of invertebrates. These observations must, however, be critically examined on the basis of the presence or absence of bottom currents approaching those occurring in the animal's natural habitat. The plasticity of an organism's feeding behavior is remarkable and many animals will substitute one mode of feeding for another in order to survive under less than optimum conditions.

For example, *Amphiodia urtica* (*A. barbarae*) has been described as both a deposit feeder (MacGinnitie 1949) and as a suspension feeder (Word 1979). Both observations have been accepted by various investigators even though these views are diametrically oppossed. The reason for the discrepancy can be found by critically examining the description of the organism's feeding behavior and the conditions of the environmemt during both observations.

In an aquarium without bottom water movement, *Amphiodia urtica* swept its arms over the surface of the sediment and captured the suspended detritus with its tube feet (MacGinnitie 1949). Those captured at sea lacked sediment grains in their stomach contents and were found at stations on the coastal shelf with low organic concentrations in the sediments (Word 1979). Both of these observations indicate that deposit feeding is not likely to be a successful means of nourishment for this animal.

In additional aquaria observations, I found indications that *Amphiodia urtica* will feed entirely upon suspended detritus when the animal is exposed to water movement which occurs near an aerating stone or the return stems of filters. All of these observations including those made by MacGinnitie are consistent with suspension feeding . MacGinnitie's observations further indicate that the animal actually had to resuspend detritus prior to recapturing it in aquaria without water motion.

This example suggests the need for caution in interpreting observations made only in aquaria without bottom water movement. Ideally, feeding behavior observations should be made in the animal's own habitat, or if this is not possible, currents should at least be simulated in the aquaria. Caution must also be used when abstracting feeding behavior observations from literature. As indicted in this example, deposit feeders are not always what they seem when only reading the literature.

CLASSIFICATON INTO FEEDING STRATEGIES

Once the prevailing feeding habits for each species have been defined, the species are grouped according to generalized feeding patterns, which I have termed "feeding strategies". The range of possible feeding habits was identified and generalized into four categories. For the purposes of these infaunal community analyses, the primary separation into groups of feeding strategies was based upon the distinction between detritus and deposit feeding animals; i.e. the type of food consumed.

Although the four categories used in the original form of the Infaunal Trophic Index method have remained the same, a better understanding of the feeding behaviors of these animals was gained from the current work. Refinements have been made that will make the analyses and results of this method more sensitive to both animal behavior and environmental conditions.

The actual scheme used to separate the groups is shown in Table 3. This table demonstrates that the groups can be further divided on the basis of the location of food items, and the relative degrees of energy required to obtain and utilize these resouces. The suggested importance of the role of energy utiization is a new consideration and is briefly discussed below.

IMPORTANCE OF ENERGY UTILIZATION TO FEEDING STUDIES

There are two principal hypotheses which are pertinent to benthic feeding studies:

1) Different feeding behavioral movements of the animals require varying amounts of energy; the most successful behavior of each species defines which benthic communities they can dominate.
2) The availability of food resources is influenced by the strength and patterns of bottom water movement and the settling rates of particulates. These may also be affected by feeding habits and dwellings of the individual species. The interaction of these factors helps determine the optimum environment for each species, i.e. potential dominance patterns.

Animals obtain organic particulates by moving their bodies to the particulates, moving a modified feeding appendage to the material, or by passively accumulating them near their dwelling due to interuptions in water flow around these dwellings. This sequence of feeding techniques appears to require lesser quatities of energy. Each of the 4 trophic groups discussd below have taxa that use at least one of the techniques outlined above.

Therefore, if an organism expends a relatively large quantity of energy in capturing its food, it must either make more efficient use of the energy required to capture its food, or live in an environment where this material is abundant. It is hoped that quantitative measures will become available in the future to better investigate these hypotheses.

DESCRIPTION OF THE FOUR TROPHIC GROUPS

The following discussion of each group includes detailed examples and illustrations of the significant behavioral differences pertinent to each group. Four sub-categories of suspension feeding are discussed, as well as three categories of surface detrital feeding and two of surface deposit feeding. These sub-divisions are based upon apparent differences in the quantity of energy required to obtain food.

Group I: Suspension Feeding

Suspension feeding organisms include those that actively pump water and suspended particulates through a filtration apparatus and those that use highly developed feeding appendages to sieve particles from the water column with the aid of bottom currents. Passive suspension feeding is an additional suspension feeding technique that results in accumulations of detrital materials near the tubes of apparent surface detrital feeders. This technique and a modification of it will be described in detail.

Table 3. Scheme used to generalize feeding habits into feeding strategies, the basis for the separation of Infaunal Trophic Index taxa groups.

WHAT IS EATEN?	WHERE IS IT OBTAINED?	RELATIVE ENERGY REQUIREMENT?
Detritus: usually lacks sediment grains in stomach contents	*Suspended*: from the water column (GROUP I)	*Passive*: Tubes or burrows concentrate materials close to the organism
		Normal: Modified appendages are held into bottom currents
		Active: Active motion of animal draws particles toward itself
	At Sediment Surface: usually from upper 0.5 cm (GROUP II)	*Stationary*: Body appendage searches surface of sediments for food
		Mobile: Animal moves to search surface of sediments for food
		Specialized: Combination of two modes—active search of sediments and passive suspension
Deposits: has either sediment and/or plant debris in stomach contents	*From Surface Sediments*: usually from upper 5 cm (GROUP III)	*Stationary*: Body appendage searches sediments for food
		Mobile: Animal moves through sediment to search for food
	Sub-Surface Sediments: usually upper 10 cm of sediment (GROUP IV)	These organisms are mainly mobile; but information is incomplete or nonexistent

Normal and Active Forms of Suspension Feeding. Different species within the amphipod genus *Ampelisca* have two principal techniques of suspension feeding (Enquist 1950). One method uses the normal sieving of water-borne particulates, and the other actively draws suspended particulates to the animal. When the first method is used, feeding antennae which have numerous setae are turned into benthic currents, and these extract particulates from the water column (Figure 1). Conversely, the active form of suspension feeding is accomplished by waving antennae in such a manner that a vortex is created which, combined with the additional movement of pleopods, draws suspended particulates in towards the feeding appendages. This active form of suspension feeding obtains surface detrital material that has been resuspended by the activities of the organism as well as those particles already in the water column. It represents an intermediate form between the two strategies of suspended and surface detrital feeding.

Passive Suspension Feeding. Small scale patterns of disturbance and eddy formation have been observed and their forces calculated around simulated tubes in benthic sediments (Eckman 1979). Kudenov (1976) demonstrated that areas immediately surrounding the tubes of certain maldanid polychaetes contained significantly higher concentrations of organic materials than in the surrounding areas. Eckman and Kudenov both theorized that small scale patterns of disturbance enhanced the rate of settling of particulate organic materials and live larvae near the tubes. These observations, coupled with the absence of sediment grains in stomach contents, support the conclusion that they are

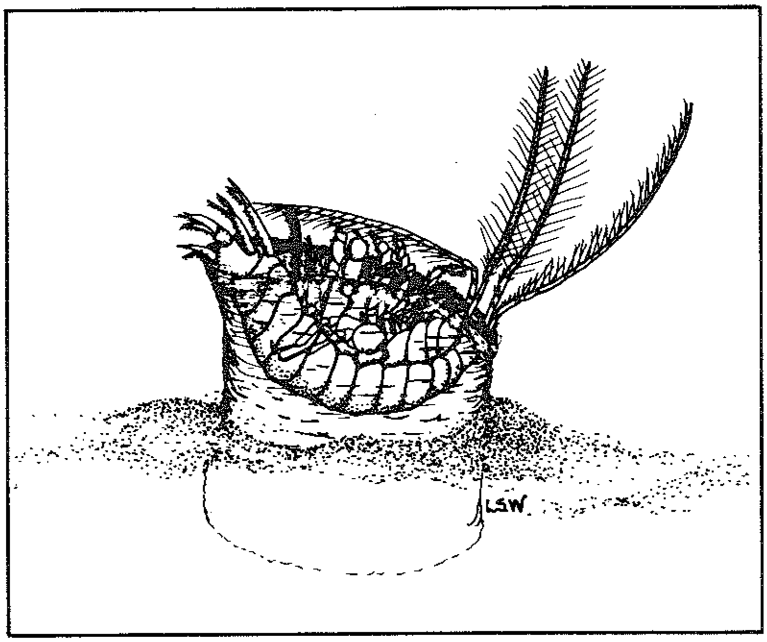

Figure 1. A "normal" suspension feeding amphipod of the genus *Ampelisca*. Note the numerous setae on the antennae which are held into the bottom water currents. These setae act as a sieve to collect suspended detritus. This illustration, and Figures 2 through 8, were drawn by Lucinda Smith Word.

detrital feeders rather than deposit feeders. The observations of feeding upon the accumulated detritus around their tubes or on the detritus falling within their tubes, rather than an active searching of wider areas of the sediment surface, support the conclusion that they represent a specialized form of suspension feeding. (Figure 2).

Gregarious Passive Suspension Feeding. The fourth technique of collecting suspended particulates is a modification of the passive suspension feeding mode. It occurs in waters where wave or current action is great enough to retain organic particulates in the water column. *Diopatra ornata*, an onuphid polychaete, exemplifies this behavior (Figure 3). This species lives in areas exposed to wave surge and requires some method to prevent being swept away. Two techniques have evolved to maintain this species in place. First, *D. ornata* anchor themselves by burying portions of their tubes in the sediment. This also serves to maintain other species often living in association with *D. ornata* but which require less dynamic conditions. *Diopatra ornata* however, requires greater holding power to remain in one location. This is probably the reason that it lives in such crowded conditions with numerous tubes intelaced. Interlacing apparently provides additional means of support similar to root systems developed by terrestrial plants.

This living arrangement, with its interlaced tube community, also aids the species in obtaining food by

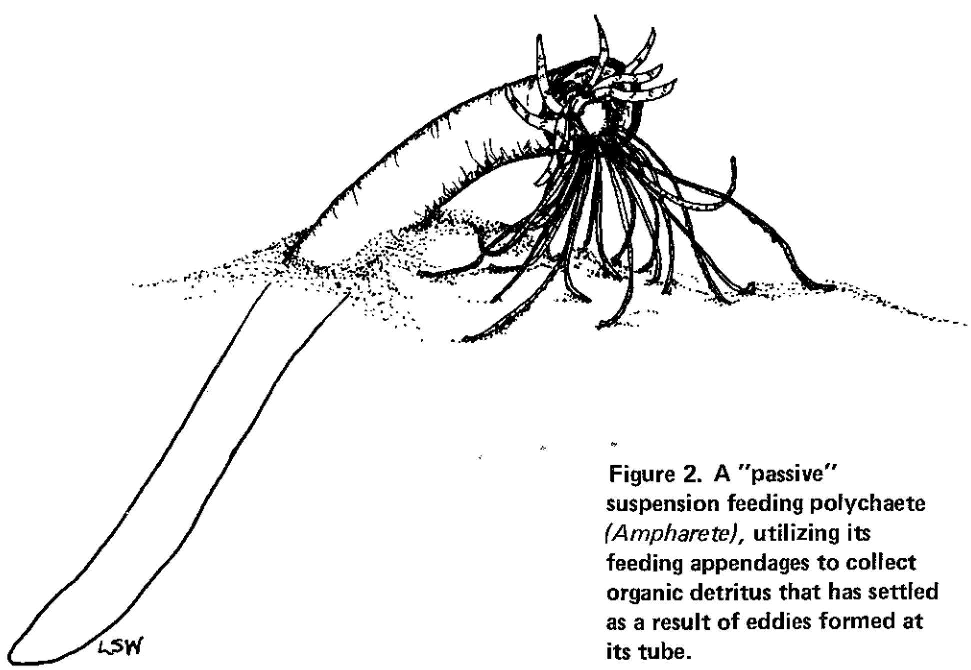

Figure 2. A "passive" suspension feeding polychaete *(Ampharete)*, utilizing its feeding appendages to collect organic detritus that has settled as a result of eddies formed at its tube.

serving as a large sieve or eddy-producing object. This sufficiently slows down the organic particulate allowing them to settle near the tubes. Direct observations indicate these animals feed on many forms of live or dead detritus around their individual tubes as well as on the neighboring tubes.

Suspension feeding species such as mussels and barnacles are commonly found near the shore on rocky coasts exposed to the turbulence of wave action. *D. ornata* is an excellent example of a specialized type of suspension feeder in wave-swept sandy beach environments.

Relative Energetics of Suspension Feeding. Three principal types of suspension feeding were discussed: active, normal, and passive. Each of these techniques of collecting suspended detrital materials appear to require different levels of energy consuming activity, and would therefore seem to require varying quantities of detritus to support the respective type of behavior.

The active suspension feeders utilize patterns of body movement that require more energy to draw particulate detritus towards themselves; the normal suspension feeding behavior allows benthic currents to bring detritus to an

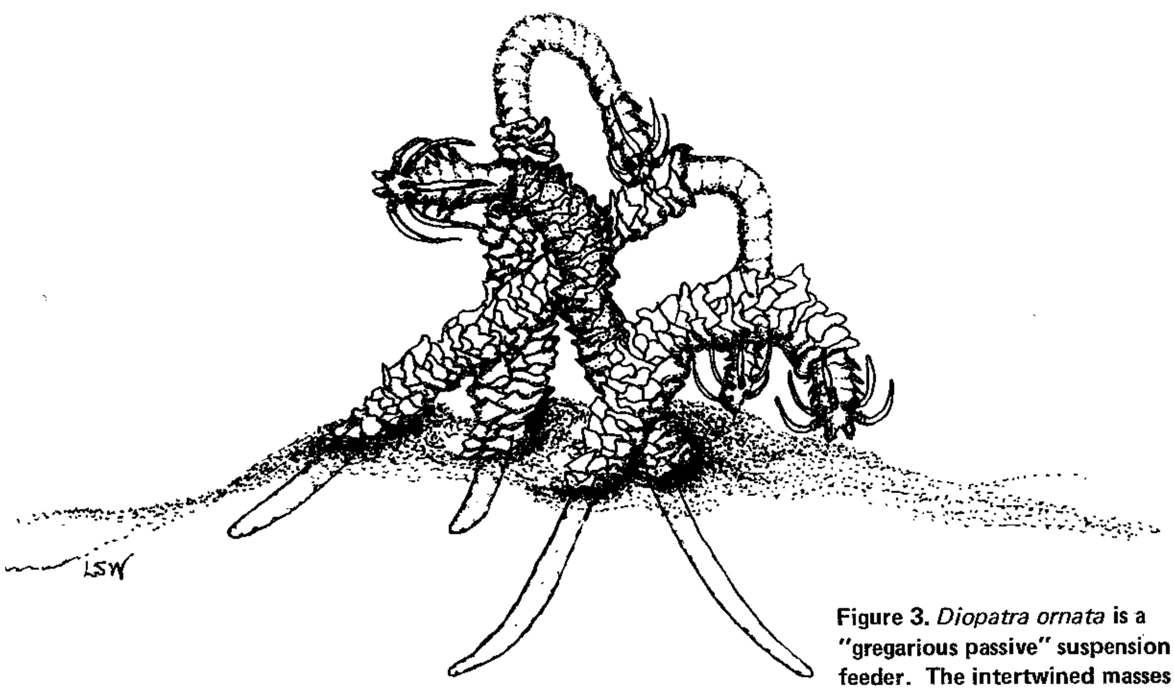

Figure 3. *Diopatra ornata* **is a "gregarious passive" suspension feeder. The intertwined masses of tubes aid in anchoring the animal in surf-influenced sediments and act as a large sieve to collect drifting detritus and cause material to deposit on and around the tubes.**

appendage held into the water column. However, supporting this appendage in the water colunm also requires energy. Passive suspension feeders which depend upon the structure of their tubes to form eddies and deposit detritus near them do not expend such energy in capturing food. Each of these categories requires a decreasing amount of activity and energy for obtaining detrital foods.

Group II: Surface Detritus Feeders

Surface detrital feeders obtain the same types of food as suspension feeders. Because their stomach contents do not reveal any major differences, behavioral observations serve as the only means of separating suspension from surface detrital feeding animals. Two typical surface detrital feeding behaviors are used by members of several different phyla. First, there are those organisms (e.g. *Photis*, *Corophium*, and *Tharyx*) that are relatively stationary surface detrital feeders. These animals have modified feeding appendages that search the surface of the sediment and then locate, capture, and convey food items to the animal (Figure 4). The second type, mobile surface detrital feeders, move from one food item to the next rather than drawing it toward themselves. Species exemplifying this type of behavior are the ostracod, *Euphilomedes*, and the polychaete, *Mediomastus*.

The polychaete, *Cistena californiensis*, employs a special modification of surface detrital feeding. It lives

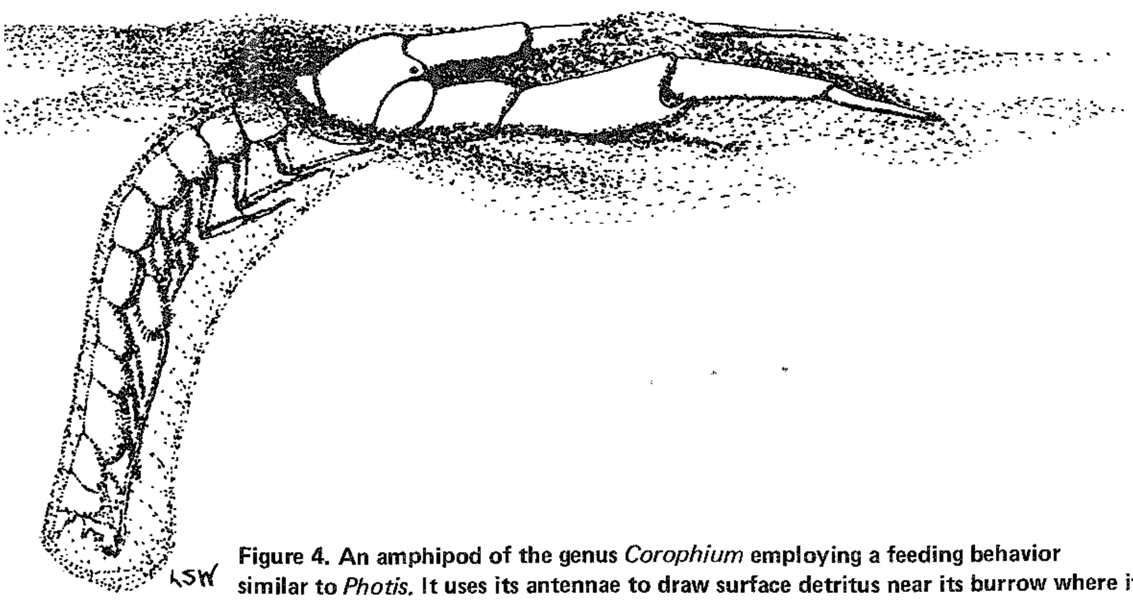

Figure 4. An amphipod of the genus *Corophium* employing a feeding behavior similar to *Photis*. It uses its antennae to draw surface detritus near its burrow where it then selects food particles with its mouth parts.

with its head burrowed to a depth of 5 to 10 cm beneath the surface of the sediment. As a result of this behavior, most researchers have considered the animal to be a sub-surface deposit feeder that feeds on the deposits surrounding the head of the species. The presence of sand grains in its stomach contents would also normally be sufficient to indicate deposit feeding. However, the following observations of its feeding behavior in aquaria and the types of fish that preyed heavily upon it support the premise that it is a detrital feeder.

C. californiensis was observed to move to the sediment surface at night by slowly rotating the tip of its tube and rising out of the sediments a distance of about 15 mm. It then lowers the tip of its tube until it is just above the surface and swings the tube in a circle until a sediment depression of approximately 1 cm in diameter had been produced (P. Striplin, personal communication). Haven and Morales-Alamo (1965), oberved that fluorescent particles placed on the surface of the sediment would be found buried to depths of 8 cm in aquaria containing this animal. It is hypothesized that these fluorescent particles and other surface detrital material fell into this pit and were forced into the sediment as the polychaete reburied itself (Figure 5).

The modification of surface detrital feeding employed by the polychaete *Cistena californiensis* appears to require a greater expenditure of energy to move through the sediments than the mobile surface detrital feeders that move through the water or surface detritus. However, the low frequency of this behavior in aquaria (observed once or twice a week for each animal) and the energy advantages obtained once the pit is constructed probably make this food collecting method energy efficient.

There is additional evidence indicating this observed behavior also occurs in the environment. When English sole (*Parophyrs vetulus*), a predator on *C. Californiensis*, were captured early in the day, they had large quantities of this species in their stomachs. No other predators containing large amounts of *C. californiensis* were found at any other time of day. It is possible that *P. vetulus* can detect movement (perhaps by means of small sensory pores near the mouth on the blind side), and thus successfully feed on *C. californiensis* while it forages at night.

Cistena californiensis becomes abundant in a variety of habitats extending from areas dominated by suspension feeders to areas dominated by surface detrital feeders.

GROUP III: SURFACE DEPOSIT FEEDING

It is often difficult to distinguish between surface and sub-surface deposit feeding animals, since both types generally have large quantities of sediment inside their stomachs. Sub-surface deposit feeders are often more mobile and contain larger quantities of plant material in their stomach contents than surface deposit feeders.

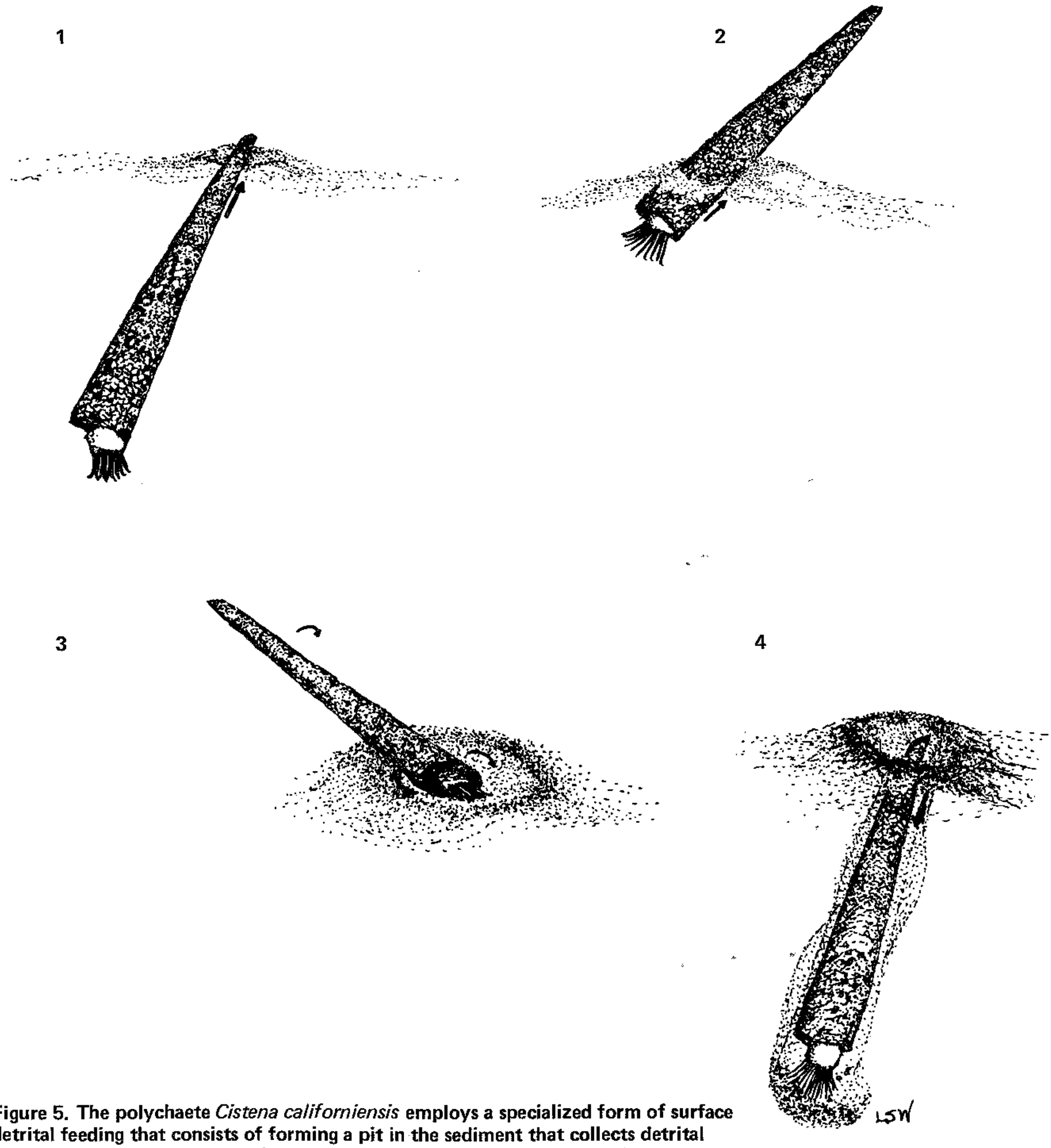

Figure 5. The polychaete *Cistena californiensis* employs a specialized form of surface detrital feeding that consists of forming a pit in the sediment that collects detrital material. The material is then forced into the sediments to depths of at least 5 cm.

Surface deposit feeders generally obtain their nourishment from the top 2 centimeters of sediment. There are two basic feeding strategies classified in this group: mobile surface deposit feeders and stationary surface deposit feeders. The polychaete genera *Travisia* and *Nereis* and the gastropods *Bittium*, *Nassarius*, and *Mitrella permodesta* are the mobile surface deposit feeders. These species all contain sediment grains in their stomach contents where they are numerically abundant and appear to be limited to the uppermost layers of the sediment. The gastropods move over the surface of the sediment with only millimeters of the foot beneath the sediment (Figure 6), while the polychaete *Travisia* is found directly on the surface of the sediment (Allan Hancock Foundation 1965). The polychaete genus *Nereis* is included in this grouping but requires additional study.

The stationary surface deposit feeders consist of several species of pelecypods that have evolved methods and appendages to help them collect deposited materials. *Macoma carlottensis* is a small clam that demonstrates such modifications (Figure 7). Its incurrent siphon or feeding appendage is as long as--or longer than--the rest of the body and moves easily over large areas of the sediment in search of food,. *M. carlottensis* is most successful on coastal slope sediments with heavy organic enrichment. At stations in these areas its stomach contents and gills are full of sediments in addition to detritus; therefore, it has been placed into the category of surface deposit feeding.

Though it does not have elongated siphons, the small clam *Parvilucina tenuisculpta* is a very successful deposit feeding organism on coastal shelves and slopes in areas with heavy organic enrichment. Its siphons are so short they do not usually extend to the surface of the sediment. Ordinarily, short siphons indicate some form of suspension feeding; but in this case, morphology does not explain the successful feeding behavior used by this species.

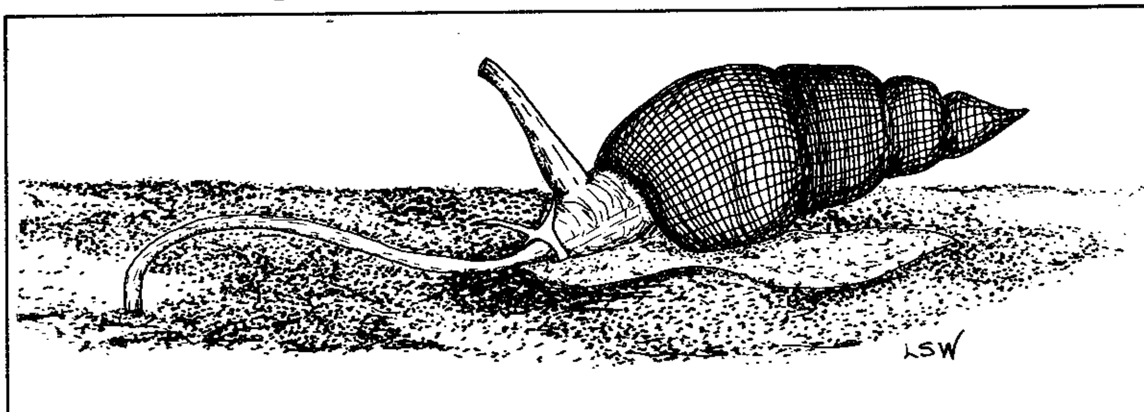

Figure 6. The gastropod genus *Nassarius* uses its proboscis to select particles while moving over the surface of the sediment. It is a mobile surface deposit feeder.

Examination of the stomach contents and the gills reveal that the quantity of sediment in these tissues is even greater than that observed in *Macoma carlottensis*. This suggests that the animal is a deposit feeder. Futher study of this species' depth of burrowing reveals that it lives within the upper 5 cm of sediment, supporting the premise that it is a surface deposit feeder.

Mobile surface deposit feeders probably use more energy to obtain their food than stationary deposit feeders. Observatons made while conducting studies at sea tend to support the conclusion that mobile forms require richer concentrations of sediment-bound organics than the stationary types. Unpublished data indicate that mobile species such as *Nassarius*, *Bittium*, and *Mitrella permodesta* become more abundant closer to outfall discharge locations in more nutrient rich sediments than the pelecypods *Parvilucina tenuisculpta* and *Macoma carlottensis*.

GROUP IV: SUB-SURFACE DEPOSIT FEEDING

Sub-surface deposit feeders are generally mobile, deep burrowers (up to or greater than 10 cm) that feed on deposited organic material and usually have sediments in their stomach contents. In addition , animals that feed mainly upon identifiable plant debris usually belong to this group.

Five of the seven taxa contained in this group ar recognized as indicators of marine pollution and disturbed environments. However, these animals are often abundant in natural marine environments. The common parameters at all of the stations where they are consistently abundant (not transient enhancement in abundance of these species) are the

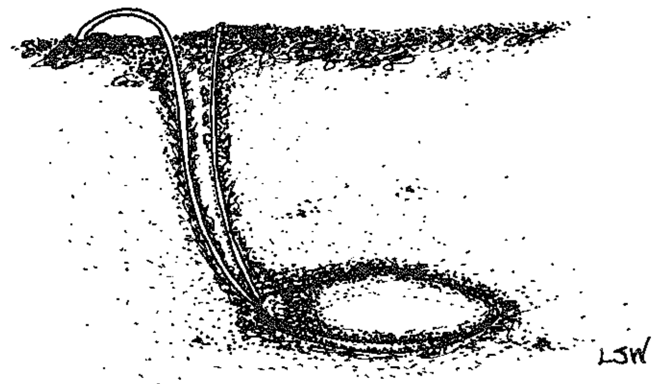

Figure 7. *Macoma carlottensis* **is a relatively stationary surface deposit feeder that actively searches the surface of the sediment for its food.**

presence of identifiable plant remains and anaerobic sediments. The common traits of the animals are: 1) their ability to live at greater than normal depths within the sediment (>10 cm), 2) the presence of sand grains and/or plant remains in their stomach contents, and 3) the requirement that plant material needs to be in their diet in order for them to successfully reproduce.

Capitella capitata is a deep burrowing deposit engulfer that nearly always has algal fragments in its stomach contents (Fauchald and Jumars 1979). Recent observations on the stomach contents of this species in the laboratories of the Coastal Water Research Project reveal they have few sediment grains in their stomachs. They have instead large quantities of plant material. *Capitella capitata* is placed in this group because of its deep burrowing activities, tolerance of anaerobic sediments and the observations of the requirement for plant materials in its diet. The plant material can be of terrestrial or coastal origin.

Schistomeringos longicornis is a dorvelleid polychaete that lives on the surface of sediments that are anaerobic (Figure 8). It requires plant material in its diet before it will spawn (Reish 1957). It is abundant in areas which naturally accumulate terrestrial or coastal plant material,

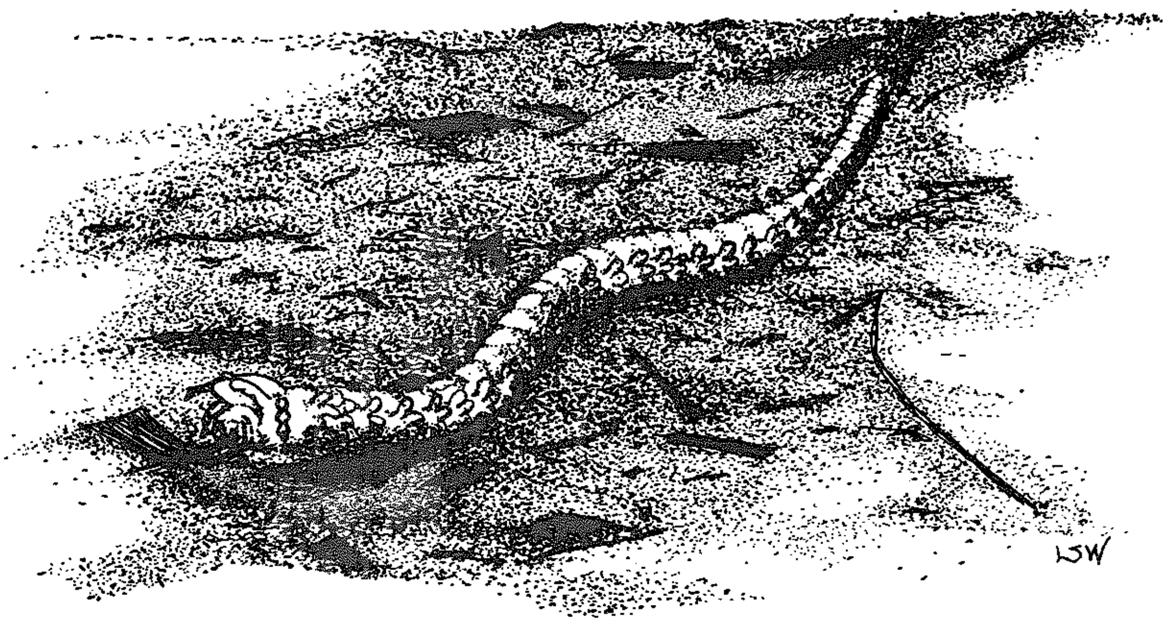

Figure 8. *Schistomeringos longicornis,* **a dorvelleid polychaete, lives on the surface of anaerobic sediments and feeds extensively on plant material.**

e.g. kelp debris (Allan Hancock Foundation 1965), at the heads of canyons with terrestrial plant debris (Hartman 1963), and in accumulations of ocean sludge particulates (identifiable plant material; Word 1976). The presence of sand grains is minimal and the placement of this species into Group IV is based upon its dietary requirement of plant material and its tolerance for anaerobic sediments.

SUMMARY

The selection of benthic invertebrates and their placement in four feeding groups has been based on extensive observations of the animals and their environment. After much consideration, 53 taxa were selected to best represent the distribution of feeding strategies over a wide range of depths and latitudes.

Of the environmental characteristics considered, the three of greatest importance are:

1. Concentrations and biological useability of organic particulates in the sediment.
2. Speed of the bottom current and the effects of turbulent-producing objects.
3. Settling rates of particulates through the water.

The character of the animals feeding can be determined by:

1. Presence of specialized feeding structures.
2. Stomach contents.
3. Observations of feeding behavior in the laboratory or the environment.
4. The depth of the animal in the sediment.
5. The relative energy used in feeding.
6. The feeding techniques of dominant animals with which it is associated.

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