FOOD HABITS AND DIETARY ADAPTATION OF THE ENGLISH SOLE (*PAROPHRYS VETULUS*) IN A RECENTLY DISTURBED HABITAT

by

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A THESIS

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

December 1986

Rec'd [illegible]

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An Abstract of the Thesis of

Dennis Keith Marks for the degree of Master of Science
in the Department of Biology to be taken December 1986

Title: DIET OF THE ENGLISH SOLE (*PAROPHRYS VETULUS*) IN A RECENTLY DISTURBED HABITAT

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Environmental changes affected the abundance of benthic invertebrates and fish in the vicinity of a newly constructed jetty. Stomach contents of 108 juvenile English sole were analyzed from the site over a 3-year period to examine food preference and dietary adaptation. The observed diet included a diversity of benthic invertebrates and appeared to be transitional between that of 0-age and adult English sole reported by others. Polychaeta annelids were the largest prey and the most important food each year (about 50% by volume). Bivalves, primarily clam siphons, were second most important. Other major prey included harpacticoid copepods and cumaceans. Excepting amphipods and nematodes, which were largely absent probably because of their small size, all invertebrate taxa were represented in the sole stomachs in roughly the same proportions as observed in the changing sediment samples, demonstrating a low degree of food selectivity and a corresponding high capacity for dietary adaptation.

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Sigma Xi Grant-in-Aid of Research, 1986

ACKNOWLEDGMENTS

For their help with this project, I wish to thank Daniel Varoujean, Michael Graybill, Jim Marks, Charlotte Coester, Michael Roberts, and especially Peter Frank.

DEDICATION

This paper is dedicated to my father, Clark Marks, because the thought of having to hear "Are you planning to finish your Masters?" once every year for the rest of my life finally induced me to finish it, and to my mother, Margaret Marks, who has, on various occasions, tolerated fish stomachs and other of nature's sacrifices in her refrigerator.

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CHAPTER I

INTRODUCTION

Basic Description of Factors Influencing Diet and Predation

Foraging and feeding almost certainly account for most of the active time of an organism's nonresting life. However, since only finite amounts of time and energy can be devoted to these activities, efforts must be sufficiently productive to meet the organism's nutritional needs for maintenance and reproduction. To obtain the optimal quantity of high-quality food, predators have evolved behavioral and morphological adaptations to increase the efficiency of locating, capturing, and eating desirable prey (which, in turn, have become correspondingly adapted to the avoidance of being located, captured, and eaten). Efficient predators forage for the prey that yields the greatest amount of nutrition for the least time and effort. Predators with efficient strategies for obtaining food have a selective reproductive advantage and ultimately become dominant food competitors (see Emlen, 1984).

The rate of predation on any given prey population has been shown to be a function of prey abundance and distribution, and although it has been reported for fishes and other animals under laboratory conditions (Ivlev, 1961), direct evidence from field situations is scanty. Steele, McIntyre, Edwards, and Trevallion (1970) examined the diets of a population of plaice[1] on the west coast of Scotland and concluded that the level of predation on clam (Tellina) siphons was a function of the relative abundance of the clam in the benthos. Similarly, the occurrence of harpacticoid copepods in the diet of certain 0-age English sole exhibited a positive correlation with the period of maximum density of copepods in the substrate (Hogue, 1982). Neither researcher was able to find any distinct annual pattern and Steele et al. (1970) attributed this lack of seasonality in diet to the lack of any overwhelming seasonal pattern in the invertebrate distribution.

Hogue (1982) found the diets of English sole taken from trawls conducted in his study area to be very similar to each other in the winter, while sole from different trawls had differing diets in the summer. The seasonal distribution of prey in the area appeared to account for the difference—randomization of the meiobenthos through the mixing of sediments by winter storms was the likely cause for widely similar diets, while the benthic fauna became increasingly aggregated in the summer, leading to diet variability between clumps of fish.

The pattern of dispersion or the degree of aggregation of the prey can be more important to the predator than the absolute numbers of

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[1] An Atlantic pleuronectid flatfish, Pleuronectes platessa.

prey. Ivlev (1961) has demonstrated, for fish in an experimental treatment, that an increase in prey concentration, apart from any other change, has the same effect on predation as increasing the absolute number of prey. Although the effect of feeding rate of variously distributed prey populations is still being examined and certainly varies for different organisms and environments, studies on sedentary prey populations suggest a randomly dispersed population with an overall lower degree of concentration is fed upon less efficiently than an aggregated, patchy one (Ivlev, 1961).

Along with distributional effects, other morphological characteristics of prey species can cause them to be more or less desirable to predators. "There are probably few, if any, animals which have a completely indifferent attitude toward food types, and selectivity is probably inherent, to some degree, in most predators" (Ivlev, 1961). Observed diet, or that subset of the available prey that the predator has actually consumed, is modified by these food preferences.

The most obvious factor influencing prey selection is a proportional size relationship. For many predators, there is an optimal prey size from which the predator will deviate only when prey within this size range are scarce (Nikolsky, 1963). Ivlev (1961) has shown experimentally with fish that there are size-related preferences—when a fish was presented with various sizes of the same type of prey, larger items were preferred, and the upper limitation on prey size appeared to be only a function of mouth size. In diet studies of northeastern demersal fish, Levings (1974) and Tyler (1972) found that selection of various sizes of prey was a function of predator size; and although the predation on large species was density dependent (and positively correlated), the consumption of smaller prey was not. Smaller prey were largely disregarded probably because of their low nutritional value. Selection of prey that are easier to locate, capture, and consume will benefit the predator by yielding a higher caloric intake per unit effort.

Finally, predators exert their own influence on the characteristics of the prey populations. Steele et al. (1970) concluded that a decrease in predation on *Tellina* siphons by plaice was due to the decreased abundance of the clams as a function of this same predation. Ivlev (1961) has also shown that the selectivity (electivity) for a given prey changes as a function of predator density, due to competitive interaction. Fluctuations in the relative abundance of prey in flatfish diets are usual and have been observed for other demersal fish.

These factors—the abundance and distribution, along with the relative size, feeding morphology, and physiology—of the prey and the predator are reflected in the search strategy and prey selection of the predator. These factors will define the range of prey types that will be utilized in a particular habitat. While some animals feed on a very restricted range of prey organisms, others use a high diversity of prey types. The ability of predators to generalize on a variety of food types is usually a result of their flexible behavior, accommodating feeding structures, and digestive physiology, or to a spectrum of prey species with somewhat similar morphologies and habits. Although food specialists have fewer prey from which to select, generalized predators feeding on a variety of prey must be adapted to cope with a greater range of predator escape tactics than more specialized predators that deal with fewer types of prey.

A substantial amount of work has demonstrated the importance of food availability on the evolution of feeding strategies and morphologies of predators, and from this have come many ideas that attempt to explain the range of diet specialization seen in nature. According to MacArthur and Pianka (1966), a more productive and stable environment should lead to a more restricted diet in terms of numbers of species or prey types eaten. Organisms will specialize, given a productive habitat, because a greater feeding efficiency can be achieved by becoming especially proficient at utilizing a narrow range of prey.

On an ecological, rather than an evolutionary time scale, the degree of predator specialization has also been found to be a function of the productivity and stability of the environment and the distribution of prey organisms (Werner & Hall, 1979). Studies on flatfish (Tyler, 1972) have shown that the diet overlap between different species of fish in the same area increased as the environment became increasingly unstable. In an environment with a scant food supply, a predator cannot afford to pass up many acceptable food items because the average search time is relatively high and the expectation of prey encounter is low. In such an environment, the consumption of a wide range of prey will probably be the most energy efficient strategy (Pianka, 1978). In a productive environment, search time is low and substandard prey items can be bypassed because the expectation of finding a superior item in the near future is high. More selective foraging might result, leading to a narrower range of food being selected. An exception is probably seen in very patchy environments where predators spend much time searching. In such a habitat a generalist strategy may be common even in a very productive area (Pianka, 1978). Zaret and Rand (1971), from a study of tropical freshwater fishes, observed a decrease in food overlap values between species when food was less abundant in the dry season. The authors suggested that when the food resource diminished, the fish adopted a more specialized feeding behavior, which resulted in the avoidance of intense competition. The reason for an organism, in a food-diminished environment, to pass over less optimal food to search for prey of a higher quality may relate more to highly visual predators in a clear freshwater habitat than to any general trend. When the abundance of prey decreases in the dry season, a predator that can identify food items quickly and at a distance may be less apt to expend critical energy capturing a low quality food, when it can identify it as such, than to wait for a more easily captured prey of a higher food value. Organisms foraging in areas of limited visibility, or searching with tactile organs, should be much more likely to adopt generalist strategy because all potential prey must be closely approached for assessment, and any acceptable prey to which the predator comes into close proximity will be eaten.

Predators foraging in overlapping feeding ranges have evolved uniquely, largely to avoid competing for very similar foods. Intra- and interspecific competition among co-occurring organisms results from this overlap and most certainly affects the quality and quantity of available food. In their observations on the effect of clam (Tellina) abundance on the predation by plaice, Steele et al. (1970) determined that the plaice predators were themselves responsible for the periodic reduction in clam abundance. In a natural system, competitive interaction is extremely important in directing the evolution and population dynamics of a community. There exists a limit to the rate at which a fish population can remove food from the available habitat and the growth rate of fish is limited by this.

The Effect of Disturbance on Diet and Predation

The effect of an environmental disturbance and subsequent change in food availability on a predator or group of predators has been studied to a very limited degree. Apart from a numerical decline due to a decline in prey abundance, several workers have determined that the dietary overlap between predators often increases as a result of perturbations in the habitat and fluctuations in prey abundance. The work of Tyler (1972) and others suggested that environmental disturbance often resulted in weakened prey partitioning within a predator community and a decrease in the degree of specialization among predators. In a tank experiment (Ivlev, 1961), the aquarium environment was subjected to an apparent stress in which the invertebrate distribution was altered but the composition was left in the original proportions. The range of prey consumed by the fish increased significantly. Likewise, over a period of time, and given environmental stability, food overlap diminishes and resource partitioning increases. This will occur as two predators reduce the abundance of their common prey and become better adapted at finding and eating the unshared items. In an examination of past studies on fish food partitioning, Tyler (1972) ranked each study by the amount of environmental disturbance and discovered the same basic trend: As environmental stability decreases, food partitioning also decreases and diet overlap increases. As unstable environments have been shown to decrease the partitioning of food resources, stable environments with constant conditions have revealed assemblages of organisms with a minimal amount of overlap in resource utilization.

Flatfish Ecology

The occurrence and distribution of fishes within Oregon estuaries has not been extensively studied or documented and little research has been conducted on the feeding habits in such areas. Food habit studies have recently been completed on flatfishes in the nearshore habitat off central Oregon, and many aspects of flatfish biology have been determined (Forrester, 1969; Allen, 1974; Hulberg & Oliver, 1979; Wakefield & Pearcy, 1980).

Food has been shown to be a common limiting factor to the growth of fishes in natural conditions, and the types, densities, and distribution of food organisms in the benthic habitat of a nursery area will have profound effects on the survival and growth of juvenile flatfish. Rae (1956) suggested that differences in the types and quantities of prey that were available between two sites in the same vicinity resulted in differential growth rates of the lemon sole (*Microstomus kitt*). Sedentary polychaete annelids were determined to be the most common organisms in the areas of most rapid growth for *M. kitt*. In estuaries and other nearshore habitats influenced by tides, many organisms fluctuate widely in abundance, due largely to patchy recruitment and sporadic mortalities. Because of the likelihood of short-term fluctuations in the abundance and availability of estuarine food items, most of the fishes which spend time here are not specialized feeders (Moyle, 1982).

While recently it has been determined that flatfish have a variety of feeding strategies, in the recent past northern demersal fishes were considered to be trophic generalists (Bigelow & Schroeder, 1953). This might have been due to the fact that early workers were not concerned with the relative abundance of prey items and that the bulk of the diet may likely have come from only a few dominant species. Some of the pleuronectids are known to be truly opportunistic feeders, regularly using a wide range of prey (Tyler, 1972; Pearcy & Hancock, 1978).

However, many species of flatfishes have since been found to specialize on a rather narrow range of food types (Edwards & Steele, 1968; Kravitz, Pearcy, & Guin, 1977; Cailliet, Antrim, & Ambrose, 1979) such that assemblages of these predatory species are able to partition the prey community, each species specializing upon only a portion of the food spectrum.

Studies of demersal flatfish have turned up a predominance of benthic feeders, although species using midwater invertebrates and fishes for food have also been studied (Kravitz et al., 1977; Richardson & Pearcy, 1977; Steele et al., 1980). Bottom feeding flatfish have been observed to utilize a variety of foraging strategies which include excavating small amounts of sediment to unearth prey, clipping off appendages just above the bottom (e.g., clam siphons, polychaete feeding appendages), or capturing free-swimming prey (Kravitz et al., 1977; Hogue, 1982).

Hatanaka, Kosaka, Sato, Yamaki, and Fuyui (1954) and DeGroot (1971) discovered specific morphological adaptations in the mouth and jaw structure and digestive morphology of demersal fishes in the Pacific Northwest which allowed different species of fish to utilize specific prey. Flatfishes that feed on benthic organisms (e.g., Rex sole, Rock sole) most often have asymmetrical jaws; gill rakers with short, blunt teeth; small stomachs; and long intestines. Fish that feed on more pelagic animals (e.g., Petrale sole, Pacific sanddab) have long, symmetrical jaws with sharp teeth, serrated gills rakers, and large stomachs. These adaptations enable the fish to feed more efficiently upon their prey organisms while providing each species with a relatively peculiar spectrum of prey organisms.

Pearcy and Hancock (1978) discovered two general feeding types among four species of syntopic flatfish off central Oregon. The Dover sole, *Microstomus pacificus*, and the Rex sole, *Glyptocephalus zachirus*, fed primarily on infaunal and epifaunal invertebrates, the major fraction composed of annelids (64%), bivalves, and crustaceans (mainly gammarid amphipods). Both the Pacific sanddab, *Citharichthys sordidus*, and the Slender sole, *Lyopsetta exilus*, preyed principally on pelagic crustaceans such as euphausids and amphipods. Fish were occasionally an important food for the sanddab. Two other locally important flatfishes, the Rock sole (*Lepidopsetta bilineata*) and the Petrale sole (*Eopsetta jordani*), were determined to be benthophagous (*L. bilineata*) and piscivorous (also pelagic invertebrates), respectively.

Partitioning of the food resource among these co-occurring fishes was obvious from the data with the possible exception of the English sole, *Parophrys vetulus* which, possibly due to the patchy nature of the bottom areas it occupied, may be a "scavenging generalist" predator (Kravitz et al., 1977).

The English Sole

The English sole, *Parophrys vetulus* Girard, is a common flatfish of the family Pleuronectidae, found to at least 200 meters in the eastern and western Pacific coastal waters of the northern hemisphere. Ranging between Baja California and Alaska, it is one of the most abundant of the flatfishes along the Oregon coast and has been relatively well studied there, largely owing to its importance in Oregon's commercial fishing industry (Westrheim, 1954).

Spawning of English sole off the Oregon coastal commences in the fall and winter (Hewitt, 1980); the gonadal condition of the female sole and the variability of the spawning season have been observed to be inversely related to bottom temperature (Kruse & Tyler, 1983). The concentrating of females in well-defined areas and their subsequent movement offshore makes them more available to the commercial fishery and has been correlated with spawning cycles (Hewitt, 1980). Planktonic eggs hatch in the winter and spring (Rosenberg, 1981) and, like all pleuronectids, English sole have planktonic larvae that drift with currents until metamorphosis into juvenile fish. More than 90% of all larvae collected in an offshore collection off Oregon were netted between February and July (Richardson & Pearcy, 1977). Young are pelagic for 6 to 10 weeks (Forrester, 1969) and are continuously recruited to the bottom over approximately a 9-month period, mostly from January to June (Pearcy & Krygier, 1980). Reproductive success varies from year to year and is possibly a function of transport, by water movement, from the spawning grounds to nursery grounds (Ketchen, 1956). Juvenile English sole, as with the young of many flatfish, are thought to settle in these well-defined "nursery areas" following metamorphosis. Estuaries and other shallow, protected inland areas are known to be important nursery grounds for English sole during the 1st year of life, although recent collections of 0-age English sole in shallow, unprotected nearshore waters suggest that open-coast nursery areas may be as important in recruitment to adult populations as are the estuarine nursery grounds (Laroche & Holton, 1979).

The growth period for English sole is March through September (~ 0.1 mm/day), is most rapid during May and June, and appears to be inversely correlated with water temperature and directly with the degree of upwelling (Kreuz, Tyler, Kruse, & Demory, 1981). From monthly length-frequencies of *P. vetulus* caught in Yaquina Bay, Oregon, Westrheim (1954) observed a modal growth to 14 cm during the first year of life. Subsequent to becoming benthic, 1- and 2-year-old fish are known to migrate by degrees to deeper waters where they concentrate in numbers, becoming available to demersal fisheries at 3 to 4 years of age. Juvenile *P. vetulus* mature to adulthood in 3 to 8 years and the natural life span may reach 20 years, as observed for Dover sole. English sole landed for filleting in Oregon range in size from 250 to 500 mm (Westrheim, 1954).

Food of English Sole

English sole, as do other flatfish, have asymmetrical jaws with a few long teeth which are used to forage in the sediment, primarily for surface-dwelling and infaunal invertebrates. With a variety of feeding behaviors, *P. vetulus* is able to find and locate many types of prey. While many, if not most, of the prey organisms are taken from the surface of the substrate, deep-living species are accessible to the sole. *P. vetulus* has been observed to dig into the sediment to extract burrowing species that are not active at the substrate surface (Hulberg & Oliver, 1979). Hogue and Carey (1982) reported two distinctly different types of foraging behaviors in *P. vetulus* in laboratory aquaria. The first strategy is a sit-and-wait tactic in which the fish remain motionless for a period before lunging forward to strike at the prey on the bottom. The second entailed a series of rapid, thrusting movements causing a few millimeters of sediment to billow into suspension, followed by a succession of rapid strikes on the suspended particles—harpacticoid copepods in this case.

P. vetulus has been consistently reported as a food generalist, typical individuals displaying a wide variety of food items in the gut.

Kravitz et al. (1977) sampled a population of adult English sole (230-450 mm SL, *n* = 37) from a nearshore, sandy bottom location off central Oregon and found polychaetes and amphipods to be the numerically dominant food. Bivalves, cumaceans, and ophiuroids were also frequent in the stomachs. Based on the wide variety of prey types in individual stomachs, Kravitz et al. (1977) proposed an opportunistic foraging strategy for English sole where the fish appear to eat, in whatever quantities encountered, most food encountered in foraging. In a diet survey on 0-age English sole (17-87 mm SL, *n* = 235) from a slightly shallower location, Hogue and Carey (1982) also reported a very generalized diet for *P. vetulus* although the food composition was significantly different, consisting primarily of small prey: juvenile bivalves and bivalve siphons, harpacticoid copepods, polychaete palps, amphipods, and cumaceans. Larger prey such as polychaetes and decapods were taken in lesser quantities as would be expected in such small fish.

Although the number of prey types found in the stomachs was high, typically one group was numerically dominant throughout the sample (e.g., polychaetes for adult fish). As documented for other pleuronectid species (Edwards & Steele, 1968), Hogue (1982) reported profound differences for English sole diets for both within and between year samples as well as between individual tows, in certain months, and suggested changes in the temporal and spatial density of prey organisms as the probable reasons for the changes in diet.

Description of Present Study

The Site

The Umpqua River has the largest drainage basin and average discharge of coastal rivers in Oregon (Hancock, 1985) and terminates in a shallow bay 180 miles south of the Columbia River. This coastal estuary is particularly influenced by freshwater effluent in the winter when it is a two-layered system, and by tidal influx and upwelling in the summer when the estuary grades from a partly-mixed system in March to a well-mixed system in July (Burt & McAllister, 1959).

Net transport of sediment material along the coast is to the south. At the mouth of the Umpqua River, the seasonal movement of sand around the north jetty and into the estuary has been observed through aerial photographs. Heavy winter runoff carries silt and mud sediments through the estuary and out of the river mouth. The mean grain size of sediments in the bay is that of fine sand (Burt & McAllister, 1959).

The study area is located at the mouth of the Umpqua River, is adjacent to a large sand beach and dune complex on the south side of the river, and at present is enclosed on both the ocean and river sides by stone jetties (Figure 1). Before October 1980, only a fragment of the northern training jetty existed and the study area was a high energy beach exposed to large swell, wave action, and both river and tidal currents.

In October 1980, an existing training jetty was extended to the beach from the main jetty, enclosing 57 hectares of water and tidal beach. The jetty extension was constructed with a 200-foot porous section and four culverts, each 4 feet in diameter, placed at mean lower low water. Swell and wave action within the impounded study site are now negligible, and circulation is limited to exchange through the jetties and culverts. Depth in the study site ranges from 0 to 15 m with mean depth for the deep water zones (B, C, and D, see Figure 1) around 7 to 8 meters.

Background of the Study

The Umpqua Training Jetty Extension Monitoring Study (Hancock, 1985) was initiated before implacement of the jetty to assess the future impact of this jetty configuration on overall water quality, bottom sediments, and biological communities. The study was developed by the Portland District Army Corps of Engineers in conjunction with

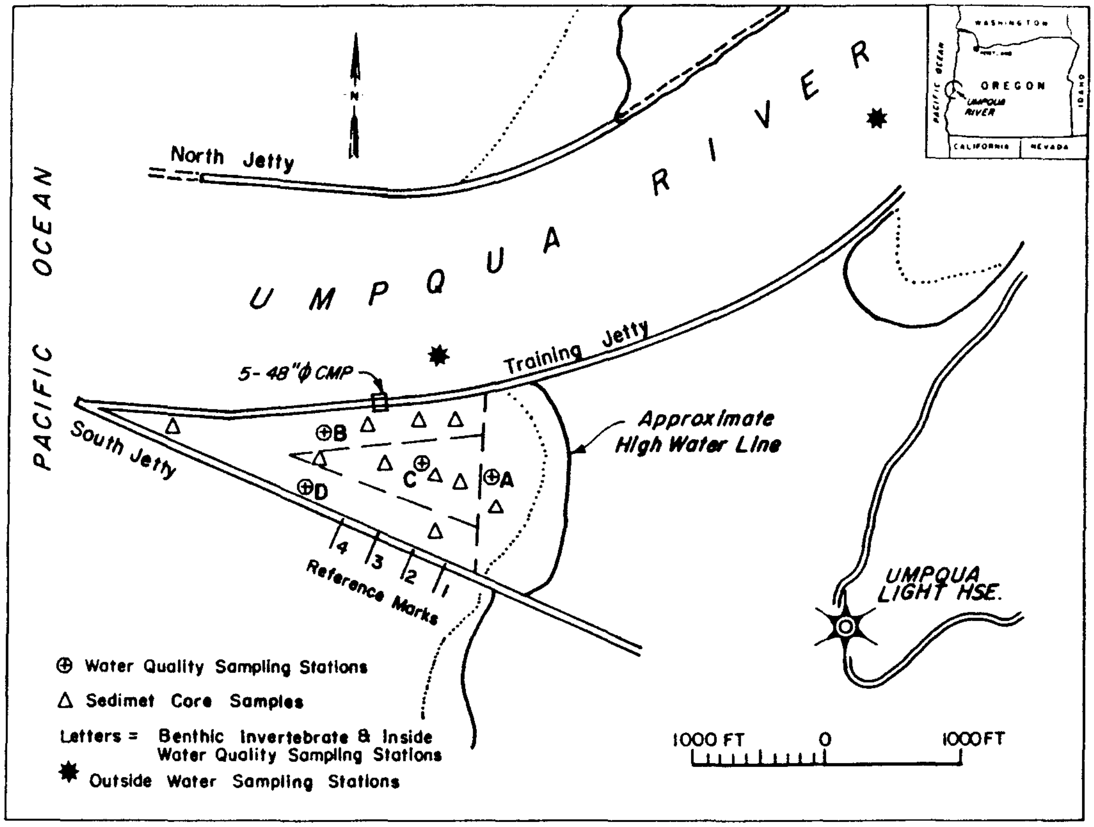


FIGURE 1. Study site at the mouth of the Umpqua River. The study area was divided into four zones (A, B, C, and D) of equal area. Transects (dashed lines) bisecting each zone were established, and reference marks were painted on the south jetty (the location of only marks 1-4 are shown). Extension of the training jetty (slash marked portion) was completed by October 1980.

Note. From Varoujean, D. H. (1984, April). Umpqua Training Jetty Extension Monitoring Study (p. 3), (Final Report to Portland District), Portland: U.S. Army Corps of Engineers.

other state and federal resource agencies. The biological monitoring was contracted to the University of Oregon Institute of Marine Biology, Charleston.

This study utilizes the data from the monitoring study with additional work in an effort to correlate changes in the site with changes in the diet of the English sole.

Purpose of Present Study

Data were analyzed from an area of a well-defined physical disturbance. An effort was made to quantify the magnitude of the change on the habitat and upon the benthic organisms used as food by the dominant demersal fish, the English sole (*Parophrys vetulus*).

English sole diets were analyzed over a 3-year period and, in addition to the goal of adding to the general information on the food habits of *P. vetulus*, the nature of the disturbance should allow for an examination of the dietary adaptability of the sole to a changing environment and food supply.

CHAPTER II

MATERIALS AND METHODS

Methods for the analysis of English sole stomach contents and for the Umpqua River Training Jetty study (physical-chemical analysis and benthic invertebrates community survey) are given below.

Sampling Methods

Samples were taken between the months of April and October 1980 through 1982. Collecting dates were scheduled to correspond to the neap tide series each month in order to maintain consistency and avoid possible complications caused by extreme tides.

The study site was divided into four zones (Figure 1) for the sampling of benthic organisms and the measurement of physical parameters, with a transect running the length of each for the repeated sampling of demersal fishes. Fish were collected monthly; benthic samples were taken every other month, beginning in May 1980.

Physical measurements were taken every month between April and October (except in 1980, when sampling began in February) and included measurements of water quality (water temperature, salinity, pH, dissolved O_2), and an analysis of water movement, along with the composition and dynamics of the sediments within the site.

Benthic samples were obtained from 15 stations (with five replicates each) using diver-held can-type corers (surface area, 125 cm^2). Samples were preserved immediately in the field and were washed over a 0.5 mm mesh screen in the laboratory. Polychaetes were identified to family, all else to more broad groups. With the single exception of harpacticoid copepods, the 0.5 mm mesh collected all types of organisms also found in the stomachs of English sole.

Beach seines and otter trawls were used monthly to collect fish. Gill nets were set during the 1st year only and were used to ascertain the effectiveness of the other two fishing methods.

Parophrys vetulus were collected from the site with a 3-meter otter trawl (with a 7-mm stretch mesh liner), towed at about 2 knots for approximately 15 minutes, along each transect (once in each zone— B, C, and D). Tows were done between 0830 and 1600 hr. which was appropriate for obtaining recently feeding fishes, based on their diurnal feeding habit (Hogue & Carey, 1982). After each set was completed, the fish to be kept for stomach content analysis were immediately placed in a 10% formalin solution buffered with sodium borate (NaH_2BO_3). The fish remained in formalin for about 48 hours, were rinsed for an equal amount of time, then measured (total and standard length) and weighed. The entire digestive tract was removed from each fish and placed in a 70% isopropyl alcohol solution. From a subsample of stomachs taken from fish between 65 mm and 180 mm total length, stomachs were randomly selected for analysis (except in very small samples where all were analyzed). This size range corresponds to

1st- and 2nd-year fish (Rosenberg, 1981) and were segregated in an attempt to minimize the variation in diet due to ontogenetic shifts in prey selection (Hogue, 1982).

A reference site was selected nearby to act as a control for the study site. The site was chosen for its similarity (in wave action, water circulation, depth, and sediments) to the study site before it was impounded. Fish were collected each month with otter trawl and beach seine during 1981 and 1982 only. The benthos was sampled using the same methodology as in the study area, bimonthly and in 1981 only.

Stomach Content Analysis

Stomachs were removed from the fish and estimates of fullness were made, subjectively, on a scale from 1 (empty) to 6 (100%+). The section of gut from the esophagus to the junction anterior to the pyloric caecum, which includes the stomach, was dissected and analyzed under a dissecting microscope equipped with an ocular micrometer. Due to the advanced state of digestion, intestinal content was examined only to add to the list of prey items and no quantitative measurements were made. Animals were identified to family when possible, or placed in broad groups and enumerated.

Polychaete feeding palps, predominately from species of the family Spionidae, and bivalve siphons are parts of prey organisms that protrude from the substrate surface. They were commonly observed alone in the sole stomachs. Based on previous findings (Tyler, 1972; Hogue & Carey, 1982; Peterson & Quammen, 1982) and laboratory observations of fish selectively cropping these parts (Steele et al., 1970), both feeding palps and siphons were considered separate food items. It was often unclear, however, as to whether the polychaete palps and tentacles were taken exclusively, as stomach contents were often a partly digested mixture of annelid segments and appendages. These parts were only counted when found alone or in clearly greater numbers than the corresponding worms. Polychaete feeding palps were counted and divided by two, since each polychaete has two palps. Each bivalve siphon was regarded as representing one individual eaten, since it has been reported (Edwards & Steele, 1968) that when whole clam (*Tellina* sp.) siphons are presented to plaice, the fish swallowed it whole, and the siphon remained intact in the stomach. The siphons were the toughest item found in the stomachs and, when manipulated with forceps, were not easily torn. Finally, often pieces were recognizable as the tips of siphons unambiguously distinguishing them from separate animals.

Polychaetes were the most difficult group to estimate when the stomach contained only fragments. If heads were recognizable, then each was counted as a whole worm. If the state of digestion prohibited the identification of heads, estimates were made of the combined lengths for pooled size (diameter) classes of fragments and the total number of worms was approximated from the length to width ratios of intact polychaetes.

The surface area of each item was estimated as it was identified by using a gridded ocular in the eyepiece of the dissecting scope. The thickness was approximated in the same way and, based on these estimates, a volume was assigned to each individual food item. Unidentifiable food was segregated into one mass and volumetrically quantified in the same way.

Finally, the degree of digestion for each stomach was estimated on a scale from 1 (whole animals) to 6 (finely digested).

Data Analysis

Diversity of prey consumed was measured with the Shannon-Wiener information index (H') using natural logarithms (Pielou, 1969). Overlap between the composite diets, between years, was calculated with Spearman's rank correlation coefficient, corrected for ties (Snedecor, 1956).

The mean percentage composition, a measure of the percentage a particular food type contributes to the individual diet, was determined by averaging this proportion for all the fish in a sample. It is a measure of the average individual consumptions and is sensitive to changes in the distribution of prey in the population but is not greatly affected by aberrant individuals.

Both numerical and volumetric computations were done to consider both large and small prey. Mean percentage composition was computed for each monthly sample (both by number and volume) and individual proportions were averaged for each year. The frequency of prey occurrence (FO) is a measure of how widely a prey item is used among a sample population and is that proportion of stomachs containing the particular food item.

One comprehensive measure of the relative importance of each prey category to a group of predators is the Index of Relative Importance (IRI) (Pinkas, Oliphant, & Iverson, 1971) given as:

$$IRI = FO\ (N + V)$$

where N = numerical percentage of given prey, or the average number of prey per fish, V = volumetric percentage, and FO = frequency of occurrence, or the proportion of fish containing this prey item.

CHAPTER III

BACKGROUND DATA: THE UMPQUA TRAINING JETTY STUDY

The following results are from data collected for the Umpqua Training Jetty Monitoring Study during 1980-1982, as described. All biological data were collected by a team from the University of Oregon Institute of Marine Biology at Charleston, Oregon and are presented in Varoujean (1984). Physical and water quality data were collected by the Portland District Army Corps of Engineers (Hancock, 1985).

Physical Changes in the Study Area

Although four culverts placed in the training jetty allow limited flushing of the site (Hancock, 1985) and the large rocks that make up the jetties permit water to pass through, the water quality and sedimentation within the jetty configuration has been altered--the riverine influence within the enclosed area has been severely reduced, wave action has been virtually eliminated, and a considerable amount of organic silt is accumulating on the bottom.

In 1980, before jetty construction, the salinity in the study area reached the lowest concentrations during the winter, dropping from an average of 30 parts per thousand (ppt) (range: 27-34 ppt) at high tide to less than 9 ppt at low tide, indicating a large degree of mixing with river water. The variation in mean salinity and daily salinity ranges were very similar between stations outside and inside the enclosure. In 1981 and 1982, the salinity regime at the outside stations remained essentially the same, given normal temporal variation, and exhibited a larger range in maximum and minimum values from the waters inside the impoundment. Salinity measurements in the study area after impoundment exhibited a diminished daily variation and a narrower absolute range between maximum and minimum values.

Spring and summer upwelling usually brings a colder, more saline and nutrient-enriched body of water to the surface from the offshore depths. Thermal stratification in the study area, before impoundment, suggests that these colder waters were allowed to flow freely into the area where the higher density of the water kept it below the warmer river water. Additionally, water temperatures outside the jetty were generally lower during high tide than at ebb tide, at all depths, reflecting the difference in the ambient temperatures of the ocean and river water. After emplacement of the jetty, the temperature data for the study side indicated a reduction in thermal stratification and a reduction in the daily temperature ranges between high and low tide. Both changes suggest a decrease in the mixing of riverine and marine waters within the enclosed site (Hancock, 1985).

Variation in the study site of other components such as nutrient concentration and dissolved oxygen (which reached greater extremes than in oceanic waters) also appeared to be similarly affected by a drastic reduction in the influence of the freshwater river water and more closely resembled oceanic water.

The elimination of vigorous surface currents, swell, and wave activity in the site after 1980 appears to have had definite effects on the sedimentation in the enclosed area. Both core samples and observations indicate that the study area is rapidly infilling. Sand is being carried, via littoral transport, through the South Jetty. Fine-grained sediments with high levels of organics are entering through the culverts and settling throughout the study site. The cores from these areas have shown a change from the poorly graded sand present in 1981 to silts and clays (Figure 2); there has been a four- to fivefold increase in the sediment organic content. A large portion of the study site now acts as a settling basin where large amounts of organic material are being deposited. Large clumps of brown algae were often brought up with the trawl samples. In many areas, a fine silt flocculus 1 to 2 feet thick was observed on the bottom.

In 1980, then, the study site existed as an interface habitat, experiencing extremes brought about by the interaction of the ocean tides and the freshwater riverine effluent and affected by the surf and vigorous circulation. After impoundment, quiet waters with less variable and more oceanic conditions prevailed, accompanied by drastic changes in the bottom sediments.

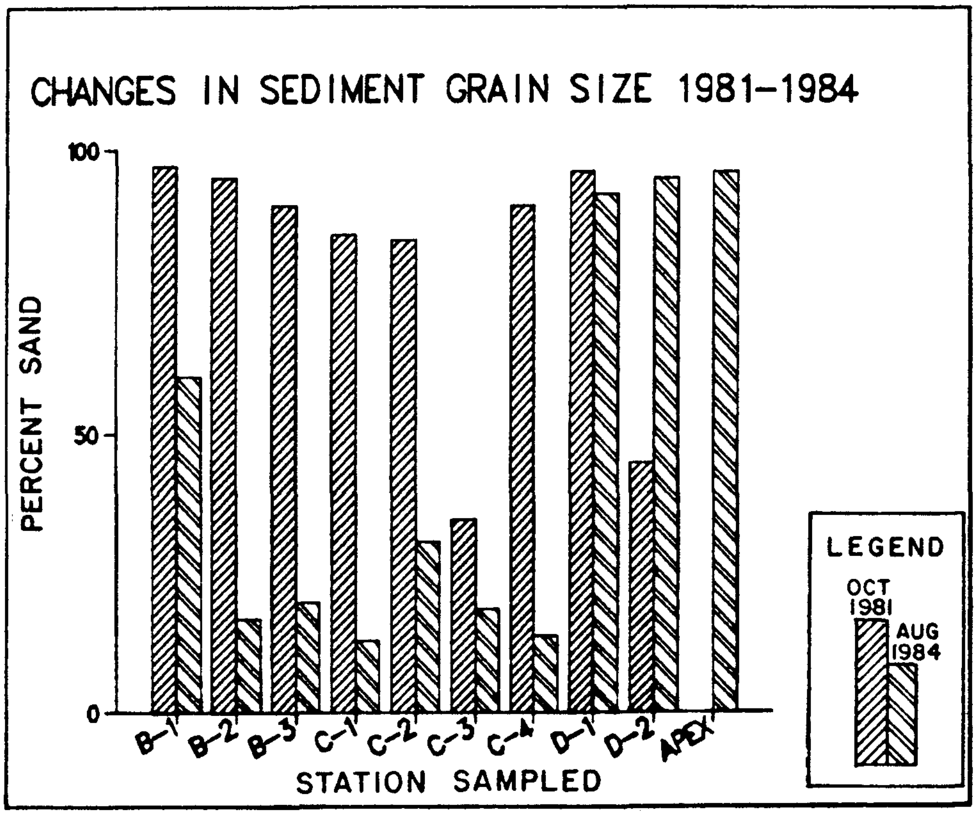


FIGURE 2. Changes in sediment grain size in study area between 1981 and 1984.

Note. From Hancock, D. R. (1985, January). Umpqua Training Jetty Extension Monitoring Study (p. 8) (Final Report, IPA #E1844077), Portland: U.S. Army Corps of Engineers, North Pacific Division.

Changes in the Occurrence of Benthic Invertebrates

Qualitative differences were found in both the study and reference sites between the intertidal benthic invertebrate community and the subtidal community (Varoujean, 1984). To avoid the complication of zonation and the influence of surf on benthic invertebrates, data from Zone A, which includes the intertidal beach, were not included here and this paper will be concerned only with the subtidal communities of Zones B, C, and D, where the majority of English sole are found.

Due to the relatively rapid infilling by current-propelled sediments, the future suitability of the site to sustain marine life is uncertain. However, at the conclusion of the study, the productivity of the area was far from decimated—the overall density of benthic organisms had increased (Tables 1 and 2) and the site appeared to contain a greater biomass on and within the bottom sediments.

Found in the benthic core samples were 11 groups of invertebrates from six phyla (Tables 1 and 2), although only specimens large enough to be caught in the 0.5-mm^2 mesh were able to be observed, and harpacticoid copepods and other minute organisms were inadvertently discarded during the sieving process.

Of the groups in Table 1, those organisms contributing less than 5% of the total number, for all 3 years, include nemerteans; oligochaete annelids; mysid, isopod and decapod crustaceans; and brittle stars—the only echinoderm found in the samples. Together, these groups make up only 6%, by number, of the benthic invertebrates

TABLE 1. Mean Densities/m^2 of Major Taxa of Benthic Organisms Recorded in Samples Taken in Zones B, C, and D in the Study Area.

	1980				1981				1982			
Taxa	April	June	August	October	April	June	August	October	April	June	August	October
Nemertea	174	88	34	69	81	184	115	124	28	20	30	23
Nematoda	539	84	32	75	130	1932	435	4574	138	677	168	236
Polychaeta	472	325	528	468	955	566	527	944	390	577	1034	843
Oligochaeta	50	16	8	13	3	54	12	56	7	41	31	31
Mysidacea	10	11	6	0	6	8	26	5	0	0	0	0
Cumacea	0	1	51	5	0	0	0	101	136	574	181	235
Amphipoda	389	178	33	7	3	1	7	177	3	24	53	126
Isopoda	4	23	3	0	0	0	0	5	3	4	1	3
Decapoda	4	1	0	263	3	2	4	2	0	4	1	0
Bivalva	0	5	472	0	413	640	375	181	189	525	224	145
Echinodermata	3	0	7	3	1	72	5	5	3	3	3	0
Number Samples	49	60	58	60	53	57	58	48	58	59	59	52

Note. From Umpqua Training Jetty Extension Monitoring Study (Final Report to Portland District) (p. 32), by D. H. Varoujean, 1984, Portland: U.S. Army Corps of Engineers.

TABLE 2. Benthic Organisms; Cumulative Yearly Densities and Percentage Contribution of Major Taxa.

	1980*		1981**		1982***	
Taxa	D	%	D	%	D	%
Polychaeta	448	37.3	760	23.2	772	43.6
Oligochaeta	21	1.7	31	1.0	20	1.1
Bivalva	185	15.4	402	12.2	271	15.3
Amphipoda	240	20.0	135	4.1	87	4.9
Cumacea	14	1.2	25	0.8	280	15.8
Nematoda	182	15.2	1768	53.8	314	17.8
Nemertea	91	7.6	126	3.8	25	1.4
Mysidacea	7	0.6	11	0.3	0	0.0
Isopoda	8	0.6	1	0.0	2	0.1
Decapoda	1	0.1	3	0.1	1	0.1
Echinodermata	3	0.3	21	0.6	2	0.1
Total Density	1200	—	3283	—	1774	—
H'		1.67		1.29		1.53

*Number of core samples for year = 227.
**Number of core samples for year = 216.
***Number of core samples for year = 228.

Note. From Umpqua Training Jetty Extension Monitoring Study (Final Report to Portland District) (p. 32), by D. H. Varoujean, 1984, Portland: U.S. Army Corps of Engineers.

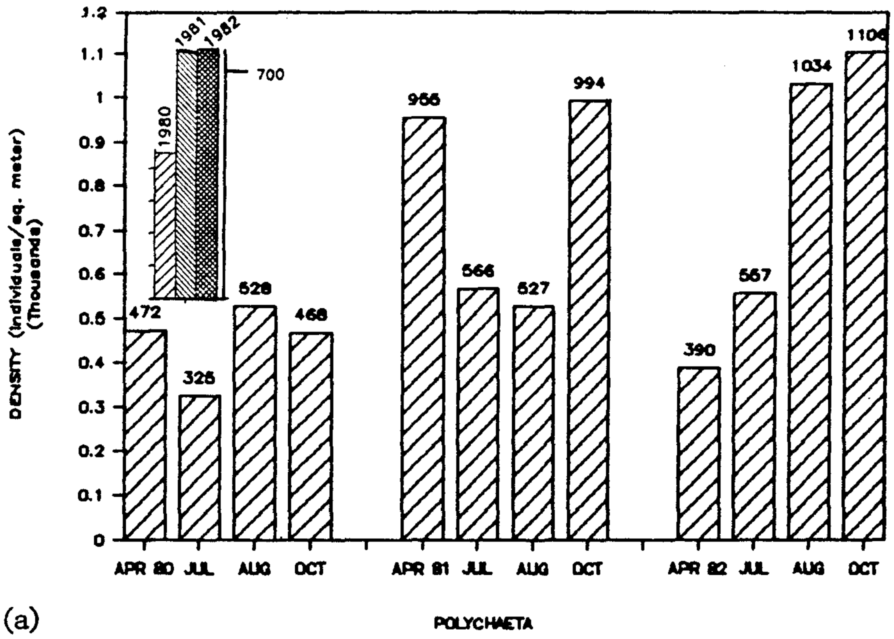
retrieved during sampling. Bay shrimp (Crangon franciscorum) and juvenile Dungeness crabs (Cancer magister) were frequently taken in the otter trawls but were much too large to be considered prey organisms for juvenile sole. The remaining organisms that are dominant in at least 1 of 3 years (and > 5% total) include nematodes, polychaete annelids, small bivalves, and cumacean and amphipod crustaceans.

Using Student's t-tests, Varoujean (1984) found no consistent pattern of significant difference in benthic invertebrate abundances between sampling stations within a sampling zone or between sampling zones in each month and between months. No significant correlation was found for the benthic community between sample years. The Spearman rank correlation coefficient for five pairs of values requires 100% agreement of the rankings between groups in order to meet the 5% significance level requirement. No two years were identically ranked (r_s, 1980-1981 = 0.75; r_s, 1981-1982 = 0.88; r_s, 1980-1982 = 0.70; r_s [0.5] = 1.00). All of the organisms that were numerically dominant in 1980 were also dominant in 1981 and 1982, and with the single exception of the cumacea, no new organisms became dominant in 1981-1982 that were not already in 1980.

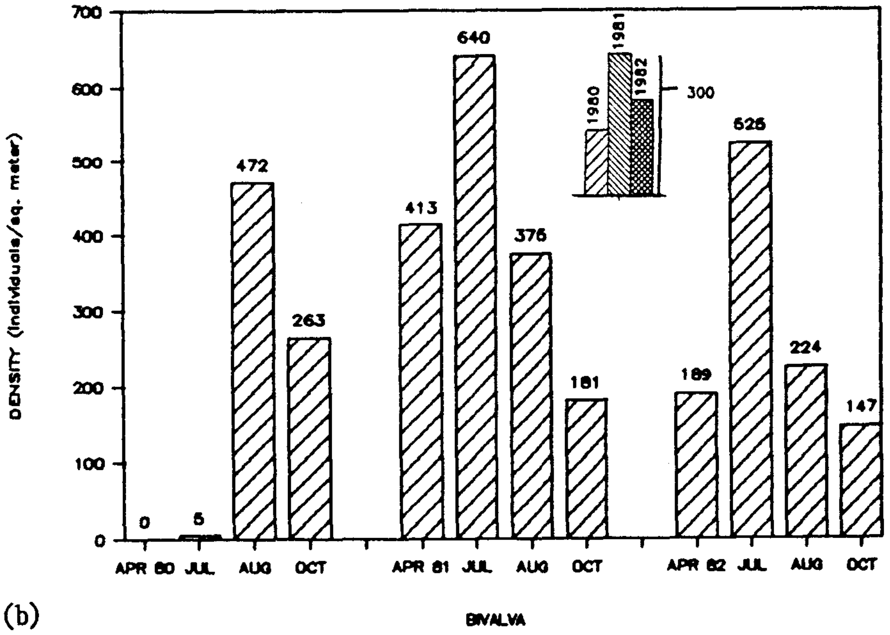
The results of the faunal analysis for the 1980 preimpoundment site describe a macroinvertebrate community typically found in the sandy substrates of the open coast. Very few epifaunal organisms were found in the samples, as would be expected where the substrate is subjected to relatively rigorous swell and wave action.

Monthly and between-year changes are evident for all the major invertebrate groups (Figure 3), and in many cases reflect obvious environmental changes—organisms typically found in the sandy substrates of the open coast (e.g., amphipods, errant polychaetes) were replaced by more opportunistic organisms and those more tolerant of the quiet waters and the fine, organic sediments present in the study site in 1981 and 1982 (e.g., certain sedentary polychaetes, bivalves). A major difficulty faced by benthic invertebrates less well adapted to the fine sediments entering the study site is that of fouling—in particular, the disruption of ventilation to the gills and brood chamber. Although some organisms were adversely affected immediately after completion of the jetty (e.g., amphipods and certain polychaete families), the benthic community generally appeared to undergo a gradual succession in species composition.

Oliver, Slattery, Hulberg, and Nybakken (1980) observed that benthic marine invertebrate communities of a subtidal high-energy beach, in Monterey Bay, California, were organized along a gradient of wave-induced substrate motion, and that this factor was the single most important factor affecting benthic invertebrate zonation. Distinct zonation patterns were found to be relative to bottom depth with small, commensal, actively burrowing deposit-feeding amphipods and ostracods dominant in the shallow, disturbed zones, with the more sedentary

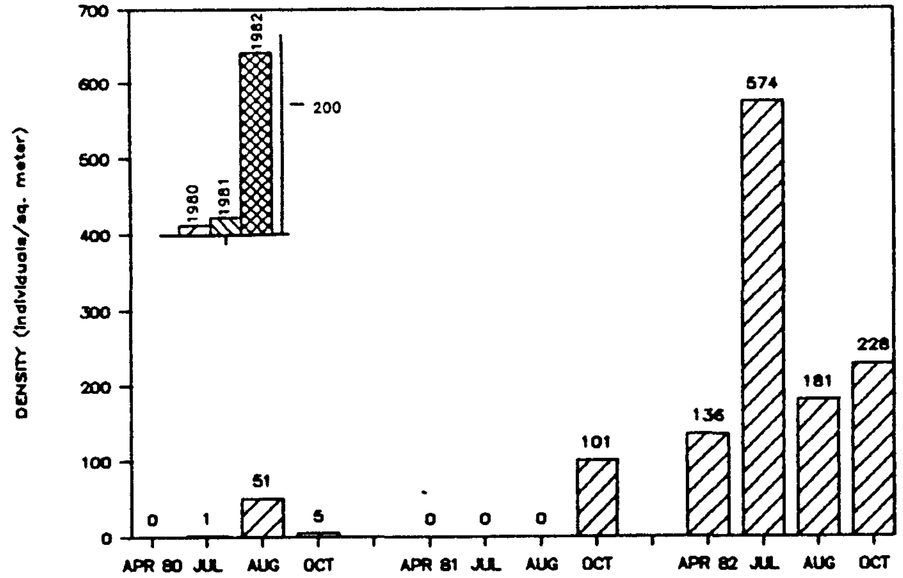


(a)

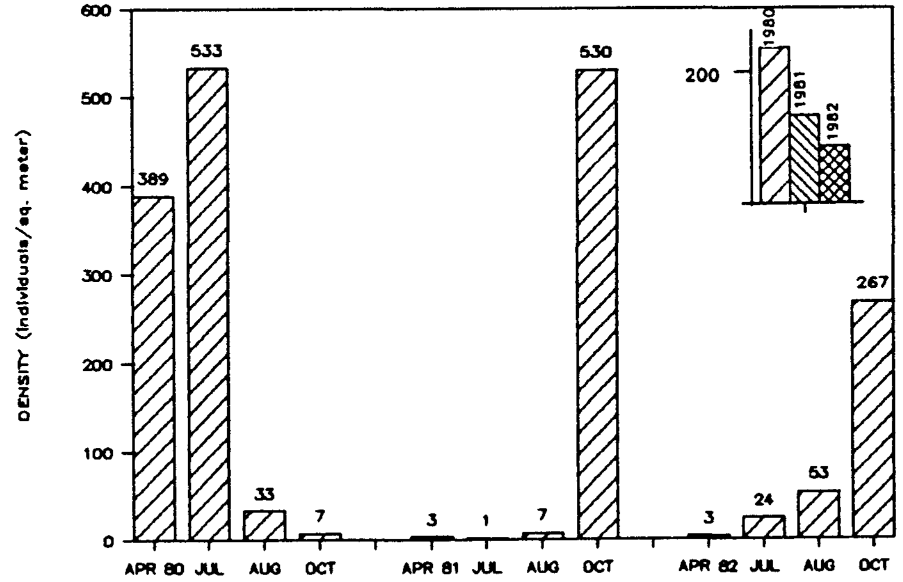


(b)

FIGURE 3. Monthly and annual mean densities (in nos./m^2) of dominant benthic invertebrates. (a) Polychaeta. (b) Bivalvia. (c) Cumacea. (d) Amphipoda. (e) Nematodes. (f) Nemertea. Yearly mean densities are also in nos./m^2.

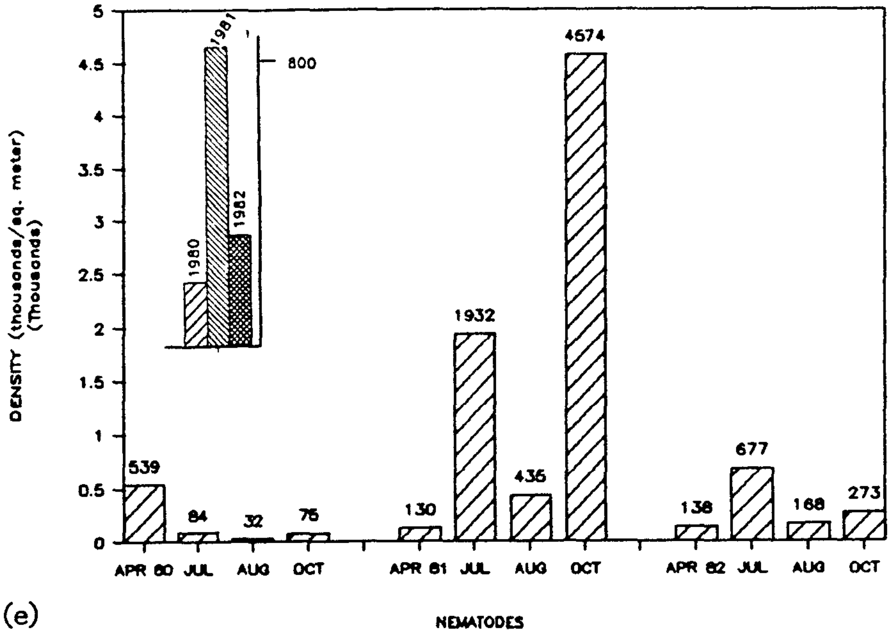


(c) CUMACEA

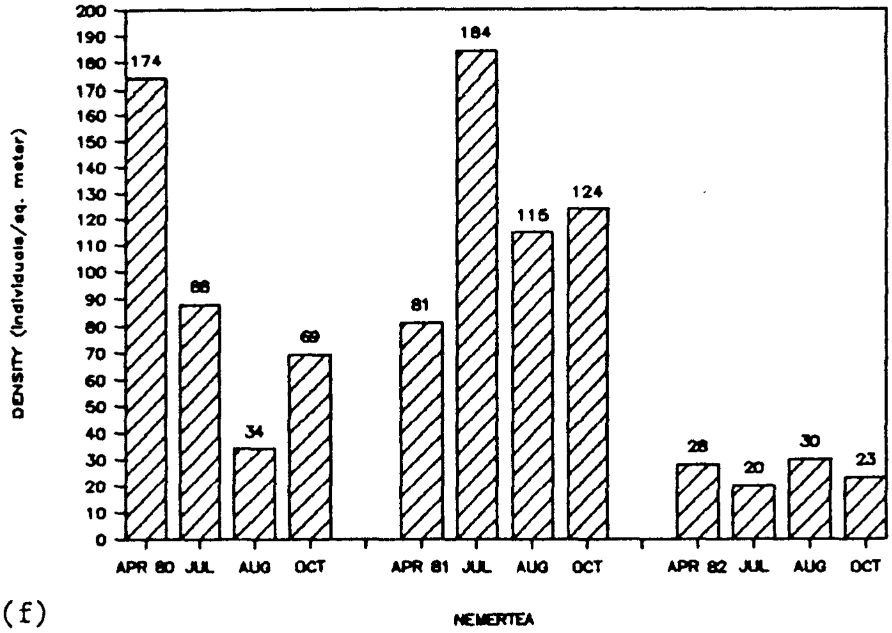


(d) AMPHIPODA

FIGURE 3. (Continued).



(e)



(f)

FIGURE 3. (Continued).

burrowing and tube-building polychaetes[1] dominant in the deeper, more stable substrate.

The polychaete community exhibited substantial changes in concentration during the 3-year study (Figure 3a); sampled densities for 1981 and 1982 were almost 70% higher than the yearly mean for the 1980 preimpounded samples. Of the polychaetes, 16 families were identified (Figure 4) and whereas most polychaete groups diminished drastically in number after 1980, 4 of the 16—the spionid, capitellid, owenid, and nereid polychaetes—increased after 1980. The most important change in the polychaete community was a significant increase ($P < 0.02$, $df = 3$) in the density of spionid and capitellid polychaetes after impoundment (Figure 4).

Spionid polychaetes, like the owenids and magelonids, are a relatively sedentary, tubicolous species with a feeding strategy that is transitional between the indirect deposit feeders and filter feeders. In addition to feeding on the bottom deposits, they have two grooved feeding palps which are used to collect suspended detritus. The tube it constructs may, among other benefits, provide the animal access to clean, oxygenated water above a muddy or sandy bottom (Barnes, 1980) and may be a very important adaptation for the new conditions in the study site. Capitellids are errant burrowers and are found, almost exclusively, in fine sands and mud. Both of these

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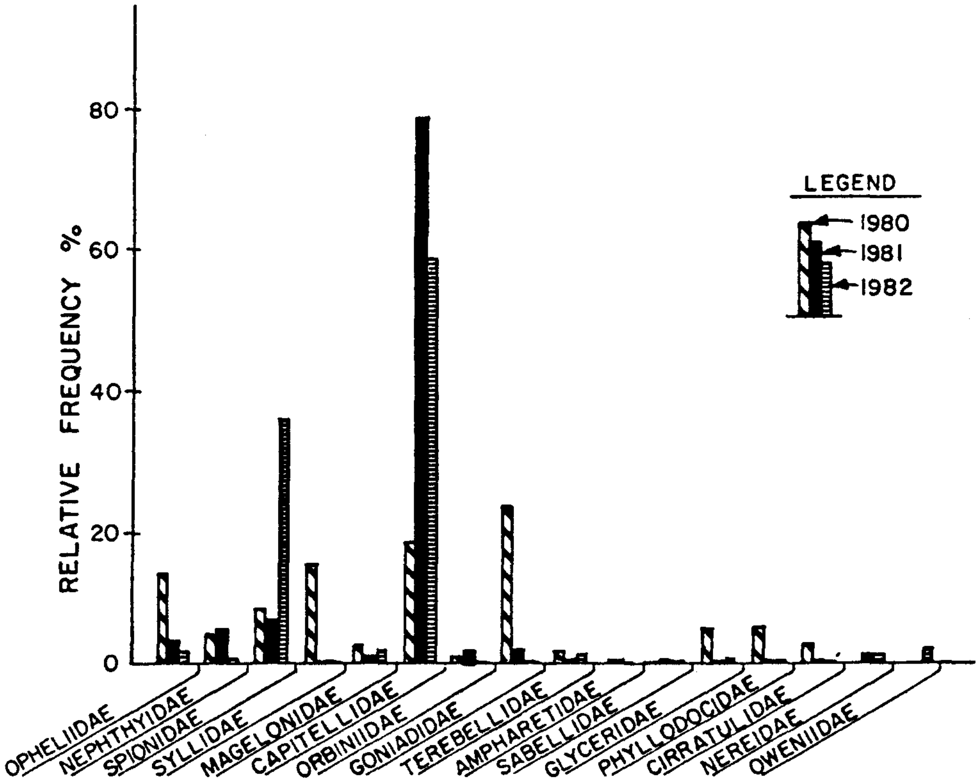
[1] Most of these were surface deposit-feeders and suspension feeders whereas the polychaetes living exclusively in the shallow, crustacean zone did not have permanent tubes or burrows.



	1980		1981		1982
spionids	44(46)		36(19)	*	203(97)
capitellids	75(32)	*	498(217)		423(181)

* = adjacent means significantly different, P<0.02 (t-test, 3 d.f.)

FIGURE 4. Changes in the frequency of polychaete families, 1980-1982: changes in the relative frequency (%) of all families sampled in the study area (top); means of monthly densities (number/m^2) of spionid and capitellid polychaetes in zones B, C, and D of the study area (bottom). Numbers in parentheses are one standard deviation from the mean.

Note. From Varoujean, D. H. (1984, April). Umpqua Training Jetty Extension Monitoring Study (pp. 30, 33) (Final Report to Portland District), Portland: U.S. Army Corps of Engineers.

families can be found, however, in a wide variety of habitats and have been previously reported associated with highly organic or frequently disturbed areas; some capitellid worms are considered pollution indicators (Light, 1975). The increase in abundance of these two families accounts for the overall increase in polychaete density for 1981 and 1982 (Figure 4).

Nemerteans showed a small, probably insignificant increase in sample abundance for the 1981 sample season before becoming much more rare in the 1982 samples (Figure 3f).

Four species of bivalves, mostly small clams between 0.5 and 3 mm long, exhibited an overall increase in density for the postimpoundment years (Figure 5), although the trend is not marked. In 1980, there were almost no bivalves in the samples during the first two sampling sessions, indicating either a barrier to recruitment into the site before construction, or unfavorable conditions (water or sediment quality) for survival in the preimpoundment environment. The reference site exhibited a similar pattern (few bivalves until the month of September) which might suggest that there is larval recruitment into the shallows, in the summer, followed by the destruction of this community or the migration to deeper waters during the winter. Large surf due to winter storms might cause such a pattern in the shallow areas.

In 1982, as the study site continued to fill in with organic sediments, the abundance of bivalves decreased somewhat (Figure 3b). With inefficient gills that double as feeding surfaces bivalves might

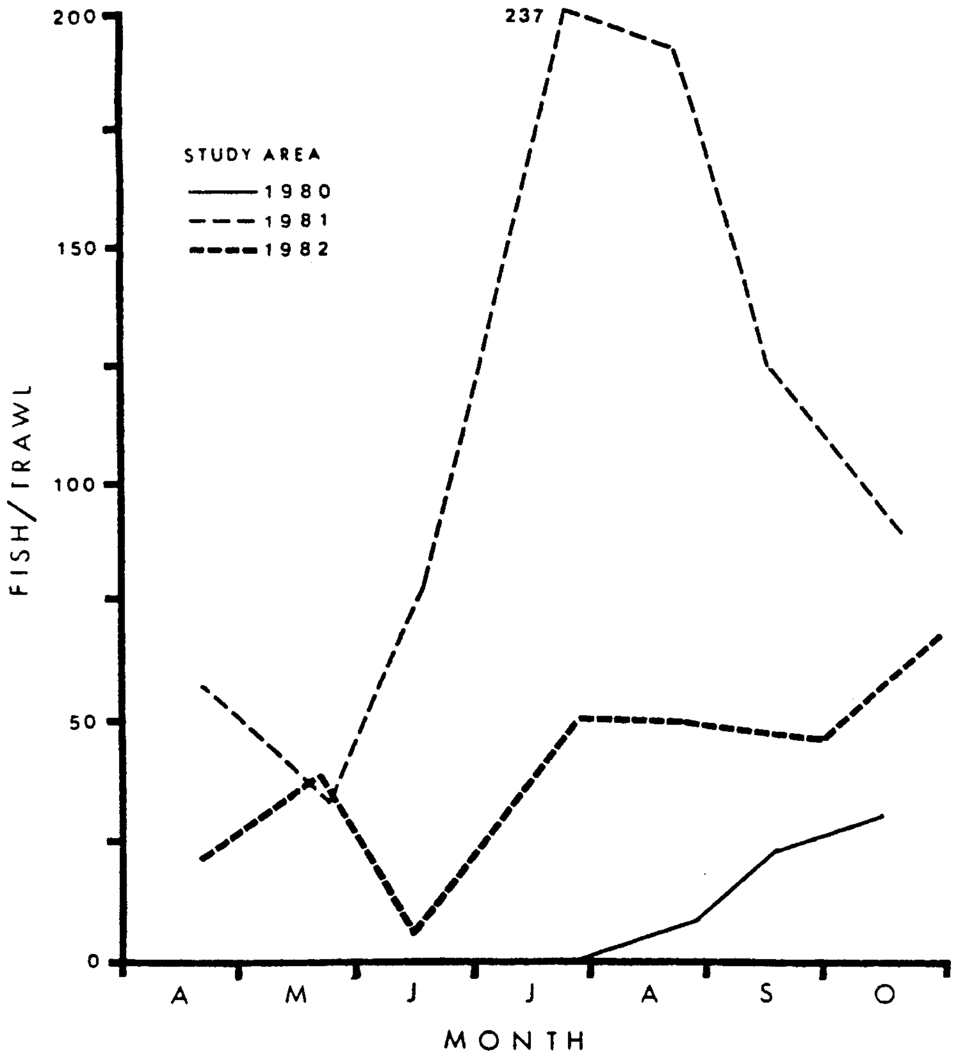


FIGURE 5. Catch/effort of English sole in the study area.

Note. From Varoujean, D. H. (1984, April). Umpqua Training Jetty Extension Monitoring Study (p. 43) (Final Report to Portland District), Portland: U.S. Army Corps of Engineers.

have begun to experience fouling problems. Barnard (1963) observed that the distribution of Tellina modesta was correlated with the percentage of silt in shallow water sediments which indicated very specific sediment-size preference in some bivalves. Species or size-specific success in dealing with the sediments in the study area might allow for a partial destruction of the bivalve population. Other factors, such as predation, may also affect the bivalve population.

At least 12 species of gammarid amphipods exhibited a dramatic decline near the end of 1980 and did not begin to reappear, in any consistent numbers, until 1982 (Figure 3d). October 1981 samples discovered a patch of amphipods (in Zone B) of extremely high concentration, but the study area generally appeared void of any substantial numbers.

The cumaceans, an order of small, bottom-inhabiting crustaceans, exhibited the most dramatic change in numbers (of individuals sampled) over the 3-year period. The data indicate nearly a 15-fold increase in population density between the end of 1981 and 1982 (Figure 3c).

Although many cumaceans feed directly from the substrate surface, most are suspension feeders and are capable of exploiting the water column in search of food. Cumaceans live buried in the sand and mud, often in tunnels, and in areas of rapidly shifting sediments; they are able to relocate when becoming too deeply buried (Barnes, 1980). In a study of benthic invertebrate zonation, Oliver et al. (1980) found that cumaceans were not abundant on the bottom but instead were successfully captured in funnel traps just off the bottom. A factor in their success in the study area might largely stem from their not being restricted to the substrate surface. That the cumaceans were so much more abundant in 1982 than the previous years suggests they prefer quiet waters. The organic sediments and detritus brought into the area are likely an ideal food supply for these organisms.

Nematodes occurred in very large numbers in the samples between July and October of 1981 (Figure 3e), with sample population densities far exceeding those of 1980 and 1982.

Spearman rank correlation coefficients were compared pooled results between years. Values indicate a significant correlation between 1981 and 1982 only (P = 0.05). The diversity (H') is relatively low in 1981 and is probably the result of the abundance of nematodes in that year.

Monthly comparison of the study site with the reference site in 1982 (the only year the reference site was sampled for benthic invertebrates) revealed little.

From trends observed in the sediment samples taken over the 3-year period, cumaceans, certain spionid and capitellid polychaetes, and diminutive bivalves appeared to thrive much better in the fine, organic sediments of the study site in 1982 than the more exposed and coarse-grained river-influenced environment of 1980. Of equal importance, the gammarid amphipods and species of many other families of polychaetes have declined dramatically in the 2 years following impoundment.

Changes in Fish Abundance

Collected from the study site in 1980 were 38 fish species, including 6 species of flatfish (Table 3). Large numbers of midwater and nonflatfish demersal species were taken by otter trawl and beach seine. Gill nets yielded several species not taken by the other methods, but these additional fishes comprised a very small percentage of the overall catch. Species composition and relative numbers of fish captured in the study site in 1980 are in agreement with data reported for the lower Umpqua River Estuary (Mullen, 1977) and Coos Bay (Cummings & Schwartz, 1971).

In the otter trawl samples, the dominant fishes were juvenile English sole (*Parophrys vetulus*) and juvenile speckled sanddab (*Citharichthys stigmaeus*). Sampling during the 1981 and 1982 seasons showed a striking decrease in the number of midwater and nonflatfish demersal species, with a concurrent increase in the number of juvenile flatfish, especially English sole, in the study area (Table 4). Sampling at the adjacent reference site in 1981-1982 showed little change in species composition from that of 1980 and closely resembled the 1980 preimpoundment study site.

Relatively few English sole were taken from the study area before August 1980, before jetty completion. Catch data for the postimpoundment years (Table 4, Figure 5) show that English sole were present in the study area during all months sampled and that there was a substantial numerical increase from 1980 levels. Only fish between

TABLE 3. Fish Species Found in Umpqua River Estuary During the Study Period 1980-1982.

Common Name	Scientific Name
Spiny dogfish	*Squalus acanthias*
Big skate	*Raja binoculata*
Green sturgeon	*Acipenser medirostris*
Pacific herring*	*Clupea harengus*
American shad	*Alosa sapidissima*
Northern anchovy*	*Engraulis mordax*
Rainbow trout	*Salmo gairdnerii*
King (Chinook) salmon*	*Oncorhynchus tshawytscha*
Silver (Coho) salmon*	*Oncorhynchus kisutch*
Surf smelt*	*Hypomesus pretiosus*
Whitebait smelt*	*Allosmerus elongatus*
Night smelt*	*Spirinchus starksi*
Longfin smelt*	*Spirinchus thaleichthys*
Pacific tomcod*	*Microgadus proximus*
Topsmelt*	*Atherinops affinis*
Threespine stickleback	*Gasterosteus aculeatus*
Bay pipefish	*Syngnathus leptorhynchus*
Black rockfish	*Sebastes melanops*
Juvenile rockfish	*Sebastes* sp.
Lingcod*	*Ophiodon elongatus*
Kelp greenling*	*Hexagrammos decagrammus*
Cabezon	*Scorpaenichthys marmoratus*
Staghorn sculpin*	*Leptocottus armatus*
Buffalo sculpin	*Enophrys bison*
Padded sculpin	*Artedius fenestralis*
Pricklebreast poacher	*Stellerina xyosterna*
Striped bass	*Roccus saxatilis*
Redtail surfperch*	*Amphistichus rhodoterus*
Spotfin surfperch	*Hyperprosopon anale*
Walleye surfperch	*Hyperprosopon argenteum*
Silver surfperch*	*Hyperprosopon ellipticum*
Shiner surfperch*	*Cymatogaster aggregata*
Striped surfperch	*Embiotoca lateralis*
Pile surfperch	*Damalichthys vacca*
White surfperch	*Phanerodon furcatus*
Penpoint gunnel	*Apodichthyes flavidus*
Saddleback gunnel	*Pholis ornata*
Pacific sandlance*	*Ammodytes hexapterus*
Sand sole*	*Psettichthys melanostictus*
English sole*	*Parophrys vetulus*
Starry flounder*	*Platichthys stellatus*
Rock sole	*Lepidopsetta bilineata*
Speckled sanddab*	*Citharichthys stigmaeus*
Pacific sanddab*	*Citharichthys sordidus*

*Indicates fish caught in study site.

Note. From *Umpqua Training Jetty Extension Monitoring Study* (Final Report to Portland District) (p. D1), by D. H. Varoujean, 1984, Portland: U.S. Army Corps of Engineers.

TABLE 4. Fish, Dungeness Crab, and Bay Shrimp Caught in Otter Trawls Conducted in Zones B, C, and D in the Study Areas (S) and Zones II, III, and IV in the Reference Site (R) by Year (Abundances Expressed as Mean Number/Trawl).

	1980	1981		1982	
Species	S	S	R	S	R
Surf smelt		5			
Whitebait smelt	2	+			
Pacific tomcod	5			+	+
Topsmelt	1				
Lingcod	1				+
Kelp greenling	1	1	+	+	+
Staghorn sculpin	4	+	1	+	+
Shiner surfperch	6	+	1	+	+
Sand sole	+	+	1	+	+
English sole	9	100	36	34	21
Starry flounder	+	1	1	+	+
Pacific sanddab		1	+	1	1
Speckled sanddab	20	6	17	2	12
Dungeness crab	49	4	16	1	13
Bay shrimp	33	15	6	5	3
Number hauls	21	21	17	21	21

+Present, but number/haul less than 1.

Note. Species for which the catch/effort was less than one in each of the three years of study are not listed.

Note. From Umpqua Training Jetty Extension Monitoring Study (Final Report to Portland District) (p. 32), by D. H. Varoujean, 1984, Portland: U.S. Army Corps of Engineers.

20 and 180 mm (SL) were captured in the study area. This size range is probably representative of the English sole community at the site, although some bias may exist as a result of large fish being better able to avoid the sampling trawl. Length/frequency data for English sole in the study site (Figure 6) indicate that smaller individuals constituted a greater proportion of the total in 1981 and 1982 than was the case in 1980, where fish smaller than 80 mm standard length were rare or not found in the samples over the year. The change in English sole size-frequency data over the 3-year study period may be owing to an abundance of larval *P. vetulus* entering the study site through the jetty as planktonic larvae, metamorphosing, setting, and maturing within the study site. Although juvenile English sole commonly inhabit relatively shallow, nearshore waters, they are probably uncommon in very shallow areas subject to heavy wave action, as in the preimpoundment study area. The stone jetty does not appear to prevent the recruitment of the planktonic larvae of flatfish into the site, and the quiet waters of the impoundment area seem to have made the site more conducive to settlement and growth.

Because the jetty will impede emigration to deeper waters, the study site might act as a trap for certain bottom fishes with planktonic larvae by providing them with favorable conditions for recruitment and early growth. Unless the study site proves to be too unproductive to support an abundant bottom-fish community, the average size of *P. vetulus* would be expected to increase in coming years.

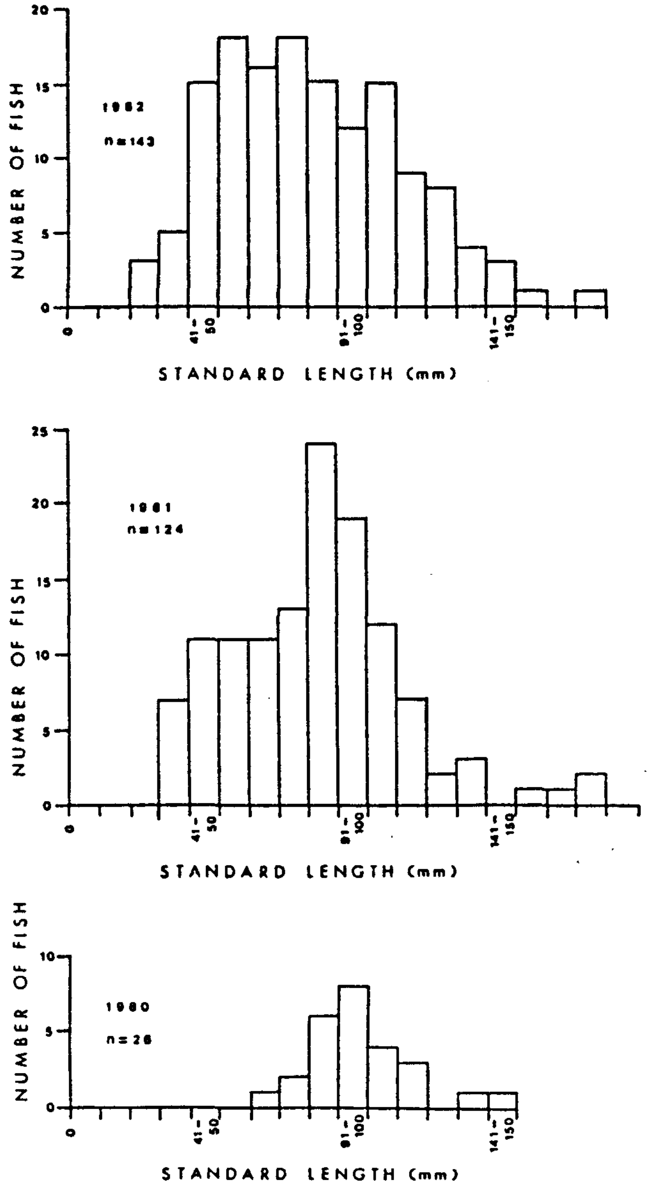


FIGURE 6. Length/frequency data for English sole caught in the study area.

Note. From Varoujean, D. H. (1984, April). Umpqua Training Jetty Extension Monitoring Study (p. 44) (Final Report to Portland District), Portland: U.S. Army Corps of Engineers.

CHAPTER IV

RESULTS OF STOMACH CONTENTS ANALYSIS

With the exception of the October samples, fish caught in 1980 were not saved. The diet analysis, then, for 1980 is based on fish captured in October of that year, just after completion of the training jetty. As with the benthic invertebrates collected from the study site, only English sole taken from Zones B, C, and D were examined in order to avoid possible complications in including the intertidal habitat in Zone A.

English Sole Diet, General

Stomachs from 128 juvenile *Parophrys vetulus* were examined over the 3-year study, of which only 12 were empty. Fish used in the diet analysis were between 68 and 178 mm total length, corresponding to 1st- and 2nd-year English sole. As is apparent from Table 5, *P. vetulus* feeds on a wide variety of benthic animals (see Figure 7). Prey from seven broad taxonomic groupings were found but the majority of prey came from only three classes of invertebrates: the Polychaeta, Bivalvia, and Crustacea. Seven prey categories from these three classes account for over 99% (numerically) of the total prey organisms taken by *P. vetulus* and are Polychaeta annelids, juvenile bivalves, clam siphons, cumaceans, harpacticoid copepods, amphipods, and

TABLE 5. Taxa Identified From Stomachs of English Sole Taken From the Study Site.

Major Group	Dominant Organisms	Incidental Organisms
Nematoda		+
Nemertea		+
Polychaeta	*	
Bivalva	Clams and miscellaneous bivalves, clam siphons	
Gastropoda		Veliger and egg case
Crustacea	Harpacticoid copepods, cumaceans, gammarid amphipods	Cladocerans, ostracods, calanoid copepods, cirripedians (nauplii) isopods, amphipods, decapods (zoea), mysids
Ophiuroidea		Brittle stars
Vertebrata		Fish eggs

+Indicates presence at site.

*Identified specimens include polychaetes from the families: Capitellidae, Magellonidae, Nephtyidae, Nereidae, Opheliidae, Owenidae, Spionidae, and Terebellidae.

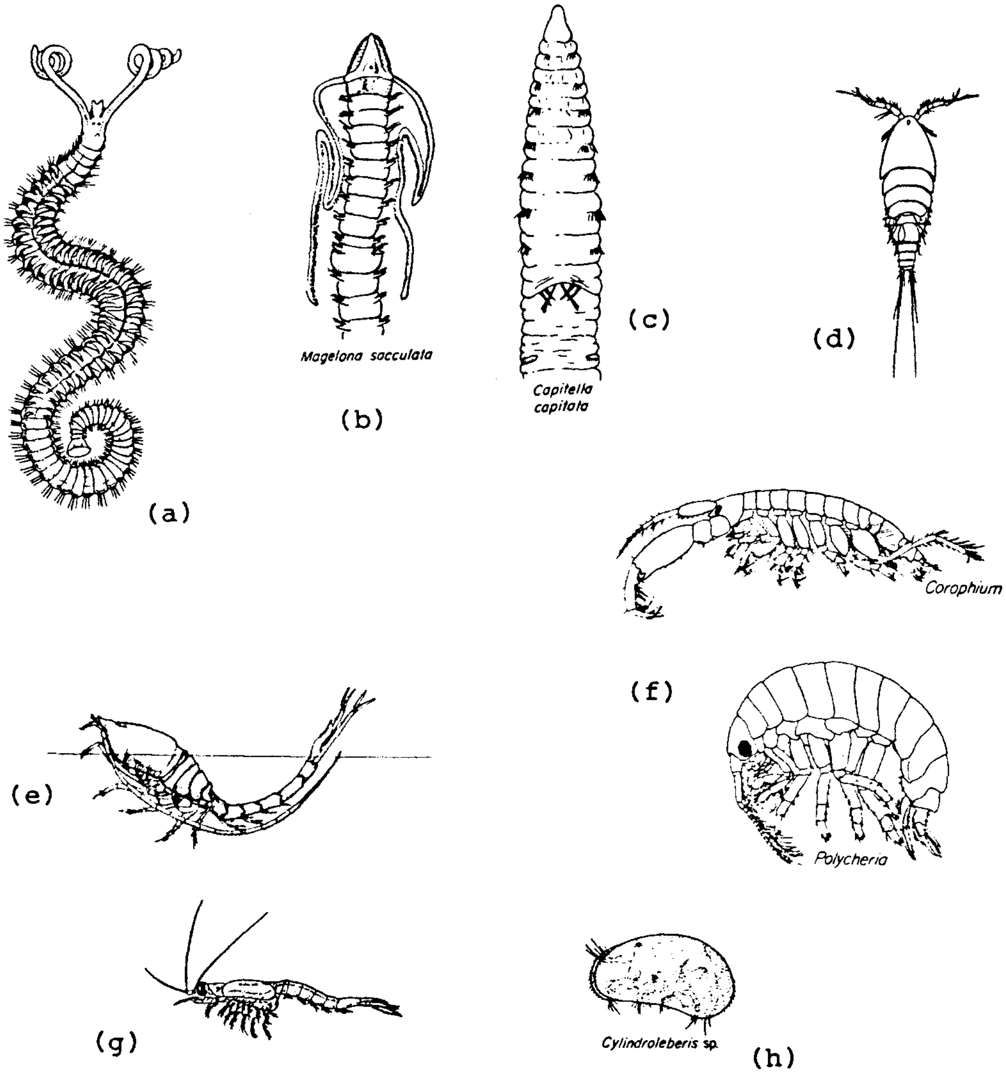


FIGURE 7. Some of the dominant invertebrate taxa found in the stomachs of P. vetulus from the study area. (a) a spionid polychaeta annelid, Polydora (note feeding palps). (b) a magelonid, Magelona (note feeding palps). (c) a capitellid polychaete. (d) a harpacticoid copepod, Tisbe sp. (e) a cumacean, Diastylis, shown buried in sediment. (f) gammarid amphipods. (g) a mysid, Mysis sp. (h) an ostracod, a less frequently observed prey item.

Note. All figures except (e) from S. F. Light, 1975, Light's Manual: Intertidal Invertebrates of the Central California Coast (pp. 165, 223, 249, 254, 329, 332), Berkeley: University of California Press. (e) is from C. P. Hickman, 1973, Biology of the Invertebrates (p. 547), St. Louis: C. V. Mosby.

nematodes. Quantitative data are summarized for these prey categories in Table 6, and the yearly mean abundances (numerical) are compared in Figure 8. Animals constituting less than 1% of the total number of prey items for all three years include cladoceran, ostracod, isopod, decapod, and mysid crustaceans; brittle stars (Echinodermata: Ophiuroidea); and gastropod and fish eggs, along with other incidental food (e.g., barnacle nauplii and gastropod veligers).

Most of the prey items were small, between 0.5 mm and 4.0 mm along their greatest dimension. Harpacticoid copepods were the smallest prey, between 0.2 and 0.3 mm in length. Gammarid amphipods, cumaceans, intact juvenile bivalves, and bivalve siphons ranged from between 0.5 mm and 4.0 mm long, with a few individuals from each of these groups being slightly larger. Polychaetes, predominantly of the families Spionidae and Capitellidae, were by far the largest prey, with pieces frequently between 6-10 mm and occasionally up to 30 mm in length. Polychaete palps and nematode worms were commonly over 1 mm long, but are very thin and constitute a much smaller volume of food than other prey of equal length. The majority of nematodes were determined to be free living, based on their appearance (often partially digested) and their position in the digestive tract (frequently a part of the food bolus), which distinguished them from the parasitic forms.

All the prey items in the stomach contents were also found in the benthic faunal sediment cores, with the exception of calanoid copepods,

TABLE 6. Summary of Stomach Content Data Collected for English Sole, *Parophrys vetulus*.

Sample Date	No. Fish Examined	Mean Length (cm) and Range	Polychaetes			Juvenile Bivalves			Clam Siphons			Harp
			N[a]	V[b]	FO[c]	N	V	FO	N	V	FO	N
12 October 1980	12	12.2 (9.0–16.5)	0.44 9.60	0.60 47.40	(0.85)	0.07 1.80	0.08 7.90	(0.39)	0.10 1.50	0.09 2.60	(0.31)	0.26 28.70
23 July 1981	9	9.0 (6.8–11.5)	0.18 10.00	0.45 47.60	(0.89)	0.20 3.80	0.29 24.70	(0.89)	0.20 6.40	0.15 12.00	(0.78)	0.24 19.10
20 August 1981	16 (2)	12.8 (9.6–17.8)	0.44 15.10	0.60 54.80	(1.00)	0.09 2.00	0.09 9.20	(0.57)	0.35 8.40	0.24 16.80	(0.93)	0.00
17 September 1981	9 (1)	11.6 (9.9–13.0)	0.56 6.80	0.80 60.80	(1.00)	0.06 0.50	0.04 2.10	(0.50)	0.29 6.30	0.15 9.80	(0.50)	0.04 1.50
21 October 1981	9 (3)	11.2 (9.6–13.6)	0.44 4.30	0.68 34.70	(1.00)	0.16 1.00	0.18 9.70	(0.50)	0.16 6.50	0.12 10.00	(0.17)	0.24 1.70
Totals & Means	43 (6)	11.4 (6.8–17.8)	0.43 10.30	0.62 51.10	(0.97)	0.12 2.00	0.14 11.50	(0.62)	0.27 7.10	0.18 13.00	(0.68)	0.10 5.20
27 July 1982	17 (3)	10.2 (8.6–13.0)	0.24 6.90	0.34 40.90	(0.93)	0.20 6.10	0.29 49.20	(0.79)	0.17 5.60	0.12 12.70	(0.86)	0.03 1.70
23 August 1982	16	12.8 (10.5–16.1)	0.39 12.60	0.57 101.80	(1.00)	0.05 1.10	0.05 5.10	(0.44)	0.38 1.10	0.05 6.60	(0.88)	0.01 0.30
29 September 1982	16	12.7 (9.5–15.3)	0.50 15.90	0.60 90.50	(1.00)	0.03 0.30	0.08 4.60	(0.19)	0.29 7.40	0.25 17.80	(0.75)	0.03 0.90
28 October 1982	15 (5)	10.9 (9.6–12.6)	0.26 8.90	0.37 37.30	(0.90)	+ 0.30	0.01 9.90	(0.20)	0.32 14.20	0.27 27.40	(1.00)	0.05 1.40
Totals & Means	64 (8)	11.2 (6.5–18.0)	0.36 11.80	0.48 71.80	(0.98)	0.07 2.00	0.11 15.80	(0.36)	0.30 10.20	0.22 22.00	(0.88)	+ 0.40

[a] Mean percentage composition by number (N) (upper) and mean numbers of organisms per stomach (lower). Same for each N in every prey category.

[b] Mean percentage composition by volume (V) (upper) and mean volume (in mm^3) of organisms per stomach (lower). Same for each V in every prey category.

[c] Frequency of occurrence (FO). Same for every prey category.

+Indicates a value for less than 0.01.

*90% of the miscellaneous organisms were mysids, all from one stomach.

Note. Numbers in parentheses under the heading "No. Fish Examined" are number of fish with empty stomachs.

Prey Categories

Clam Siphons		Harpacticoid Copepods			Cumacea			Amphipods			Nematodes			Miscellaneous		
V	FO	N	V	FO	N	V	FO	N	V	FO	N	V	FO	N	V	F
0.09 2.60	(0.31)	0.26 28.70	0.15 17.10	(0.46)	0.00	0.00	0.00	0.00	0.00	0.00	0.05 0.46	+ 0.40	(0.23)	0.08* 5.90	0.08 22.00	(1.
0.15 12.00	(0.78)	0.24 19.10	0.06 3.90	(0.67)	0.02 0.80	0.01 0.90	(0.44)	0.03 1.10	0.02 0.22	(0.67)	0.01 0.20	+ 0.01	(0.22)	0.01 0.40	0.01 1.10	
0.24 16.80	(0.93)	0.00	0.00	0.00	0.01 0.30	+ 0.30	(0.14)	0.00	0.00	0.00	0.10 2.70	0.02 1.00	(0.36)	0.01 0.10	0.04 8.60	
0.15 9.80	(0.50)	0.04 1.50	+ 0.40	(0.13)	0.00	0.00	0.00	0.01 0.04	0.60	(0.13)	0.06 1.10	+ 0.40	(0.25)	+ +	+ +	
0.12 10.00	(0.17)	0.24 1.70	0.03 0.50	(0.33)	0.00	0.00	0.00	0.02 0.20	0.02 0.30	(0.17)	0.00	0.00	0.00	+ +	+ +	
0.18 13.00	(0.68)	0.10 5.20	0.01 1.10	(0.24)	+ 0.30	+ 0.30	(0.16)	0.01 0.40	+ 0.80	(0.22)	0.05 1.30	0.01 0.20	(0.24)	+ 0.20	0.20 3.50	(1.
0.12 12.70	(0.86)	0.03 1.70	+ 0.60	(0.21)	0.34 14.30	0.23 19.90	(0.93)	0.01 0.60	0.02 1.10	(0.29)	0.01 0.90	+ 0.50	(0.29)	+ 0.70	+ 0.10	
0.05 6.60	(0.88)	0.01 0.30	+ 0.10	(0.19)	0.12 4.90	0.06 5.90	(0.56)	0.03 1.20	0.03 3.10	(0.38)	0.01 0.30	+ 0.20	(0.13)	0.01 0.40	0.01 2.90	
0.25 17.80	(0.75)	0.03 0.90	+ 0.30	(0.19)	0.07 0.90	0.05 1.10	(0.44)	0.01 0.50	+ 0.90	(0.25)	0.04 0.10	0.01 0.20	(0.13)	+ 0.10	+ 0.10	
0.27 27.40	(1.00)	0.05 1.40	+ 0.30	(0.50)	0.25 13.20	0.24 30.90	(0.80)	0.11 4.30	0.09 8.40	(0.80)	0.00	0.00	0.00	+ 0.30	0.02 2.80	
0.22 22.00	(0.88)	+ 0.40	0.03 1.20	(0.25)	0.19 7.60	0.13 12.70	(0.66)	0.04 1.40	0.03 2.90	(0.39)	0.02 0.30	+ 0.20	(0.66)	+ 0.20	0.01 0.91	(1.

ry prey category.
V in every prey category.

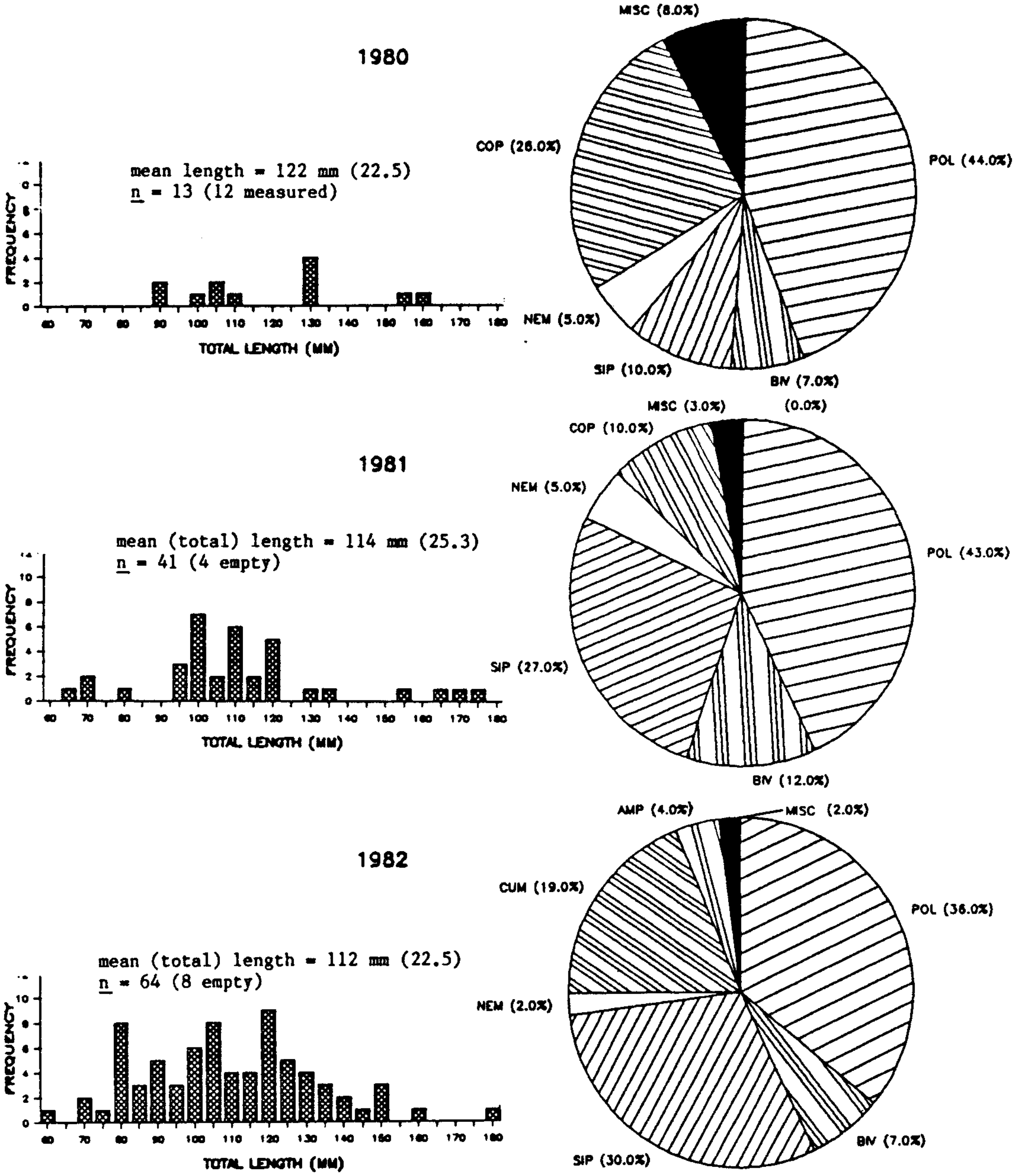


FIGURE 8. Right: Mean percentage composition for major prey taxa found in P. vetulus from the study site, 1980-1982 annual means based on numerical abundance. Polychaetes, POL; bivalves, BIV; bivalve siphons, SIP; nematodes, NEM; cumaceans, CUM; amphipods, AMP; and all other minor taxa present in stomachs, MISC (Note: 90% of the MISC in 1980 were mysids). Left: Length versus frequency histogram for all P. vetulus examined (n = number of fish/sample). Numbers in parentheses are one standard deviation from the mean.

barnacle nauplii, and gastropod veligers, which are pelagic. Mysids also migrate vertically into the water column.

Typically high frequencies of occurrence in the stomach samples, for most prey groups, indicate a wide range of prey types were consumed by a majority of fish in the samples. Polychaetes were found in nearly all stomachs (frequency of occurrence [FO] for each year, respectively, was 84%, 97%, and 98%), and bivalves and/or bivalve siphons were found in well over 50% of the stomachs examined.

The average diversity H' (Shannon-Weaver, 1949) of food consumed per sampling date was computed using the same eight major groupings[1] for each calculation and so is really a measure of evenness. H' was 0.704, 0.716, and 0.764 for 1980, 1981, and 1982, respectively. The difference in the value of H' between years is probably not significant.

The Spearman rank correlation coefficient, r_s, has been corrected for ties (Fritz, 1974) and eight pairs of ranked values produced significant correlation (at 5% significance) between diets in successive years only (r_s 1980-1982 = 0.48, r_s 1980-1981 = 0.82, r_s 1981-1982 = 0.77; r_s [0.05] = 0.714;), indicating that the prey consumed in 1981 were transitional between those of the 1st and 3rd years.

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[1] The seven major prey categories already mentioned, plus the mysids which contributed 7% of the prey to the 1980 diet samples.

Relative Importance of Prey Types

The importance of amphipods and nematodes to the P. vetulus diet was relatively low throughout the study, their combined numbers never exceeding 6% of the total prey consumed in any year. Although the numbers of some prey, particularly some of these less abundant organisms, did not change much over the 3-year study, some of the important prey in the diet of the English sole did change in a consistent fashion, as can be seen in the yearly comparison (Figure 9).

Polychaetes, bivalves (whole and their siphons), copepods, and cumaceans dominated the sampled diets over the 3-year period accounting for 91%, by number, of the diet for all years: Polychaetes and bivalves were major dietary organisms all 3 years; copepods were very important in 1980 only, and cumaceans were a dominant food in 1982 only.

Polychaete annelids were the most important prey for all 3 years, both in number and biomass (Figure 8). Roughly 30% to 60%[2] of the diet (by number) over the entire 3 years was composed of polychaetes.

The proportion of the diet comprised of polychaetes was the highest in 1981, dropping somewhat in 1982. These differences are probably not significant, however, and may in part be due to the increased consumption of other prey, particularly the cumacea and bivalves, which increased substantially. Although the majority of polychaetes in the stomachs were of the families Capitellidae,

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[2] Not including feeding palps eaten separately, a small but consistent contribution to the diet.

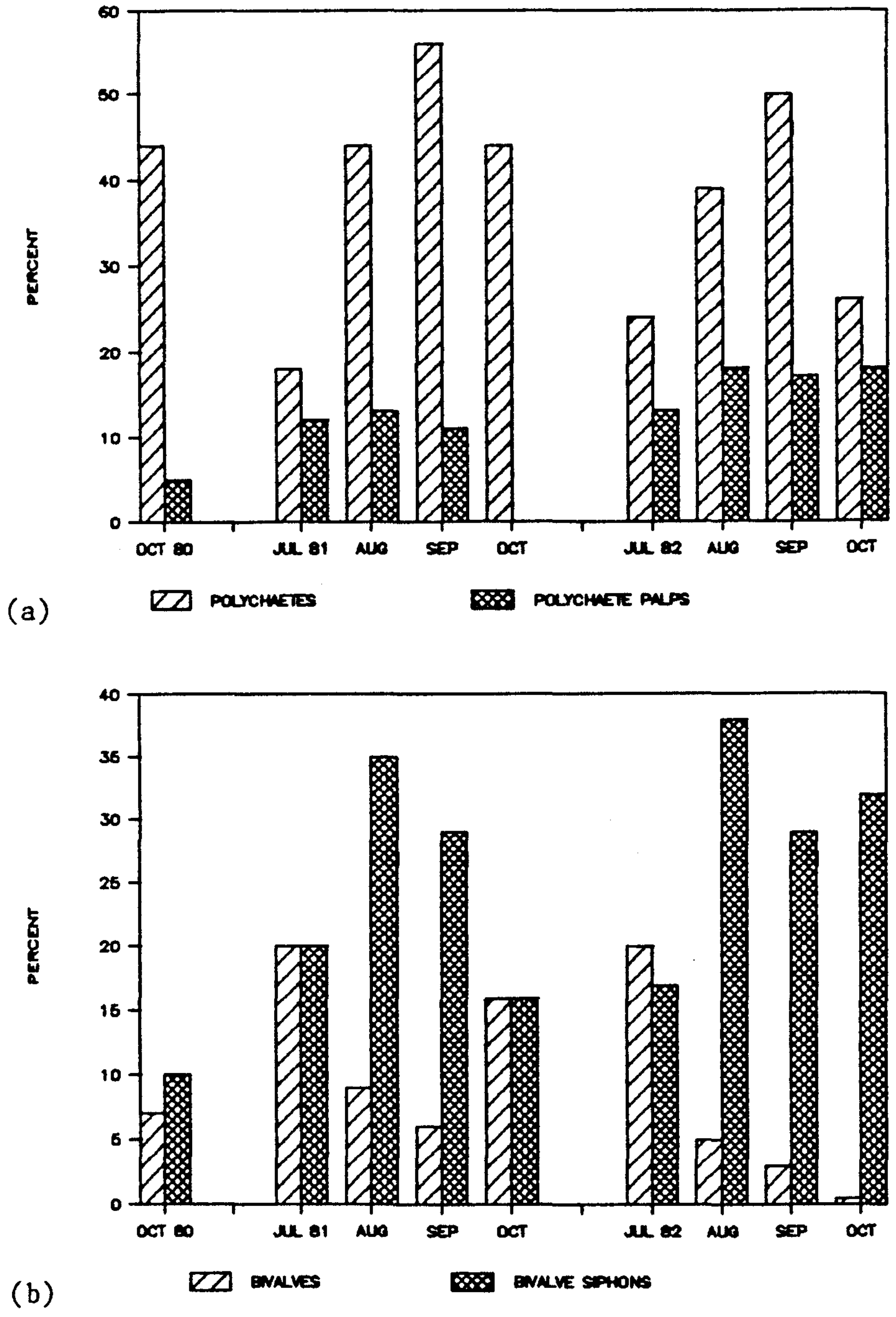
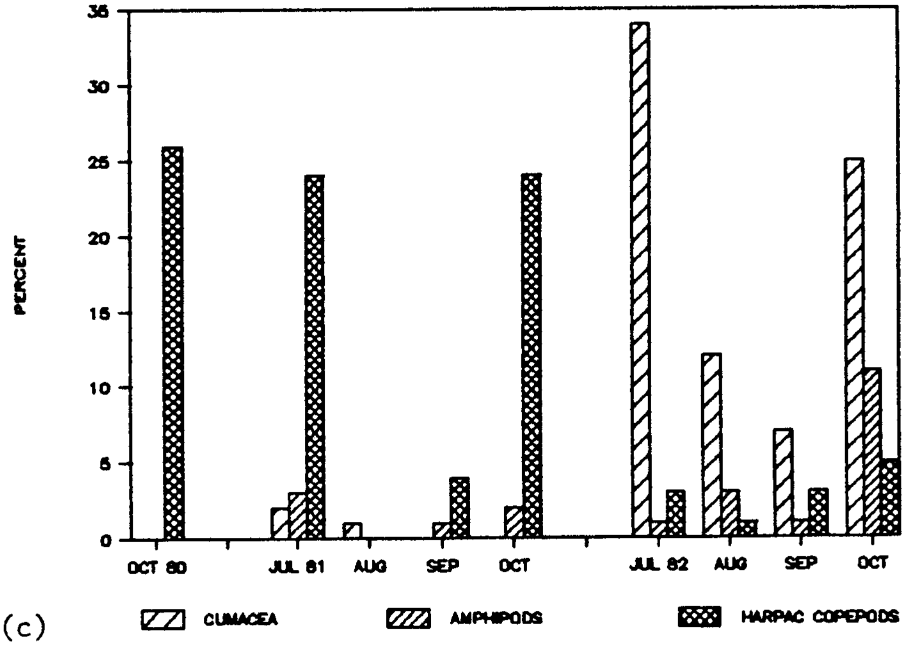
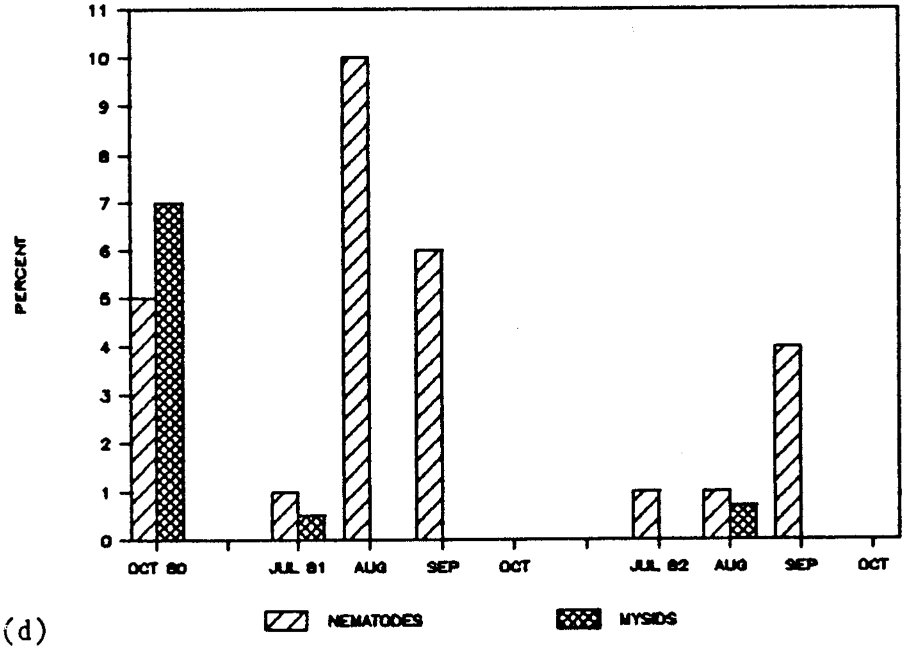


FIGURE 9. Monthly mean percentage composition for major prey taxa found in *P. vetulus* from study site, 1980-1982 based on numerical abundance. (a) Polychaeta annelids and feeding palps taken separately. (b) Juvenile bivalves and clam siphons taken separately. (c) Cumacean, amphipod, and harpacticoid copepod crustaceans. (d) Nematodes and mysids.



(c)



(d)

FIGURE 9. (Continued).

Spionidae, and Owenidae, a large proportion of polychaete material was not identifiable and the proportions of polychaete families consumed each year could not be determined. However, the number of spionid feeding palps that were taken separately from whole specimens did increase each year (Figure 9a). Feeding palps of the magelonid polychaete, *Magelona sacculata*, were also discovered in the sole stomachs.

Most of the intact bivalves found in the stomachs were clams of the genera *Tellina*, a small clam commonly observed as prey for *P. vetulus* (Hogue, 1982), and *Siliqua*. The yearly means of the frequencies of occurrence indicate that almost twice as many fish had intact clams in their stomachs in 1981 than in the other two years. The numerical abundance of bivalves in the diet was highest in 1981 (12%) (Figure 8) and a consistent decline in their numbers was observed for 1982, as seen in the monthly comparison (Figure 9b). Bivalve siphons eaten separately were much more important as food than whole clams and contributed about 20%, by number and volume, to the diets over the 3-year study (3-year mean). Bivalve siphons, as a separate food, became increasingly important in the diet (Figures 8 and 9b) as the number and volume of siphon pieces found in the stomachs increased each year (10%, 27%, and 37%, by number, for 1980, 1981, and 1982). Even more significantly, the proportion of fish using siphons for food, measured by the frequency of occurrence, increased substantially each year: 31%, 68%, and 88% for each consecutive year (Table 6).

Cumaceans were an important food in 1982 only (19% of the total diet, by number), probably reflecting the 1st year they were present in substantial numbers in the benthic community. P. vetulus was eating large numbers of cumaceans each month during the sampling period in 1982 (Figure 9c) but very few before that—less than 1% in each of the previous years.

Mysids and harpacticoid copepods, both important prey in 1980 (7% and 26%, by number, respectively), became rare food items in the postimpoundment environment (less than 1% each in 1982). Apparently a more important food than the mysids, the feeding on harpacticoid copepods gradually declined (Figure 9c); in 1981 they still contributed 10% to P. vetulus diets. Mysids were only occasionally found in the stomachs after the October 1980 sampling (Figure 9d).

The volume of food eaten by P. vetulus over the 3-year period (Figure 10) does not appear to have changed substantially; the total volume of food per fish, at the time of collection was 173 mm^3 and 159 mm^3 for the first and last years (1980 and 1982) respectively (Figure 10). The average was only 100 mm^3 for 1981, but probably does not represent a significant difference. The volume of identifiable prey consumed was higher in the 1982 samples than for the previous 2 years and is probably attributable to a greater number of large, durable prey (e.g., polychaetes, clam siphons, intact bivalves, and cumaceans) in the diet. Numbers also increased, but the volumetric gain was not accompanied by a comparable numerical increase in the

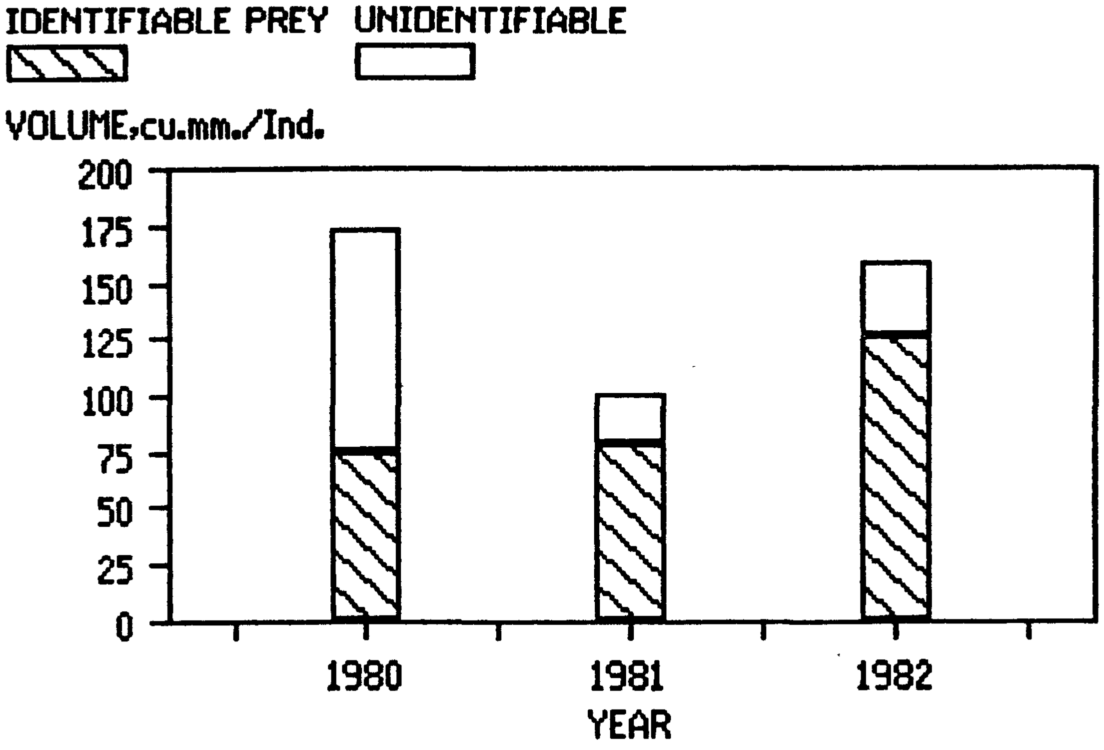


FIGURE 10. Volume of prey consumed (in mm^3/fish) by *P. vetulus* for each of the 3 years.

polychaetes and the bivalves, very possibly indicating growth in the size of these prey over the study period.

CHAPTER V

DISCUSSION

Conclusions

Although immediately following completion of the jetty some organisms were very adversely affected (e.g., amphipods and certain polychaete families), the benthic community appeared to undergo a gradual succession in species composition. Certain dominant open-coast species were replaced by others more tolerant of the new conditions, while previously excluded organisms (e.g., bivalves) were able to tolerate the new set of conditions and recruited into the site. Because of the rapid infilling by current-propelled sediments, the future suitability of the site to sustain marine life is not certain. However, at the conclusion of the study the productivity of the area was not greatly impaired—the overall concentration of benthic organisms had in fact increased and the site appeared to contain a greater density of organisms on and within the bottom sediments.

The resultant effect of these changes on the English sole population at the site was not surprising given the feeding capabilities of the sole. Although annelids remained the dominant food over the entire 3-year period, other prey organisms commonly eaten by *P. vetulus* in the open-coast environment of 1980 (e.g., copepods and mysids) were replaced by prey that became more abundant in the following years (e.g., cumaceans and bivalve siphons).

The contention that the English sole is a roving generalist, feeding on a wide range of prey types, is supported by this study. Prey organisms were almost exclusively benthic, varied greatly in size, and consisted of fossorial organisms which were retrieved from the sediment, epibenthic animals, and pelagic invertebrates.

P. vetulus taken from the study area had fed upon all the organisms known from the benthic samples (within the size range limitations for potential prey) including the relatively rare invertebrates (decapods, brittle stars). The data revealed only a few weak preferences during the 3-year study; nearly all prey items were represented in the diet of _P. vetulus_ approximately in the proportions found in the substrate. Exceptions were the nematodes and amphipods, neither of which were consumed in any substantial quantity (regardless of their abundance in the sediment) and which were largely ignored probably because the energy expenditure for locating and consuming the small prey is great compared to the relatively small benefit. Large prey, specifically polychaetes and clam siphons, appear to have been positively selected for, in the sense that these organisms were probably rarely disregarded. Generally, however, the stomachs of _P. vetulus_ appeared to be proportional subsamples of the benthic community, except for the minute organisms and animals too large to capture.

Foraging at close range in a low-visibility medium, the English sole probably consumes almost every prey it encounters. P. vetulus did not appear to be adversely affected by the almost complete removal of an important food item, harpacticoid copepods, from the site immediately after jetty completion; they simply consumed more of the other prey organisms. They fed extremely efficiently on many prey types by substituting one dominant organism for another as the prey abundances fluctuated over the 3-year period (e.g., as the copepods were a major food in 1980 and the cumaceans, in 1983). Additionally, there was no apparent minimal threshold of prey concentration below which the prey were ignored. P. vetulus continued to feed on prey (such as cumaceans, amphipods, mysids, and brittle stars) even when it occurred in very low densities. The suggestion that the English sole is an opportunistic feeder (Pearcy & Hancock, 1978) is supported here.

The diet of the 1st- and 2nd-year English sole (68-178 mm TL) examined in this study was more similar to the diet observed for the adult English sole (230-450 mm SL) examined by Hogue (1982) than that of the recently settled fish (17-87 mm SL) studied by Kravitz et al. (1977). The juvenile fish studied here contained elements of both these diets and probably represent a typical diet of intermediate-sized English sole. Hogue (1982) found a significant difference in the prey consumed by 0-age English sole and those greater than 35 mm standard length. Feeding data from the present study appear to represent a transitional diet between the small fish which concentrate on a high diversity of exclusively small prey types (approximately

0.5-1.5 mm long: copepods, nematodes, juvenile bivalves, and polychaete palps) and juveniles and adults which utilize a few dominant and larger prey (1.5-4 mm: amphipods, cumacea, and polychaete annelids).

Interactions Between the Predator and Prey Populations: Implications and Suggestions

The Index of Relative Importance (IRI) (Figure 11) (Pinkas et al., 1971) for the polychaetes was higher in 1980 than might be expected, considering their relatively low (apparent) density in the benthic samples in that year (Figures 5 and 11). This discrepancy might reflect a degree of selectivity for polychaetes so that a more constant level of predation is maintained in spite of fluctuations in the relative densities of polychaetes in the benthos. Almost as a rule, Polychaeta annelids present the predator with a large, very nutritious item with very little indigestible hard parts. As opposed to many smaller prey, probably few predators, if any, even in a very productive environment would disregard a polychaete to search for alternative prey. Additionally, *P. vetulus* may have adopted a new strategy to forage for certain polychaetes that were numerous after 1980. In 1980, when there was a more even distribution of polychaete families in the study site, English sole may have had a more general foraging strategy, feeding on a wide range of worms. As spionid and capitellid worms began far to outnumber the rest, fish may have become efficient at finding and eating these worms.

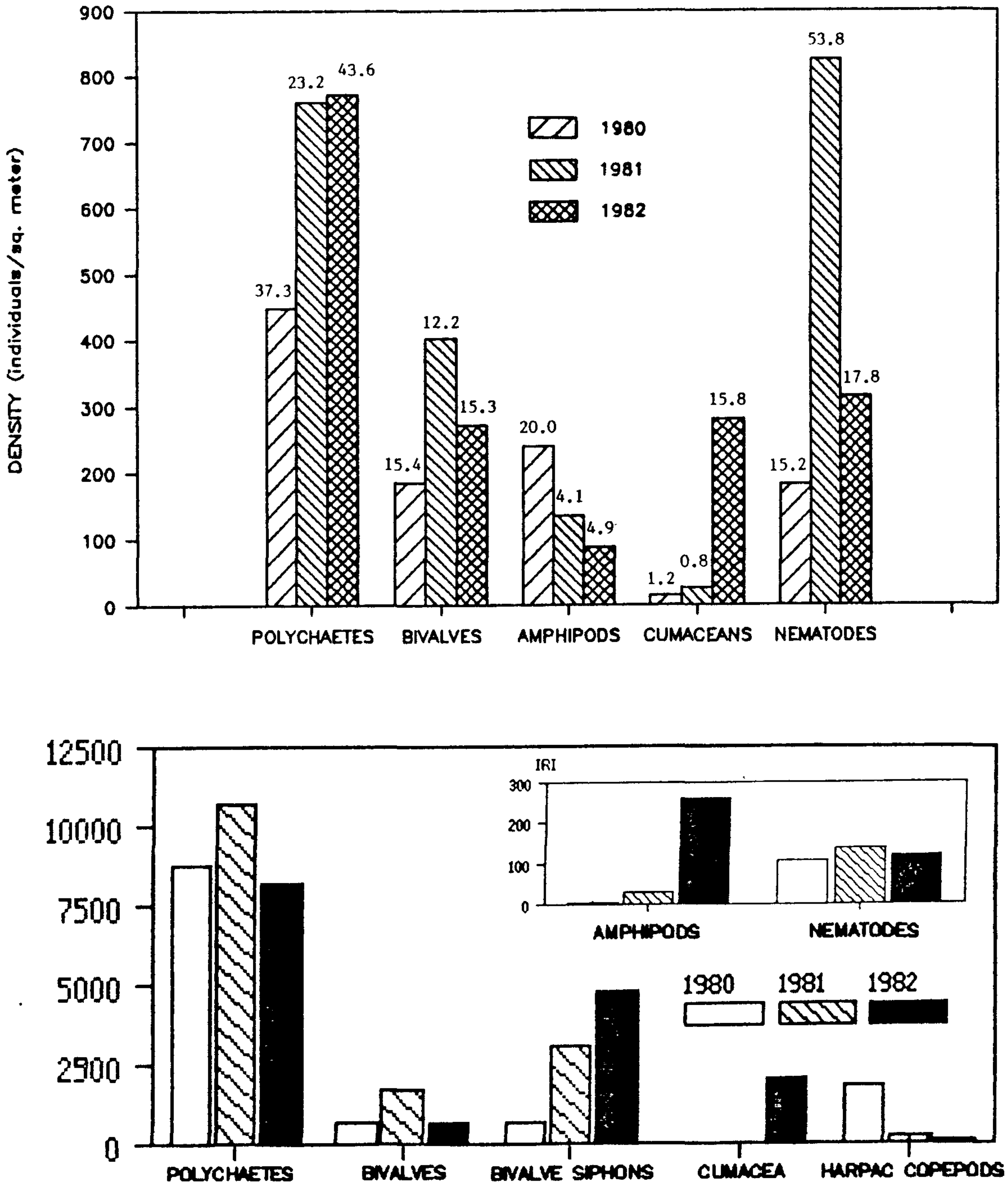


FIGURE 11. Percentage numerical abundance for major prey taxa found in P. vetulus from the study site (top); Indices of Relative Importance (IRI) for all major prey (bottom).

Although the degree of significance is questionable, data for the number of intact clams and clam siphons consumed suggest that the sole likewise exhibited a preference for clam siphons. Despite an apparent decrease in the density of bivalves in the sediment in 1982 (and a concurrent decrease in the numbers of intact bivalves eaten by _P. vetulus_), the proportion of siphons observed in the diet appeared to have increased during this time.

A similar but less marked trend was observed for polychaete annelid palps between 1981 and 1982.

Hogue (1982) suggested that the consumption of parts of macrobenthic organisms (e.g., clam siphons, polychaete palps) rather than the whole animal is related to the maximum size of food capable of being captured and consumed. Large polychaetes and bivalves might be difficult to displace from the sediment due solely to their mass and depth; ingestion of these large items may be inefficient or impossible for juvenile fish. As the size of these animals increases, the available appendages become not only a more nutritious item but also a more noticeable one. As these items get larger and easier to locate, the sole might also become more efficient behaviorally at locating and clipping these prey.

It was suggested earlier that the mean size of bivalves in the study site increased between 1980-1982. A size increase in the bivalve population, making the siphons a more preferable food and the whole clams increasingly unavailable, would help to explain the trend observed for clam siphons and possibly the polychaeta palps.

Furthermore, a learned foraging behavior which concentrated on this abundant new food source may have allowed the sole to forage efficiently for them even in the case of a decline in the bivalve abundance. The apparently contradictory trends, then, may reflect the increased use of the siphons in lieu of the larger, more difficult to get, and less nutritious whole clams. If this was in fact the case, then the increase in the proportion of siphons in the diet might support the suggestion made by Hogue of size-related prey selection—a feeding preference for food of a greater nutritional value per unit effort expended by the predator (larger prey). Although it is conceivable that polychaete palps were also eaten in greater numbers for similar reasons, the increase might be more simply explained by the increase of palp-bearing polychaetes (in particular, the spionids) in 1981-1982.

As mentioned briefly, the number of amphipods eaten by the sole did not vary much from year to year, in spite of the substantial decrease seen in their abundance between 1980 and 1982. Steele et al. (1970) found that even in an environment in which amphipods were a large proportion of the total biomass suitable to plaice as food, amphipods formed only a small but relatively constant part of the diet. He proposed that their availability is effectively low due to the fish's difficulty in capturing the amphipods[1], but that the stimulus to

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[1] Supported by observations of plaice feeding in aquaria (Steele et al., 1970).

feed on them always exists due to their constant and substantial numbers.

Summary

Foraging along the bottom, *P. vetulus* probably encounters a somewhat patchy, productive, but interspersed distribution of mixed prey types and, with a variety of feeding behaviors, is able to locate and capture many types of prey. The data indicate a substantial increase in the density of benthic invertebrates in the disturbed study area, suggesting that a relatively productive area now exists there. Because a food-dense environment offers a lower mean search time per item than does a food-sparse environment (and the study site appears to be relatively food dense), Pianka (1978) predicted that an optimal consumer should restrict its diet to only the better types of food items in a food-dense environment. As no such obvious preferences were apparent in the diet of *P. vetulus*, a number of concessions might be made. English sole may not be optimal foragers under any conditions; they may search randomly and capture anything they can as it is encountered. Secondly, the benthic invertebrate community may not present the density of organisms to the fish that the benthic samples suggest. Although 90% of all benthic forms occur in the upper 1 cm of the substrate, only part of the constituents are probably available at any one time. Additionally, any given prey type is not likely to be distributed evenly or randomly through the sediment, and the fish may only encounter certain prey in patchy and unpredictable intervals.

Lastly, there may not be a great deal of variability in the quality of prey; until such a level is reached where the energy spent capturing and eating an item exceeds its worth, the fish will eat anything it encounters, only foregoing one item to search for a second if the second is abundant and available enough.

The data suggest, and observations support, the notion that *P. vetulus* feed at close proximity to the substrate and the associated prey organisms. In the low-visibility environment of a bottom fish, particularly in the fine sediments of the study site, prey organisms would be encountered in a fairly random and density-proportional fashion, especially given a patchy distribution of invertebrates, as in the study site. In this low-visibility environment, the predaceous fish will necessarily closely approach all prey items just to recognize it. At this point, so little additional energy need be spent to capture the prey that it generally will be. Therefore, *P. vetulus* would be expected to demonstrate a generalized diet, and food preference will probably be minor and will not be commonly observed. If a high enough density of predictable prey types (e.g., sedentary polychaetes or bivalves) is available, then a simple modification in the predator search and capture strategies will likely provide the predator with a greater feeding efficiency on that abundant prey. A preference might also be observed in the situation proposed for *P. vetulus*, if less nutritious and/or more difficult prey (e.g., amphipods) are occasionally disregarded, making the remainder of the prey relatively preferred.

Finally, the effect that the benthic fish population will have on the invertebrate communities within the site can only be open to speculation. The feeding intensity of the juvenile English sole seems great enough, and their densities high enough, to have a profound effect on the abundance of the benthic invertebrates in the area. Although no such trend has been observed, or can easily be distinguished from the effects of the jetty alteration, the diet, growth, and reproductive success of *P. vetulus* and other bottom fishes[2] will surely be affected by the effect of predation and the subsequent changes in prey abundance.

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[2] Besides English sole, Starry flounder, Sand sole, Speckled and Pacific sanddab, among other nonflatfish demersal species, utilize benthic invertebrates to some extent or depend entirely on these organisms.

LITERATURE CITED

Allen, M. J. 1974. Functional structure of demersal fish communities South. Calif. Coastal Water Res. Proj. Ann. Rep. 69-73.

Barnard, J. L. 1963. Relationship of benthic Amphipoda to invertebrate communities of inshore sublittoral sands of southern California. Pac. Naturalist 3:439-467.

Barnes, R. 1980. Invertebrate zoology. 4th ed. W. B. Saunders Co., Philadelphia. 1089 p.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Mexico. U.S. Fish and Wild. Serv. Fish. Bull. 53(74):1-577.

Burt, W. V., and W. B. McAllister. 1959. Recent studies in the itychology of Oregon estuaries, Vol. 1, No. 1, July 1959, p. 14-27. Oreg. Fish Comm. Res. Briefs.

Cailliet, G., B. S. Antrim, and D. S. Ambrose. 1979. Trophic spectrum analysis of fishes in Elkhorn Slough and nearby waters. In S. J. Lipovsky and C. A. Simenstad (editors), Gutshop '78 fish food habits studies. Proceedings of the Second Pacific Northwest Technical Workshop, October 10-13, 1978, p. 118-128. Univ. of Washington Press, Seattle.

Cummings, T. E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary (Information Report No. 70-11). Fish Commission on Oregon Coastal Powers Investigations.

DeGroot, S. J. 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behavior in flatfishes. Neth. J. Sea Res. 5(2):121-196.

Edwards, R., and J. H. Steele. 1968. The ecology of 0-group plaice and common dabs at Loch Ewe. I. Population and food. J. Exp. Mar. Biol. Ecol. 2:215-238.

Emlen, J. M. 1984. Population biology: The coevolution of population dynamics and behavior. Macmillan Co., New York.

Forrester, C. R. 1969. Life history information on some groundfish species. J. Fish. Res. Board Can. Tech. Rep. No. 105.

Frame, D. W. 1974. Feeding habits of young winter flounder (Pseudopleuronectes americanus): Prey availability and diversity. Trans. Am. Fish. Soc. 2:261-269.

Fritz, E. A. 1974. Total diet comparison in fishes by Spearman rank correlation coefficients. Copeia 210-214.

Hancock, D. R. 1985. Umpqua Training Jetty Extension Monitoring Study (Final Report, IPA #E1844007). U.S. Army Corps of Engineers, North Pacific Division, Portland.

Hart, J. L. 1973. Pacific fishes of Canada. Fisheries Research Board of Canana. Ottawa. 740 p.

Hatanaka, M., M. Kosaka, Y. Sato, K. Yamaki, and K. Fuyui. 1954. Interspecific relations concerning the predacious habits among the benthic fish. Tohoku J. Agric. Res. 5:177-189.

Hewitt, G. R. 1980. Seasonal changes in English sole distribution: An analysis of the inshore trawl fishery off Oregon. M.S. Thesis. Oregon State Univ., Corvallis.

Hickman, C. P. 1973. Biology of the invertebrates. 2nd ed. C. V. Mosby, St. Louis. 757 p.

Hogue, E. W. 1982. Seasonal changes in the abundance and spatial distribution of a meiobenthic assemblage on the open Oregon coast and its relationship to the diet of 0-age flatfishes. Unpublished doctoral dissertation, Oregon State Univ., Corvallis.

Hogue, E. W., and A. G. Carey, Jr. 1982. Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon coast. Fish. Bull. 80(3):555-565.

Horn, H. J. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100(914):419-424.

Hulberg, L. W., and J. S. Oliver. 1979. Prey availability and the diets of two co-occurring flatfish. In C. A. Simenstad and S. J. Lipovsky (editors), Fish food habits studies: Proceedings of the 2nd Pacific Northwest Technical Workshop, October 10-13, 1978. Univ. of Washington Press, Seattle. 29-36.

Hurtubia, J. 1973. Trophic diversity measurement in sympatric predatory species. Ecology 54:885-890.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven.

Ketchen, K. S. 1956. Factors influencing the survival of the lemon sole (Parophrys vetulus) in Hecate Strait, British Columbia. Fish. Res. Board Can. 13:647-694.

Kravitz, M. J., W. G. Pearcy, and M. P. Guin. 1977. Food of five species of co-occurring flatfishes on Oregon's continental shelf. Fish Bull. 74(4):984-990.

Kreuz, K. F., A. V. Tyler, G. H. Kruse, and R. L. Demory. 1981. Variation in growth of Dover soles and English soles as related to upwelling. Trans. Am. Fish. Soc. 111:180-192.

Kruse, G. H., and A. V. Tyler. 1983. Simulation of temperature and upwelling effects on the English sole (Parophrys vetulus) spawning season. Canadian Journal of Fisheries and Aquatic Science 40:230-237.

Laroche, J. A., and R. L. Holton. 1979. Occurrence of 0-age English sole, Parophrys vetulus, along the Oregon coast: An open coast nursery area? Northwest Sci. 53:94-96.

Levings, C. D. 1974. Seasonal changes in feeding and particle selection by winter flounder (Pseudopleuronectes americanus). Trans. Am. Fish. Soc. 4:828-832.

Light, S. F. 1975. Light's manual: Intertidal invertebrates of the central California coast. 3rd ed. Univ. of California Press, Berkeley. 716 p.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. Am. Nat. 100:603-609.

Moyle, P. B. 1982. Fishes: An introduction to ichthyology. Prentice-Hall, Inc., Englewood Cliffs, N.J. 593 p.

Mullen, R. E. 1977. The occurrence and distribution of fish in the Umpqua River estuary, June through October 1972. Oregon Department of Fish and Wildlife Info. Report Series, Fisheries No. 77-3.

Nikolsky, G. W. 1963. The ecology of fishes. Academic Press, New York, London. 352 p.

Oliver, J. S., P. H. Slattery, L. W. Hulberg, and J. W. Nybakken. 1980. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. Fish. Bull. 78(2):437-454.

Pearcy, W. G. 1962. Ecology of an estuarine population of winter flounder, Pseudopleuronectes americanus (Walbalm). Food habits of larvae and juveniles. Bull. Bingham Oceanogr. Collect. Yale Univ. 18:1-78.

Pearcy, K. L., D. P. Bella, C. Sutterlin, and P. C. Klingeman. 1974, May. Descriptions and information sources for Oregon estuaries. Sea Grant College Program, Oregon State Univ., Corvallis.

Pearcy, W. G., and D. Hancock. 1978. Feeding habits of Dover sole, Microstomus pacificus; rex sole, Glyptocephalus zachirus; slender sole, Lyopsetta exilis; and Pacific sanddab, Citharichthys sordidius in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 75:641-651.

Pearcy, W. G., and E. E. Krygier. 1980. Ecology of 0-age group English sole. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State Univ., Corvallis.

Peterson, C. H., and M. L. Quammen. 1982. Siphon nipping: Its importance to small fishes and its impact on growth of the bivalve Protothaca staminea (Conrad). Exp. Mar. Bio. and Ecol. 63:249-268.

Pianka, E. C. 1978. Evolutionary ecology. 2nd ed. Harper & Row, New York. 397 p.

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York. 286 p.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California water. Calif. Fish Game Fish Bulletin 152:1-105.

Rae, B. B. 1956. The food and feeding habits of the lemon sole. Scott. Home Dep. Marine Res. (3) 32 p.

Richardson, S. L., and W. G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay. Ore. Fish. Bull., U.S. 75:125-145.

Rosenberg, A. A. 1981. Growth of juvenile English sole, Parophrys vetulus, in estuarine and open coastal nursery area. Unpublished master's thesis, Oregon State Univ., Corvallis. 51 p.

Rosenberg, A. A., and W. G. Pearcy. 1980. The growth of English sole from two nursery grounds (Sea Grant Annual Report, 1979-1980, Project R/OPF-1). Oregon State Univ., Corvallis.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Univ. of Illinois Press. 117 p.

Snedecor, G. W. 1956. Statistical methods. 5th ed. Iowa State Univ. Press, Ames. 593 p.

Steele, J. H., A. D. McIntyre, R. R. C. Edwards, and A. Trevallion. 1970. Interrelations of a young plaice population with its invertebrate food supply. Symposiums of the British Ecological Society 10:315-388.

Tyler, A. V. 1972. Food resource division among northern marine demersal fishes. J. Fish. Res. Board Can. 29:997-1003.

Varoujean, D. H. 1984. Umpqua Training Jetty Extension Monitoring Study (Final Report to Portland District). U.S. Army Corps of Engineers, Portland.

Wakefield, W. W., and W. G. Pearcy. 1980. Feeding relationships within an assemblage of demersal and nektobenthic fishes on the Oregon shelf (Sea Grant Annual Report 1979-1980, Project R/OPF-1). Oregon State Univ., Corvallis.

Werner, E. E., and P. J. Hall. 1979. Foraging efficiency and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869-876.

Westrheim, S. J. 1954. Size composition, growth, and seasonal abundance of juvenile English sole (Parophrys vetulus) in Yaquina Bay. Research Briefs of the Fish Commission 7:73-79.

Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52:336-342.