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Opportunistic Life Histories and Genetic Systems in Marine Benthic Polychaetes[1]

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ABSTRACT

The decline in benthic marine fauna following an oil spill in West Falmouth, Massachusetts, permitted us to follow the responses of a number of polychaete and other invertebrate species to an environmental disturbance. Species with the most opportunistic life histories increased and declined at the two stations with the greatest reduction in species diversity. The stations with an intermediate reduction in diversity showed increases and declines of somewhat less opportunistic species. Electrophoretic studies of the malate dehydrogenase loci of the most opportunistic species, *Capitella capitata*, indicated short-term selection for a single genotype in the large populations present in Wild Harbor following the oil spill. The life histories of the most opportunistic species are summarized. Initial response to disturbed conditions, ability to increase rapidly, large population size, early maturation, and high mortality are all features of opportunistic species. Using these criteria, the species are ranked in order of decreasing degree of opportunism as: 1. *Capitella capitata*, 2. *Polydora ligni*, 3. *Syllides verrilli*, 4. *Microphthalmus aberrans*, 5. *Streblospio benedicti*, 6. *Mediomastus ambiseta*. We propose using mortality as the best single measure of degree of opportunism. A definition based on mortality emphasizes the portion of the life cycle involved in adaptation through short-term selection. Two types of marine benthic opportunists are described: 1. a mixed strategy variety with obligate planktonic dispersal where selection within local subpopulations occurs in a single generation, 2. a response-to-selection type with direct development or settlement shortly after release from brood structures allowing selection within local populations through more than one generation.

1. INTRODUCTION. Species may be classified according to the response of populations to differing scales of temporal and spatial heterogeneity (Frank 1968). Those species that can rapidly respond to open or unexploited habitats

have variously been called opportunistic (MacArthur 1960, Hutchinson 1967); fugitive (Hutchinson 1951); colonizing (Lewontin 1965); weedy (Baker 1965, Harper 1965) or r-selected (MacArthur and Wilson 1967). Some of their characteristics are: 1. lack of equilibrium population size (MacArthur 1960); 2. density-independent mortality (King and Anderson 1971, Gadgil and Bossert 1970); 3. ability to increase rapidly or high r (Lewontin 1965, MacArthur and Wilson 1967); 4. high birth rate (Hairston, Tinkle and Wilbur 1970); 5. poor competitive ability (Hutchinson 1951, MacArthur and Wilson 1967, Pianka 1972); 6. dispersal ability (Hutchinson 1951, Baker 1965); 7. high proportion of resources devoted to reproduction (Gadgil and Bossert 1970).

None of these features alone is adequate to define an opportunist. For example, MacArthur (1960) equates an opportunist with a species which does not reach equilibrium. Yet, even extreme opportunists may appear to be at equilibrium under optimum circumstances. Similarly, a non-opportunistic species will be in nonequilibrium state following a disturbance. Wilson and Bossert (1971) propose a preferable, broader definition, defining an opportunist (r-strategist) as a species "adapted for life in a short-lived unpredictable habitat" by relying on a high r to make use of ephemeral resources. In a new habitat such a species would: "1. discover the habitat quickly, 2. reproduce rapidly to use up the resources before other, competing, species could exploit the habitat, and 3. disperse in search of other new habitats as the existing one began to grow unfavorable." This is similar to Mozley's (1960) definition of pests or species invading disturbed areas: "1. They occupy new territory readily. 2. Their rate of reproduction is relatively high, so that— 3. They tend to take over the exclusive occupancy of a disturbed area i.e. they become predominants. 4. They are transient (or fugitive) features in a landscape. They seldom continue to occupy a site exclusively for a long period of time." In the subsequent discussion we will refer to such species as opportunists or relatively opportunistic. This avoids confusion with the more narrowly defined processes of r-selection and K-selection (Hairston, Tinkle and Wilbur 1970, MacArthur 1972, Roughgarden 1971).

The tremendous reduction in benthic marine fauna that resulted in the aftermath of an oil spill in West Falmouth, Massachusetts permitted us to follow the response of a number of polychaete and other invertebrate species to an environmental disturbance. Our findings for one of the most opportunistic species, *Capitella capitata*, strongly suggest that genetic variation and high mortality resulting in intense selection are important components of adaptation to unpredictable environments. We propose using mortality as a measure of the degree of opportunism. A definition based on mortality emphasizes the portion of the life cycle involved in adaptation through short-term selection. High mortalities and intense selection each generation would evolve under circumstances where a general purpose genotype would be at a selective disadvantage, i.e., in an unpredictable environment (Grassle 1972).

2. METHODS. Following a spill of #2 fuel oil off Fassetts Point in West Falmouth September 16, 1969, a series of intertidal and subtidal stations were established in Wild Harbor and along the Wild Harbor River (Sanders, Grassle and Hampson 1972). Figure 1 shows the sampling localities; intertidal Stations II, IV and V along the Wild Harbor River estuary, Station 31 in the inner harbor at 3 m depth, Station 9 at about 10 m depth, Station 10 at 13 m depth and Station 20 at 7 m depth.

A 1/130 m² corer was used to sample the intertidal river stations and a 1/25 m² van Veen grab was used at the subtidal stations. All samples were washed through a 0.297 mm standard mesh screen, preserved in 5% formalin and transferred to 80% ethanol after 24 hours. All animals were stained with rose bengal and removed under a dissecting microscope from sediment and detritus retained by the screens.

Experiments were set up in the field using mud from an unoiled area made

Figure 1. Localities sampled following the West Falmouth oil spill, Sept. 16, 1969.

azoic by freezing and thawing. The animals killed in the freezing and thawing rapidly decompose so that they are readily distinguished from animals preserved alive. A m² surface area box of sediment (100 × 100 × 10 cm) was placed level with the surrounding sediment at Wild Harbor Station IV in May of 1970. During each sampling period four 4 × 4 cm samples were taken in the lower left corner of 10 cm quadrats picked at random from a 10 × 10 grid. In June, 1970 1/4 m² boxes (50 × 50 × 10 cm) were placed at Wild Harbor Station IV and in a similar environment at Greater Sippewissett Marsh, an area not affected by the oil spill. Paired 2 × 2 cm cores were taken in 5 × 5 cm quadrats chosen at random approximately every three days for one month, then every week.

Samples of the polychaete worm *C. capitata* were collected at Wild Harbor Station II in December of 1969, frozen and stored at −30°C for electrophoretic studies. Other collections of *C. capitata* were made at Wild Harbor Station IV in July, 1970 and April, 1971; at Wild Harbor Station 31 in July and August, 1970, and at Greater Sippewissett Marsh in August, 1970. Samples of 26–163 worms were sorted from the sediment alive, homogenized and electro-
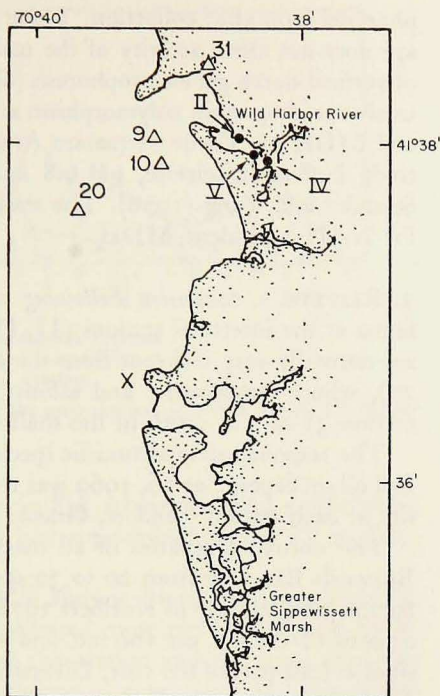
phoresed soon after collection. These analyses indicated that freezing and storage does not affect activity of the malate dehydrogenases. Standard techniques of vertical starch gel electrophoresis (Shaw and Koen 1968, Brewer 1970) were used to study protein polymorphism at two malate dehydrogenase loci (MDH 1 and MDH 2). Tissue extractant (tris-EDTA-NADP, pH 7.0) gel and electrode buffers (triscitrate, pH 6.8 and 6.3 respectively) were those used by Selander and Yang (1970). The staining mixture was that of Brewer (1970) for NAD dependent MDH.

3. RESULTS. a. *Succession Following an Oil Spill and Field Experiments.* The fauna at the intertidal stations (II, IV, and V) along the Wild Harbor River are normally very different from the offshore communities (Stations 9, 10, and 20), where temperature and salinity are less variable and more predictable. Station 31 at 3 m depth in the shallow inner harbor is intermediate.

The response of opportunistic species to conditions following the spill of #2 fuel oil on September 16, 1969 was related to the extent of reductions in diversity at each station (Sanders, Grassle and Hampson 1972).

The normal diversities of all macrofauna at the three offshore stations in Buzzards Bay vary from 20 to 30 species per 100 individuals (using the rarefaction methodology of Hurlbert 1971). The inner harbor Station 31 has diversities of 12–16 spp. per 100 ind. and intertidal Station IV reaches similar diversities at least part of the year. Diversities dropped to 1 sp. per 100 ind. at Station IV and 2 per 100 at Station 31. Further offshore, at Stations 9 and 10 diversities were reduced to 6 and 8 spp. per 100 ind. respectively and at Station 20 the minimum was 12 spp. per 100 ind. The most opportunistic species settled only at Station 31 and the river Stations II, IV and V. Stations 9 and 10 were less heavily affected and showed a different pattern from that found at the nearshore stations. The effect of the oil as reflected in faunal composition was even less marked at Station 20 (Sanders, Grassle and Hampson 1972).

At each station, species were ranked according to their time of appearance, rate of increase and decline. The animals discussed in the following pages, unless otherwise stated, are members of the polychaete component of the benthic fauna.

At the muddy sand flat Station IV, *Capitella capitata* increased most rapidly followed in order by *Microphthalmus aberrans, Polydora ligni, Syllides verrilli* and *Streblospio benedicti* (Fig. 2). In contrast to these relatively opportunistic species, adult *Nereis succinea*, although surviving the oil spill best, did not show the very large increase and decline characteristic of the other species. In all the more opportunistic species a high rate of increase was followed by a sharp decline. The maximum population size tended to be higher in the most opportunistic species, although this trend was reversed in the second, third, fourth, and fifth ranked species at Station IV. This reversal may be related to the average tolerance of the individuals to the continued presence of oil in the environment.
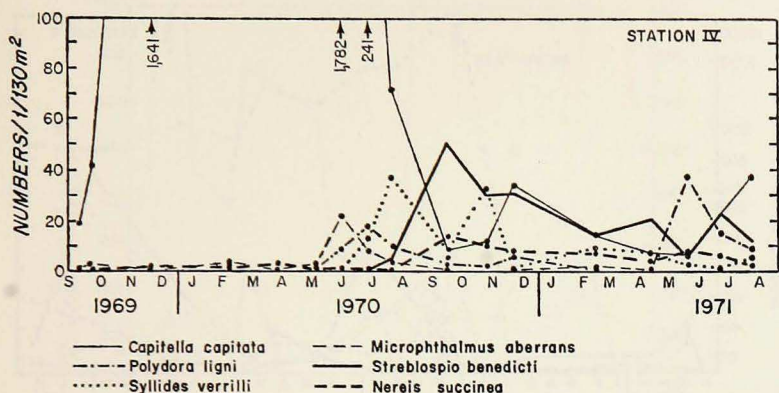
Figure 2. Abundance in numbers per 1/130 m² of the most common species at Station IV. Muddy sand flat at about mean low water.

All of the polychaete species not shown in Fig. 2 have less than 5 individuals per 1/130 m² except *Spio filicornis* which first appeared at Station IV in July, 1971.

Station 31 at 3 m depth outside the Wild Harbor River area showed a similar pattern (Fig. 3). *Capitella capitata* increased most rapidly followed by *P. ligni*. *Syllides verrilli* was not common at this station and the third most opportunistic species was *M. aberrans*. The time of appearance and rate of in-
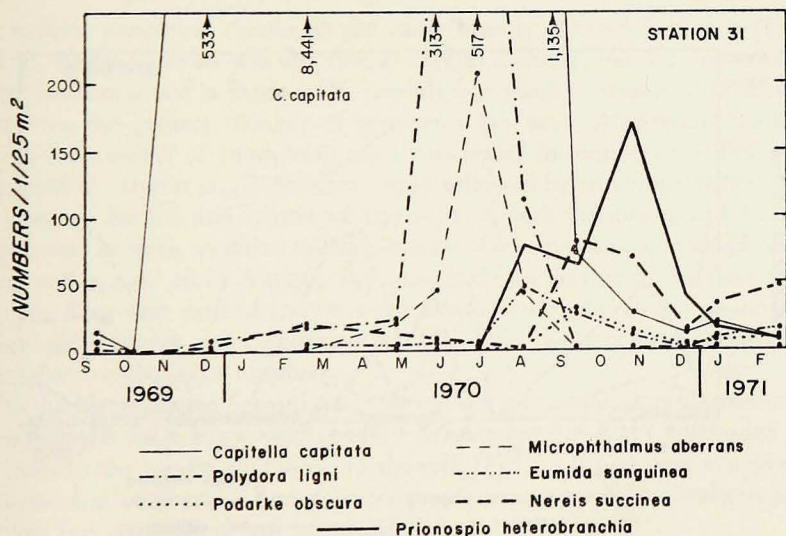

Figure 3. Abundance in numbers per 1/25 m² of the most common species at Station 31. Mud bottom at 3 m depth.

Figure 4. Abundance in numbers per 1/25 m² of the most common polychaete species at Station 9. Sandy mud bottom at about 10 m depth.

crease was directly related to the maximum population size. *Nereis succinea* followed a pattern similar to that at Station IV. It came in and stayed, not showing the large increase and almost complete decline characteristic of the more opportunistic species. The next most common species, *Platynereis dumerlii* and *Mediomastus ambiseta* (not figured) reached abundances of 21 ind. per 1/25 m².

The offshore Stations 9 and 10 have a different sequence of opportunists with

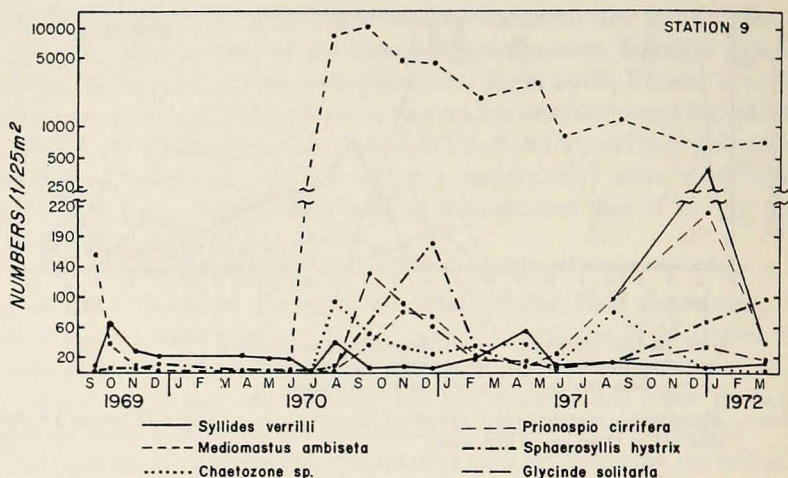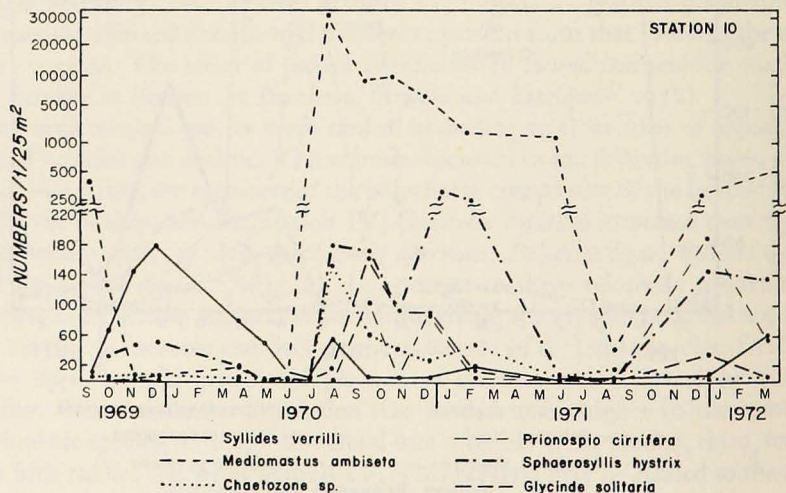Figure 5. Abundance in numbers per 1/25 m² of the most common polychaete species at Station 10. Sandy mud bottom at about 13 m depth.
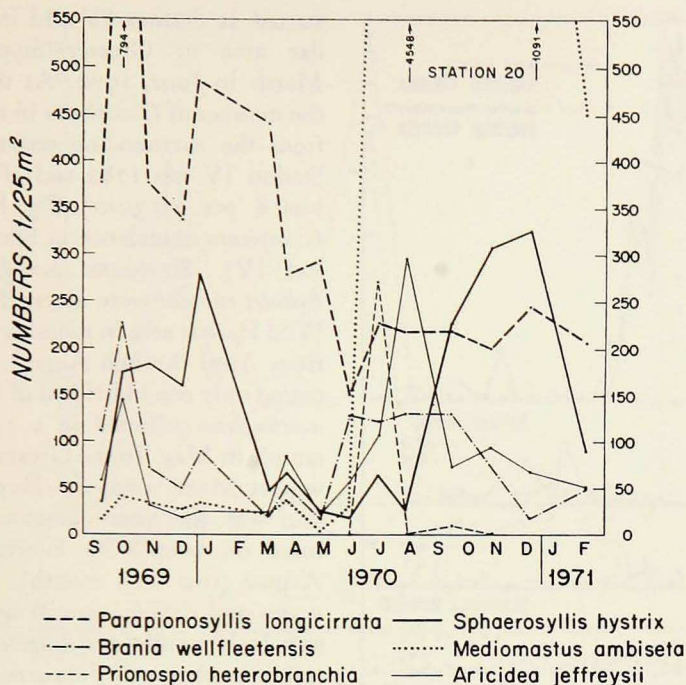
Figure 6. Abundance in numbers per 1/25 m² of the most common polychaete species at Station 20. Sandy mud bottom at about 7 m depth.

the pattern somewhat clearer at the more heavily affected Station 9 (Figs. 4 and 5). *Syllides verrilli* was the first species to increase, but did not reach the large numbers found at Station IV, possibly as a result of competition or predation from the greater number of species in this area. *Mediomastus ambiseta*, during the summer of 1970, very rapidly increased in numbers reaching a very high peak in August and September, 1970 followed by an abrupt drop in numbers during the fall and winter of 1970–71 at both Stations 9 and 10. This species may be quite sensitive to the presence of oil since a new infusion of relatively undegraded oil in August, 1971 resulted in a decline in numbers at Station 10. The next ranked species were *Glycinde solitaria*, *Prionospio cirrifera*, *Sphaerosyllis hystrix* and *Chaetozone* sp. The latter two species appear to show a seasonal oscillation in numbers.

At the least affected Station 20 most species were continuously present but *Parapionosyllis longicirrata* and possibly *Mediomastus ambiseta* responded with increases to the conditions following the spill (Fig. 6). The extreme opportunists present at Stations IV and 31 were present in these offshore stations (9, 10 and 20) but occurred in low numbers.

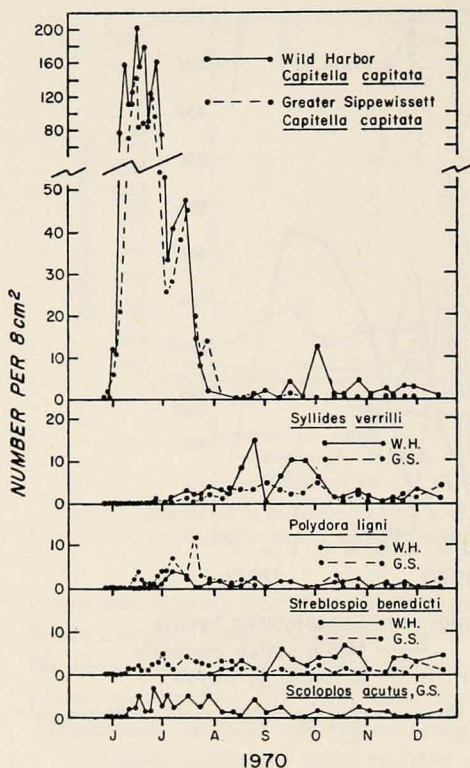The colonization experiments (1/4 m² boxes of unoiled sediment) were

Figure 7. Abundance in numbers per 8 cm² of polychaete species settling in experimental boxes of azoic mud. *Scolopolos acutus* was not found in Wild Harbor.

started at Station IV and in a similar area in Greater Sippewissett Marsh in June, 1970. At this time the number of *C. capitata* in a sample from the surrounding sediments at Station IV was 1782 and of *P. ligni* was 8 per 1/130m² (Fig. 8 shows *C. capitata* abundance at Stations II and IV). *Streblospio benedicti* and *Syllides verrilli* were absent from the Wild Harbor area in monthly samples from April through August. In this period only one individual of *Scoloplos acutus* was collected in a 1/130 m² sample in May. In the Greater Sippewissett Marsh area, *Streblospio benedicti* was the most common species based on samples in February and August (two each month). *Scoloplos acutus* and *Syllides verrilli* were present both months and *Capitella capitata* was absent in February.

Despite the differences in background numbers, both areas showed the marked initial increase in *C. capitata* (Fig. 7). Each species appeared first as postlarval juveniles settling from the plankton. If the two areas are considered together, *P. ligni* responded next most rapidly followed by *S. verrilli* and *S. benedicti*. When Greater Sippewissett is looked at separately, the responses of *P. ligni*, *S. benedicti* and *S. acutus* were similar. Although the background numbers affected the rate of response, the sequence was very similar in the two areas. The main difference was in *S. acutus*, the only species in the list without planktonic larvae.

Fig. 8 shows the number of *C. capitata* at Stations II, IV and V along the mud and sand flats bordering the Wild Harbor River Marsh. Station II is a muddy sand flat at about mean low water and is normally dominated by the bivalve, *Gemma gemma*. Station IV is a muddier sand area at mean low water and Station V is a muddy area just above mean low water along the river bank. The *C. capitata* at these three stations showed a similar increase in numbers followed by a decline coinciding with icing of the Wild Harbor River. The ice came in contact with the sediments at Stations II and IV only at low tide and the sediments did not freeze. Along the bank at Station V the ice was un-
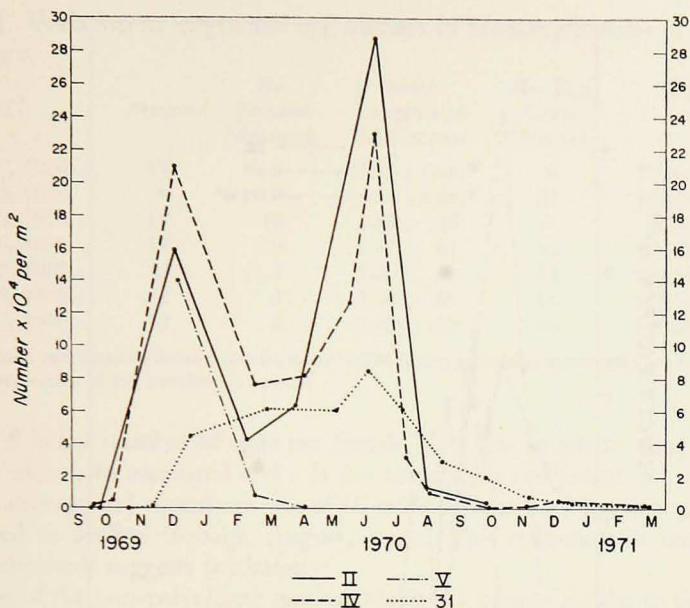
Figure 8. Numbers per m² of *Capitella capitata* at the three Wild Harbor River Stations and Station 31 (see Fig. 1).

even and the exposed sediment froze. This accounts for the disappearance of *C. capitata* at Station V while it continued to be present at Stations I I and IV. Large numbers of dead *C. capitata* were found in the sediment in February, 1970 suggesting that the kill resulted from the cold conditions rather than predation. The decomposing animals would probably have been used as a source of food for the deposit feeding *C. capitata* if the decline had resulted from resource depletion. Since only a few uncommon species were present in the winter, competitive interactions are also unlikely. The subtidal inner harbor Station 31 is not subject to the extreme low temperatures found intertidally. The numbers at this station did not show the bimodal peak and continued to rise throughout the winter reaching a peak coinciding with the second peak at the river stations.

After the spring increase, the decline resulted from any one or a combination of resource depletion, predation, and, possibly, accumulation of toxic metabolites. The sediments were almost entirely composed of faecal pellets of *C. capitata*. Estimates of predation rates were not possible but an examination of the stomach contents of the shrimp, *Crangon septemspinosus*, and the fish, *Fundulus heteroclitus* indicated that both were important predators.

By conducting additional experiments with azoic sediment we were able to study the role of depletion of food resources in population decline. In May, 1970 a 100 × 100 × 10 cm box of azoic sediment was placed at Station IV.
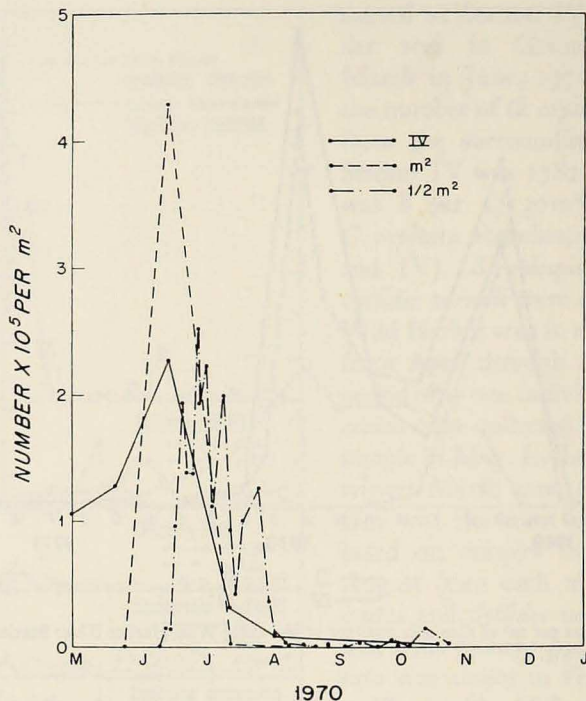
Figure 9. Abundance in numbers per m² of *Capitella capitata* in two experimental boxes of azoic sediment placed at Station IV. The solid line shows the background numbers of *C. capitata* in the surrounding sediments at Station IV.

The number of *C. capitata* increased to greater than 400,000 per m² within a month (Fig. 9). Concurrent with the population peak in the first box, a second box (50 × 50 × 10 cm) was placed at the same locality. While the numbers in the first box were crashing the second box increased to nearly 250,000 per m² remaining at over 100,000 per m² when the numbers in the first box were nearly zero. Since no significant numbers of competitors or predators occurred in either box the decline in density in the first box resulted from a density-dependent depletion of food resources or accumulation of toxic substances.

The role of food resource depletion was also indicated by a decreased fecundity and a smaller size for mature females at high population densities. Table 1 shows the decrease in size of brooding females accompanied by a reduction in egg number per female. Fig. 10 illustrates this reduction in egg number per female during the population increase at Station 31 and during the population peaks at the river stations. There is a linear correlation of egg number per female with length of adult females with broods:

$$E = 59.22\,L - 112.92 \quad \text{with} \quad N = 41 \quad \text{and} \quad r = .855.$$

Table I. Variation in length and egg number in brooding females of *Capitella capitata*.

Date	Station	No. Females Measured	Mean Length and S.D. in mm	No. Egg Cases Counted	Egg No. and S.D.
Dec. 7, 1969...	IV	0	(3.17 ± 1.88)*	6	180.50 ± 40.02
Jan. 3, 1970...	V	0	(4.03 ± 3.28)*	21	161.48 ± 62.13
May 20, 1970...	IV	10	$1.33 \pm .18$	45	55.67 ± 28.66
June 15, 1970...	IV	10	$1.27 \pm .01$	13	49.85 ± 18.54
Dec. 22, 1969...	31	7	$3.60 \pm .90$	14	493.57 ± 81.74
March 3, 1970...	31	5	$3.28 \pm .85$	14	301.14 ± 150.27
June 12, 1970...	31	9	$2.03 \pm .60$	10	146.90 ± 52.63

* On these two dates all females abandoned the tubes during processing and lengths are reconstructed from the regression of egg number on length.

Where E is the number of eggs per female, L is the length in mm, N is the number of worms measured and r is the correlation coefficient.

Both average and maximum size of all individuals at both Stations 31 and IV continued to decline through August, 1970. This reduction in numbers of large individuals suggests predation.

Three of the non-polychaete species exhibited a pattern similar to that of the most opportunistic polychaetes. The best example is the bivalve, *Mulinia lateralis*. Very small, recently metamorphosed juveniles of *M. lateralis* were present subtidally throughout the Wild Harbor area during the summer following the oil spill. Their peak abundance occurred at Station 10 in August, 1970 (265
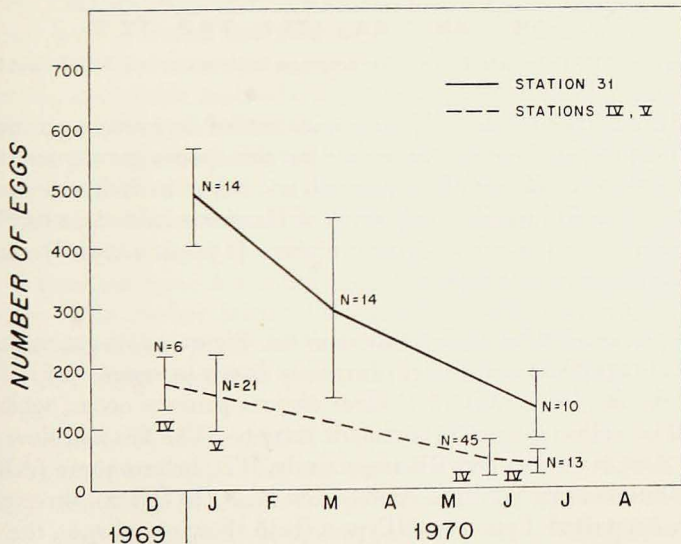
Figure 10. Egg number per brooding female at Stations IV, V, and 31.
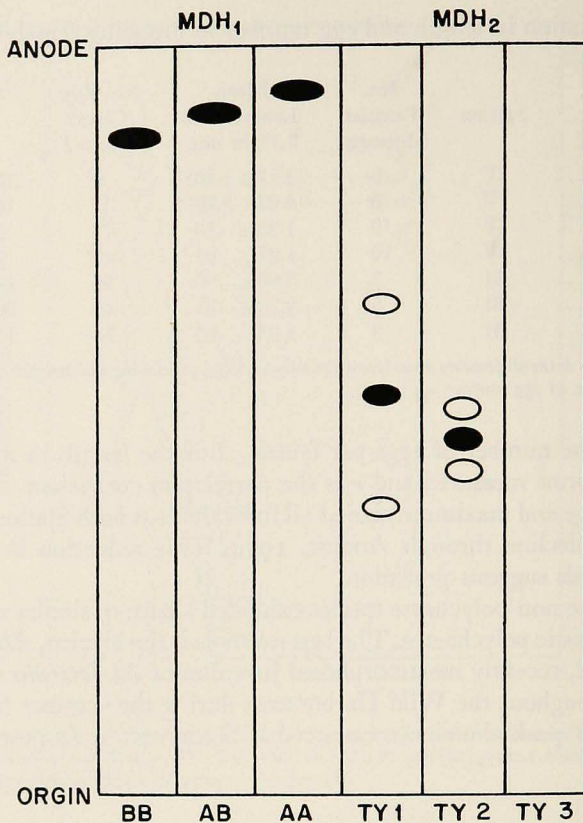
Figure 11. Diagram of NAD-dependent malate dehydrogenase bands at two loci, MDH 1 and MDH 2.

per 1/25 m²). Another bivalve, *Macoma tenta* settled in even larger numbers (2,554 per 1/25 m²) at about the same time but this species grows more slowly, so that by the time *M. lateralis* had spawned, and begun to decline in numbers, the *M. tenta* were still juveniles. Postlarvae of *Haminoea solitaria*, a tectibranch gastropod, also were present in large numbers (151 per 1/25 m²) and subsequently declined at Station 31.

b. *Electrophoretic Studies of Capitella capitata*. Figure 11 diagrams the position of NAD-dependent malate dehydrogenase bands in samples of individual worms. At the fast locus (MDH 1) three distinct patterns occur, which fit a hypothetical two allele system for a dimeric enzyme. The fast and slow homozygotes are designated AA and BB respectively. The heterozygote (AB) band occupies an intermediate position. At the slow locus (MDH 2), three patterns were found, designated Type 1 and Type 2 (both showing 3 bands, the middle one heavily stained and the other two bands faintly stained); and Type 3,

Table II.

Location and Date	Total Number of Individuals	Fast Locus MDH 1			Slow Locus MDH 2		
		BB	AB	AA	Type 1	Type 2	Type 3
Wild Harbor Station II December 1969	76	.987	–	.013	.381	–	.619
Wild Harbor Station IV July 1970	40	1.000	–	–	–	–	1.000
Wild Harbor Station IV April 1971	26	.538	.462	–	.307	.462	.231
Wild Harbor Station 31 July-August 1970 . . .	53	.962	.038	–	–	–	1.000
Gr. Sippewissett Marsh August 1970.	163	.994	.006	–	.245	.006	.749

where no activity occurred. The patterns found at this locus do not ob-
viously fit a simple genetic system. Since the simplest explanation is a two-
allele system with one of the alleles silent, the three patterns will be referred
to as products of a single locus.

Table 2 shows the frequencies of the various MDH genotypes at the fast
and slow loci in worms collected at Wild Harbor and Greater Sippewissett
Marsh.

The electrophoretic study of collections from Wild Harbor intertidal stations
indicates two genotypes at each locus in December, 1969, when the *C. capitata*
population was at its peak, but only a single genotype at each locus in the July,
1970 sample collected after the second population peak (Fig. 8). A collection
from Station 31 at the same time as the July Station IV sample revealed two
individuals variant from the single July Station IV genotype at the MDH
locus. These genotypic frequencies contrast with the frequencies for a collec-
tion from Wild Harbor Station IV taken in April, 1971 when conditions in
the marsh were closer to normal and the numbers of *C. capitata* were very low.
At this time there were two genotypes common for MDH 1 and three for
MDH 2.

The presence of single MDH 1 and MDH 2 genotypes in Wild Harbor
worms collected in July, 1970, also contrasts with the two MDH 1 genotypes
(although one of the genotypes is represented by a single individual) and three
MDH 2 genotypes present in worms collected at Greater Sippewissett at the
same time.

4. DISCUSSION. a. *Ranking of Opportunists.* The relative degree of oppor-
tunism for the polychaete species can be determined from the time of appear-
ance, rate of increase and total mortality at the two most affected stations (IV
and 31), and in the experimental boxes at both Wild Harbor and Greater Sippe-
wissett intertidal areas. Their ranking is as follows: 1. *Capitella capitata* 2.
Polydora ligni 3. *Syllides verrilli* 4. *Microphthalmus aberrans* 5. *Streblospio
benedicti.* Offshore the ranking is *S. verrilli* (1) and *Mediomastus ambiseta* (2).
There is little doubt about the rank of the two most opportunistic nearshore
species, but the order of the next three species may vary according to the hab-
itat studied or time of year. Neither *C. capitata* nor *P. ligni* were very responsive
to substratum differences whereas *S. verrilli*, *M. aberrans* and *M. ambiseta* have
more distinct habitat preferences. After the spill, *C. capitata* was present in al-
most equal numbers in sandy and muddy areas (Fig. 8). Wolff (1973) also
showed that *C. capitata* was not very responsive to sediment differences, and
Reish (1971) even found *C. capitata* settling on blocks of wood placed 1 m
above the bottom in Los Angeles Harbor. *P. ligni* like *C. capitata* settled prima-
rily on muds or muddy sands but it is also known from hard substrata such as
shells. *Microphthalmus aberrans* is normally present on well-sorted sands (Wolff
1973, Westheide, 1967), but is also found in muddy sand.

In a study of benthic succession, Reish (1962) followed the sequence of
species settling in a boat channel in Southern California following dredging.
Capitella capitata and *P. ligni* reached a maximum four months after dredging
and were not present during the subsequent two years of the study. The area is
normally dominated by *M. ambiseta.*

In an analysis of the data of Reish and Winter (1954), Wass (1967) ranked
the species from Alamitos Bay in Southern California as indicators of organic
pollution. He lists them in order as *C. capitata*, *P. ligni*, *S. benedicti* and *N. suc-
cinea* on the basis of abundance and presence in the most polluted stations. The
only difference between this and our successional ranking from Wild Harbor,
is in the absence of *S. verrilli* and *M. aberrans.* If these, or related species, had
been present in Alamitos Bay they would probably have been missed by the
relatively coarse (0.85 mm) screens used in the study. *Capitella capitata*, *P.
ligni*, *N. succinea* and *S. benedicti* characterize the most polluted areas in San
Francisco Bay (Felice 1959). *Capitella capitata* numerically dominated the
most polluted areas of the Long Beach-Los Angeles Harbors while *Polydora
paucibranchiata*, *Dorvillea articulata* and *Cirriformia luxuriosa* were the abun-
dant species in less polluted zones (Reish 1959). When bottles of fresh sediment
were placed in these same harbors, *C. capitata*, *Podarke puggettensis*, *P. pauci-
branchiata* and *D. articulata* settled in that order (Reish 1961). In polluted parts
of Gothenburg Harbor, Sweden, *C. capitata* is the most abundant species fol-
lowed by *Polydora ligni* (*Polydora ciliata* = *Polydora ligni* – Rasmussen, 1973),
Nereis diversicolor and *Scolelepis fuliginosa* (Tulkki 1968). In the recovery of
a Swedish fjord following the closing of a pulp mill the pioneer species settling

in formerly azoic areas were *C. capitata* and *S. fuliginosa* (Rosenberg 1972). In the repopulation of the Raritan River Estuary, *P. ligni*, *S. benedicti*, *N. succinea* and the bivalve *Mya arenaria* were the most abundant colonists the first year and three subsequent years (Dean and Haskin 1964). The absence of *C. capitata* as well as *S. verrilli* and *M. aberrans* may be an artifact resulting from the large-meshed screens (1.5 mm) used in processing the samples.

In summary, the rank of abundance in polluted areas or the sequence of settlement of azoic areas results in a similar sequence of species with *Capitella capitata* first, followed by *Polydora ligni* (= *P. ciliata*) or another spionid species, *Streblospio benedicti* in North America and *Scolelepis fuliginosa* in Europe. *Syllides verrilli* and *Microphthalmus aberrans* and their relatives are likely to have been overlooked in other studies owing to their small size. The following sections consider the life histories of the most opportunistic species from the Wild Harbor study. Emphasis is placed on *C. capitata* since its life history has been studied in the greatest detail.

b. *Capitella capitata.* This species is known from a variety of habitats. It is not only an indicator of pollution but also an indicator of unpredictable environments in shallow-water areas all over the world in both high and low latitudes (c.f. Muus 1967, Schulz 1969, Wolff 1973).

The species is known from areas of normal disturbance such as basins following a period of oxygen depletion (Leppakoski 1969), in clumps of detached algae (Muus 1967, Wolff 1973) and in parts of estuaries where the greatest mixing and heavy sedimentation occurs (Wolff 1973). It is even found in numbers up to 60,000 per m² at depths below 200 m (up to 637 m) off California where freshwater aquifers disturb the normally highly diverse deep-sea fauna (Hartman 1961). Where *C. capitata* is common in these deep-sea samples the other kinds of animals are absent or uncommon.

In the Oresund, Henriksson (1969) demonstrated a linear correlation (r = .929, N = 37) between counts of bacterial indicators of pollution and the abundance of *C. capitata*. It is common in harbors (Bellan 1967, Felice 1959, Reish 1959, Tulkki 1968). present near sewage outfalls (Henriksson 1969, Kitamori and Funae 1959, Kitamori and Kobe 1959, Reish 1956), and in bottoms where pulp mill effluent is discharged (Bagge 1969, Pearson 1972, Rosenberg 1972), in sludge dumps (Halcrow, Mackay and Thornton 1973), subtidal excavations (Eagle and Rees 1973), and in sediments contaminated by oil (Reish 1965, Sanders, Grassle and Hampson 1972). In Kingston Harbor, Jamaica, Wade, Antonio and Mahon (1972) found gradual replacement of the normal fauna with a community dominated by *C. capitata.*

Capitella capitata and the other relatively opportunistic species discussed may be continuously present if the environment is unpredictable or may disappear as in the case of recovery following the oil spill. In normal estuarine areas similar to Station IV, *C. capitata* is present in low numbers. Sanders, Mangelsdorf

and Hampson (1965) found this species patchily distributed in the muddy portions of estuaries. In 21 samples from seven stations in the Pocasset River Marsh, *C. capitata* was present in only two, at densities of $250/m^2$ and $1500/m^2$. The population studied by Tulkki (1968) is thought from examination of records at the Gothenburg Museum to have been present since 1922.

Both large population size and a high reproductive rate are advantageous in an unpredictable environment (Slobodkin 1972). The species responding to the disturbed environment following the oil spill (or in the experiments) have a high rate of increase, high mortality and large population size. For *C. capitata* to achieve large population sizes, the populations of other species must be reduced or absent suggesting that it is a poor competitor (Barnard 1970, Hartman 1961, Leppakoski 1969). The Wild Harbor oil spill study indicates *C. capitata* is present in low numbers or absent wherever samples are more diverse, presumably as a result of competition and/or predation (Sanders, Grassle and Hampson 1972).

Capitella capitata fits the definitions of Wilson and Bossert (1971) and Mozley (1960) quite closely. It is able to discover new habitats quickly through planktonic larvae which are produced primarily in the summer but may be present all year. Benthic larvae are produced as well, and by this alternative mode of reproduction *C. capitata* can rapidly exploit local concentrations of organic matter. When present, *C. capitata* is usually the numerically dominant species and frequently it plays the role of a transient or fugitive species.

The life history is quite variable. Egg number in our field studies varies from 6 to over 600 (Muus 1967, found an average of 130 eggs). In the laboratory under conditions of severe resource depletion we have found as few as 2 eggs in egg cases of very small mature females. The adults can produce one or several broods (in contradiction to the generalization that *r*-selected species have a single reproductive period each generation—Pianka 1970). Adult size can vary from about 1 mm (under laboratory conditions of resource depletion) to 100 mm (Fauvel 1927—the largest we have seen are about 30 mm). The time to maturity is fairly constant at about 30–40 days (literature estimates are 30–60 days), thus emphasizing the importance of rapid maturation in opportunistic species even where resources permit production of only a few eggs.

Newly settled larvae have been observed from April through November They have been observed in the Woods Hole plankton in June (Simon and Brander 1967), in spring in the Isefjord, Denmark (Rasmussen 1973), and in late summer and early fall in the Elbe Estuary (Giere 1968). In Wild Harbor settlement of planktonic larvae has been observed in both winter and summer with the greatest settlement from May to October. Larvae have been collected from the plankton essentially year around in the Oslofjord (Schram 1968), at Banyuls sur mer (Bhaud 1967) and the Gulf of Marseille (Casanova 1953). Possibly the planktonic larvae are produced only in dense populations or when food is scarce.

Sexes are normally separate with the males readily distinguished by large copulatory setae on the eight and ninth setigers. In laboratory and field populations we have found that some genetically distinct individuals change sex from male to female and may be self-fertilizing before the transition is complete. This is of obvious advantage to individuals where the pattern of dispersal and the distribution of suitable habitats results in only a few individuals reaching a particular unexploited habitat.

Population size in *C. capitata* is controlled both by density dependent and density independent causes. Rather than classify life histories on the basis of density independent or density dependent mortality, it is more informative to know whether mortality has been selective as a short-term adaptive response to a unique set of conditions. Density independent mortality is not necessarily random removal of individuals nor is selection necessarily density independent (Charlesworth 1971, Roughgarden 1971, Clarke 1972).

The cosmopolitan distribution and broad tolerance of *C. capitata* cannot be explained solely on the basis of the average tolerance range of individual animals. The species has been collected from waters with salinities from 0.3°/oo to 36°/oo and is known from tropical and boreal environments. In Buzzards Bay where we have observed it reproducing all year, the water temperature ranges from −0.5° to 27°C (Driscoll 1972). *Capitella capitata* can withstand low oxygen and a variety of conditions toxic to other organisms. Yet despite this pattern of distribution, laboratory studies do not show unusual ranges of tolerance to any of these environmental variables. For example, Reish (1970) compared *C. capitata* with three other species of polychaetes on the basis of their tolerance to different concentrations of nutrients, salinity and oxygen. *C. capitata* was most sensitive to increased concentrations of silicates, second most sensitive to reduced oxygen conditions, and the most tolerant of increased phosphates and reduced salinities. Henriksson (1969) found *C. capitata* to be less tolerant of low oxygen conditions than *Nereis diversicolor* or *Scoloplos armiger*. Mangum and Van Winkle (1973) demonstrated that *C. capitata* had no unusual regulatory ability in decreasing oxygen concentrations (although Mangum, personal communication, found that *C. capitata* could repay an oxygen debt whereas *P. ligni* could not). Laboratory studies do not reveal any unusual tolerance to toxic chemicals such as detergents (Bellan, Reish and Foret 1972, Kaim-Malka 1970), and the Wild Harbor studies (Sanders, Grassle and Hampson 1972) indicate that *C. capitata* is more sensitive to high concentrations of oil than *Nereis succinea*. These studies suggest that short-term selection from the range of genotypes available for settlement may be more important in adaptation than the range of tolerance of the average individual.

c. *Polydora ligni*. *Polydora ligni* produces large numbers of planktonic larvae that are present in the plankton of the Woods Hole area from March until September (Simon 1967). In a study of larval abundance in the Oslofjord, Schram

(1968/1970) found *Polydora ligni* (= *P. ciliata*, Rasmussen 1973) to be the most abundant larval species every month of the year except December. *Polydora ligni* is also the most abundant larval polychaete of the Elbe Estuary (Giere 1968). In Maine waters, egg capsules have been collected from April to July with up to 132 eggs per capsule. The developing larvae sometimes use other eggs as a food source (adelophagia). Simon (personal communication) finds the number of capsules ranging from 4–29 with up to 216 eggs per capsule, or 26–86 3-setiger larvae per capsule in the Woods Hole area. This agrees well with observations in the Isefjord of up to 30 capsules with 25–225 eggs per capsule (Rasmussen 1973). Two or more broods may be produced by each female in a season (Blake 1969, Daro and Polk 1973). The life cycle may be completed in six weeks (two weeks in the plankton and three weeks to maturity following settlement (Daro and Polk 1973). Some adults live for at least a year.

d. *Syllides verrilli.* In the syllid subfamilies Exogoninae and Eusyllinae sexually mature representatives develop swimming setae. In the Wild Harbor study, individuals of *S. verrilli* were observed to have swimming setae at all seasons of the year. Yet, for six other less common eusyllid and exogonid species included in the same study, reproduction was more seasonal and the eggs developed attached to the female. Although hundreds of individuals have been examined, eggs have not been observed attached to the adult as in other members of these two subfamilies (Squadroni and Grassle in preparation). This suggests a short planktonic development in *S. verrilli.*

e. *Microphthalmus aberrans.* *Microphthalmus aberrans* deposits its eggs in a mucous mass and the resulting trochophores have a short larval life (Westheide 1967). Each female produces about 400–500 eggs and the species is hermaphroditic with sperm produced in the anterior and eggs in the posterior segments. Reproduction has been reported throughout the winter and spring months (Rasmussen 1956 1973, Westheide 1967) and the life cycle takes about 4–5 months. In the Wild Harbor area, winter water temperatures are lower than in Europe and settlement occurs only in the summer months.

f. *Streblospio benedicti.* *Streblospio benedicti* has a life history similar to *P. ligni* but the period of spawning is shorter. Larvae have been collected in the Woods Hole area in September (Simon and Brander 1967) and in Connecticut spawning occurs in the Mystic River Estuary from June to October (Dean 1965). In our collections egg numbers varied from 144 to 365 and reproduction was observed from May to October. Maturity is reached in about a month following settlement. The eggs are incubated in brood pouches for 4–5 days and pelagic life is usually less than three days but may be up to two weeks (Dean 1965). Individual adults can reproduce more than once in a season.

g. *Nereis succinea*. *Nereis succinea* grows to a much larger size and lives longer than the other polychaete species discussed here in detail. Unlike the more opportunistic species *N. succinea* requires nearly a year to reach maturity. Egg numbers are of the order of one million. Fertilization takes place in the plankton from June to September (Pettibone 1963). This species is very tolerant of polluted environments, but adaptation occurs at the individual level (the tolerance of the average individual is high). Thus, population response does not include the tremendous increase and decline in numbers characteristic of opportunists.

h. *Life History of Opportunists*. All of the polychaete species that responded most rapidly to environmental perturbations (*C. capitata*, *P. ligni*, *M. aberrans*, *S. verrilli* and *S. benedicti*) have planktonic larvae but they do not release large numbers of eggs into the plankton as, for example in *N. succinea* and the opportunistic bivalves (c.f. Levinton 1970). Instead, they have some sort of brood protection so that newly released larvae can settle to the bottom almost immediately or delay metamorphosis for widespread dispersal. The two spionids, *P. ligni* and *S. benedicti*, produce greater numbers of larvae than the others. *P. ligni* is generally the most abundant larval polychaete species in the near-shore plankton and is usually followed by other spionid species. *C. capitata* (and possibly *M. aberrans* and *S. verrilli*) produce larvae which may be either benthic or planktonic.

The important characteristic of the extreme opportunists is that each larva is important in building up the local population. This is somewhat at the expense of wide dispersal since the most widely dispersed species have no brood protection. The other two features are ability to respond to disturbance at any time of the year (*C. capitata*, *P. ligni*, and *S. verrilli* breed year around) and the short period required for maturation. In the sense of being able to rapidly exploit an open environment these species are certainly *r*-strategists.

i. *Definition of an Opportunistic Species*. We propose defining degree of opportunism both in terms of ability to respond to unpredictable events and the mortality rates sustained by the species (c.f. Grassle and Sanders 1973). We would ideally like to have instantaneous mortality rates, but the total mortality represented by the decline in numbers (or seasonal turnover) is sufficient to compare species. By utilizing mortality in our definition we can measure the relative opportunism of species whether or not the species are continuously present (Gadgil and Solbrig 1972, also include more than colonists in their definition of *r*-strategists). Furthermore, a definition based on mortality focuses on the part of the life cycle involved in short-term selection. By emphasizing the adaptive process there is no contradiction in the fact that many marine invertebrates have a high fecundity, yet, are relatively long-lived with low recruitment. These latter species have a high mortality in the dispersal phase (and may be thought of as opportunistic if the focus of interest is the plankton) but should

be regarded as specialist species after they settle on the bottom. High reproductive rate accompanied by a high death rate (c.f. Gadgil and Solbrig 1972) enables the species (or offspring of individuals of the species) to adapt through short-term selection.

Along a gradient of environmental predictability (at whatever spatial scale is being studied), each species has some point on the gradient where it is at peak abundance. On either side of this optimum the species is less common either because it is replaced by more specialist species (in the population sense) or are less able to survive under the more rigorous conditions on the less predictable side of the optimum. For a particular life history, populations on the less predictable side of the optimum will show greater variation in numbers (Green 1969).

The predictability of the environment is lowered if deviations from the mean occur sporadically and without autocorrelation within the life span of an individual. Changes occurring within the physiological tolerance of every individual, i.e., that do not result in mortality or reduced viability of some portion of the population do not affect predictability (Grassle 1972). For most species the variance and severity of sudden environmental change are sufficient to define differences in predictability (Slobodkin and Sanders 1969).

j. *Other Definitions.* Each of the seven characteristics of opportunists listed in the introduction are valid and may be used in comparisons between species. Other characteristics could be mentioned (Pianka 1970). Some criteria are difficult to apply without data from very large areas over a period of several generations. The results with *C. capitata* indicate that density independent vs. density dependent mortality or equilibrium vs. nonequilibrium population size is difficult to use in specific circumstances. The life history characteristics of populations such as fecundity, time to maturity, and total mortality are easier to follow and are less dependent on the environment studied.

k. *Short-term Selection.* There are many examples of adaptation through intense short-term selection (Ford 1964, Dobzhansky 1970, 1971). The importance of short-term selection for adaptation to local conditions has been documented in plants by Antonovics (1971, 1972) and Bradshaw (1971). Koehn and Mitton (1972) have demonstrated coadaptation to local environments at a single gene locus in two species of mussels. Selection for DDT resistance is another good example—it is far more likely in the relatively opportunistic pest species than in the pests' natural enemies (Georghiou 1972). Hebert, Ward and Gibson (1972) have shown that populations of the opportunistic limnetic crustacean *Daphnia magna* undergo short-term selection for electrophoretic variants at both malate dehydrogenase and esterase loci. Tamarin and Krebs (1972) document changes in gene frequencies at a transferrin locus during an increase and decline in vole populations which they attribute to short-term selection.

The life history features involving a combination of wide dispersal and short-term selection are likely to lead to high genetic variability (the gene-flow variation hypothesis of Soulé 1971). The large effective population size of most opportunists is in itself, a basis for maintenance of high genetic variability (Grassle 1972). Thus, high abundance, high reproductive rate and high mortality are all part of the life history of the opportunist. A high reproductive rate with planktonic larvae allows for wide dispersal and rapid exploitation of open environments. The high mortality is related to the short-term selection process in each local environment.

Our studies of the malate dehydrogenase loci indicate that changes in population size are assocaited with intense selection as predicted by Carson (1968), Mayr (1963) and Ford (1964). With *C. capitata* selection occurred during the population increase as well as during the decline. The variation at the loci observed the second year after the spill when *C. capitata* numbers were low is more representative of the variety of genotypes in the plankton (Table 2). We cannot demonstrate the relevance of the genotypic changes to the conditions present following the spill but we can say that the changes were in the direction of a single genotype. The population became monomorphic while the population was still very large—30,000/m². Populations in nearby unaffected localities were variable at the same time (Table 2). This indicates that selection rather than random loss of alleles resulted in the single genotype.

There are two major life history patterns in marine benthic opportunists. Each of the most opportunistic polychaetes are both able to disperse widely by means of planktonic larvae or rapidly exploit local resources through direct development or a brief planktonic existence. The brooding or other larval protection allows semi-isolated subpopulations to be maintained (and selection to occur) through several generations. Short-term selection in species with obligate planktonic development may only be important during a single generation as in *Mytilus edulis* (Koehn and Mitton 1972). In species such as *Mytilus edulis*, *Mulinia lateralis* and *Nereis succinea* the local differentiation of populations would be lost during the dispersal phase. The polychaetes with brood protection, *C. capitata*, *P. ligni*, *M. aberrans*, *S. benedicti*, *S. verrilli*, and (probably) *M. ambiseta*, may respond to selection in a particular direction for more than one generation as in Levin's (1965) "response to selection" species. Such species are more subdivided into genetically differentiated subpopulations with a shorter generation time and less individual homeostatic ability than Levin's "mixed strategy" species. The latter are more outcrossing species with obligate dispersal that prevents local genetic differentiation for more than a single generation.

Although the frequent extinction of subpopulations suggests the possibility of interdemic selection (Lewontin 1965) it is not necessary to explain the evolution of opportunistic life histories in this way. In an unpredictable environment an individual will contribute more genes to subsequent generations if its offspring are sufficiently variable so that some individuals of the next generation

will be of relatively optimum genotype. In other words, all individuals of an average genotype might succumb to an unpredictable event. Contribution to future generations may depend on the mating of individuals of different sub-populations. Maynard Smith (1971) in a discussion of the advantages of sexual reproduction, contrasts circumstances where the genetic variation would be important in short-term selection to those where variation is primarily critical in maintaining the long term evolutionary potential of the species. He concludes that the short term advantage of sex (the argument applies equally well to genetic variation in general) will be realized only if new environmental combinations arise each generation. This is the circumstance in which opportunistic species evolve. Even in populations generally at equilibria, a single period of intense selection may maintain an allele for a number of generations (Haldane and Jayakar 1963).

1. *Opportunists and Community Characteristics.* More predictable environments should have more specialized (less opportunistic) species and less predictable environments should have more opportunistic species (Slobodkin and Sanders 1969). This generalization is supported by the results presented.

The species with the most opportunistic life histories increased and declined at the two stations with the greatest reduction in species diversity, Stations IV and 31. The stations with an intermediate reduction in diversity (9 and 10) showed increases and declines of somewhat less opportunistic species. Johnson (1970) found that species collected in samples of low diversity, from habitats of relatively low predictability (along an intertidal gradient in Tomales Bay, California), respond most rapidly following a local disturbance.

MacArthur and Wilson (1967) and Pianka (1970) have argued for the greater importance of r-selection in temperate environments and K-selection in tropical environments. The carrying capacity, K, is usually expressed in units of population size (MacArthur and Wilson 1967) or density (MacArthur 1972, Pianka 1972). Contrary to some of the presentations of r-and K-selection, r does not vary inversely with population size (Slobodkin 1972).

To relate life histories of individual species to properties of communities it is necessary to consider population size (Grassle 1972). Communities with higher diversity generally have smaller average population size as may be inferred from the lack of dominance of a few species and the larger number of species (c.f., MacNaughton and Wolf 1970). In tropical bird communities there is a lower mean population size (Karr 1971) and reduced reproductive capacity (Cody 1966). This is in keeping with specialization in the more predictable parts of the tropics that results in occupancy of smaller three dimensional space (Howell 1971, Karr 1971, Kohn 1971, MacArthur 1972). The examples usually given for an inverse density-fecundity relationship in r- or K-selection come from studies of intraspecific decline in fecundity at increased densities (Fujita 1954, Lack 1966, Lotka 1925, Pearl and Parker 1922). This

relationship occurs in *C. capitata*, where reduction in egg number and size of adult affect the probability of survival less than increases in maturation time under conditions of food resource depletion. Differences in population size between species resulting from adaptation on a long-term evolutionary time scale however, are related to the degree of opportunism.

Some other measure of population size would be preferable to the use of local densities. We would ideally like to use effective population size (Grassle 1972) even though only comparative statements on the size of breeding populations are usually possible. The relationship between reproductive capacity and population size is in need of further study. From a detailed comparison of two land snail species, Randolf (1973) found that the species with the greatest reproductive capacity and greatest proportion of resources devoted to reproduction, had the largest population size as indicated by the dependence of the diversity indices on the abundance of this species. In the African cichlid fish, the populations of species belonging to the genus *Tilapia* are larger and have greater fecundities and rates of population growth in comparison to those of the genus *Haplochromis* (Fryer and Iles 1969). *Haplochromis* species are much greater specialists with respect to both food and habitat and the spectacular species diversities characteristic of the African Great Lakes results from radiation within this genus. The commercial species of fish with the highest reproductive rates are often those with the largest standing stocks. The numerically dominant pest species tend to have a greater reproductive capacity than other insects (Mozley 1960). The same is true of weed species. Total mortality (and hence the possibility for selection) is likely to be greater in species with a large population size.

Dominant species (in terms of abundance) are less opportunistic than true fugitives (in the sense that the species is never continuously present in the same place) but still survive by sustaining a high mortality and high reproductive capacity. Thus, *Mytilus edulis* appears more opportunistic than *Mytilus californianus* (c.f. Harger 1972) but both species are more opportunistic than many of the dominant subtidal bivalves (Levinton 1973). When a local environment has been predictable for a long period of time a less opportunistic species will become dominant. This is most easily observed in relatively predictable environments such as coral reefs where locally undisturbed areas become covered with single species of coral.

m. *Mortality and Demand-to-Resources Ratio.* The low demand-to-resources ratio (Pianka 1972) and high productivity-to-biomass ratio (Margalef 1963) found in communities characterized by species with high reproductive capacity is the product of a high turnover of individuals. Conversely, the lower productivity to biomass ratio of high diversity communities is a direct consequence of the longer life span of the species (Frank 1968). Owing to their relative inability to escape environmental extremes, terrestrial plants are frequently more

opportunistic than the most opportunistic of terrestrial animals. This is an explanation for the accumulation of plant material discussed by Hairston, Smith and Slobodkin (1960).

The poor competitive ability of the polychaete opportunists may result from a shortage of the most labile food components. A species such as *C. capitata* may digest only the parts of the sediment that may be most readily converted to tissue to sustain the high growth rate. In this way the species would be more severely limited by competition than other species. Tenore, Goldman and Clarner (1973) found that the more opportunistic *Mytilus edulis* is a much less efficient feeder than *Mercenaria mercenaria*.

n. *Zoogeography. Capitella capitata* and *Polydora ligni* (= *P. ciliata*) are cosmopolitan—in all oceans at all latitudes. *Streblospio benedicti* and *Nereis succinea* are widespread on the western and eastern coasts of North America and in Europe. *Microphthalmus aberrans* is known from both sides of the North Atlantic. Until recently, the species of *Polydora*, *Streblospio* and *Microphthalmus* have been thought to be different on either side of the Atlantic. Other opportunistic species are likely to be shown to be cosmopolitan as more detailed sampling of other regions is accomplished. Rasmussen (1973) has recently described *Mediomastus filiformis*, a species very similar to *Mediomastus ambiseta* known from the east and west coasts of North America (Hobson 1971). The genus *Syllides* is an exception since *Syllides verrilli* is known only from New England (see review by Banse 1971).

Although there is considerable genetic differentiation in the opportunistic polychaetes, there is unlikely to be much speciation because of dispersal as larvae and, in some instances, as adults. In this regard, it will be interesting to do breeding experiments with the hermaphroditic forms morphologically very similar to *C. capitata* and *P. ligni* found in Europe. These have been described as separate species, *Capitella hermaphroditica* and *Polydora hermaphroditica* (Boletzky and Dohle 1967, Guerin 1973, Hannerz 1956). Our results show that a single female of *C. capitata* may produce hermaphroditic and normal offspring indicating that the hermaphroditic forms are not separate species.

5. SUMMARY. 1. Species with the most opportunistic life histories increased and declined at the two stations with the greatest reduction in species diversity. The stations with an intermediate reduction in diversity showed increases and declines of somewhat less opportunistic species.

2. Electrophoretic studies of the malate dehydrogenase loci of the most opportunistic species, *Capitella capitata*, indicate short-term selection for a single genotype in the large populations present in Wild Harbor following an oil spill.

3. Initial response to disturbed conditions, ability to increase rapidly, large population size, early maturation, and high mortality are all features of oppor-

tunistic species. Any one of these characteristics can be used to provide an approximate ranking of species.

4. The most opportunistic species live in environments of low predictability. According to our definition of predictability, adaptation to unpredictable environments is through short-term selection. The ability to survive where other species are excluded depends on the variety of larval genotypes rather than the physiological tolerance of an average individual. This variability is maintained by mixing of genotypes from a variety of local selection regimes during dispersal.

5. Since adaptation is based on short-term selection, emphasis is placed on large population size and the means of dispersal that allows maintenance of high genetic variability and, particularly, the mortality that is a direct result of the selection process.

6. Two types of marine benthic opportunists may be recognized. The mixed strategy variety has obligate planktonic dispersal, thus preventing genetic differentiation for more than a single generation. The second type includes the most opportunistic polychaetes *C. capitata*, *P. ligni*, *M. aberrans*, *S. benedicti* and *S. verrilli*, and corresponds more to Levin's (1965) "response to selection" genetic system since selection operates through several generations in each subpopulation. The larvae are not lost to the subpopulation or swamped by larvae from surrounding areas since they are ready to settle shortly after release from brood structures.

7. Community characteristics such as species diversity and ratio of productivity to biomass in unpredictable vs. predictable environments are directly related to the spectrum of life histories or degree of opportunism of the component species. Species diversity indicates the spectrum of population sizes and the productivity/biomass ratios are related to total mortality.

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