Temporal Adaptations in Sibling Species of *Capitella*

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ABSTRACT

Previously thought to be a single species, *Capitella capitata* is a complex of at least six sibling species. These species show virtually no genetic similarity at 10 loci studied electrophoretically. Close examination of the species in culture revealed life history differences and slight morphological differences between the types. As a result of life history differences the species partition the environment temporally, with each life history adapted to a somewhat different pattern of environmental uncertainty. The classification and evolution of temporal adaptations are discussed.

INTRODUCTION

From the sequence of events following an oil spill (Sanders et al. 1972; Grassle and Grassle 1974) we identified opportunistic species in marine benthos by (1) ability to increase rapidly in an unexploited environment, (2) large maximum population size, (3) early maturation and (4) high mortality. The most opportunistic species according to these criteria was *Capitella capitata*. This species has been widely regarded as a cosmopolitan indicator of pollution or environmental disturbance (Bagge 1969; Bellan 1967; Eagle and Rees 1973; Felice 1959; Halcrow et al. 1973; Henriksson 1969; Kitamori and Kobe 1959; Pearson 1972; Reish 1959; Rosenberg 1972; Tulkki 1968; Wade et al. 1972; Wass 1967). Our studies show that what we and others considered a single species, is actually a complex of at least six sibling species.

This finding raises a number of questions. How well separated are these species? How do these sympatric species with very similar food requirements subdivide the environment? How might they compare in rank on a scale of opportunism?
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CAPITELLA SIBLING SPECIES

Table 1 lists some features of morphology and life history in the six sibling species of Capitella so far distinguished. Length

<table>
<thead>
<tr>
<th>Species</th>
<th>No. with capillary metane</th>
<th>Shape of head</th>
<th>Shape of call</th>
<th>Av. wet wt. mature worms (mg)</th>
<th>Egg diameter (µ)</th>
<th>No. eggs/brood</th>
<th>Time larvae spend in plankton</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>7</td>
<td>proct. &amp; perist. relatively short, proct. broadly triangular, head not depressed</td>
<td>plain</td>
<td>3-12</td>
<td>oval 216 x 180</td>
<td>30-400</td>
<td>several hrs</td>
</tr>
<tr>
<td>Ia</td>
<td>7</td>
<td>proct. &amp; perist. largely fused, head depressed, sharply triangular</td>
<td>plain</td>
<td>10.1</td>
<td>75</td>
<td>200-2000</td>
<td>several days</td>
</tr>
<tr>
<td>II</td>
<td>7</td>
<td>proct. &amp; perist. long, not distinctly separated, proct, broadly triangular, eyes somewhat ventral</td>
<td>lined, with dorsal cleft</td>
<td>12.0</td>
<td>230</td>
<td>30-400</td>
<td>6-24 hrs</td>
</tr>
<tr>
<td>IIa</td>
<td>7</td>
<td>not distinguished from II</td>
<td>plain</td>
<td>11.9</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>III</td>
<td>3</td>
<td>proct. &amp; perist. distinct. Proct. broadly triangular</td>
<td>flared with dorsal cleft</td>
<td>1-4</td>
<td>50</td>
<td>200-1000</td>
<td>up to 2 wks</td>
</tr>
<tr>
<td>IIIa</td>
<td>7</td>
<td>proct. &amp; perist. partly fused not depressed</td>
<td>not flared, with dorsal cleft</td>
<td>1.7</td>
<td>&gt;250</td>
<td>30-50</td>
<td>none</td>
</tr>
</tbody>
</table>

of larval life was determined by observing the time from hatching to settlement of larvae which hatched spontaneously in the laboratory and were maintained at 20° over azoic mud. Type III larvae were also maintained in cultures free of sediment and were fed Isochrysis and Phaeodactylum, but successful settlement and metamorphosis were never observed. The number of eggs per brood is highly dependent on the amount of food available, and, for each species, the low end of the quoted range represents counts from starved laboratory individuals. The high end of the range for each species is representative of field-caught animals for which food is relatively abundant. Type III animals can readily be identified, but the other five species are very similar in morphology. However, each species is characterized by a set of enzymes with unique electrophoretic mobilities. Considering the eight loci most studied (PHI, XDH, PGM, IDH1, IDH2,
MDH1, MDH2, aGPDH), only one allele is shared between any pair of species, that is the monomorphic PGM found in types I and Ia. More limited results on single esterase and leucine aminopeptidase loci also indicate that no alleles are common to all six species. The species in Table 1 have been numbered according to the relative mobilities of their most common PHI alleles using bovine serum albumin as a standard: I (.48), Ia (.50), II (.29), IIa (.36), III (.18), and IIIa (.16). A complete description of the electrophoretic results is in preparation.

The discovery of six species in Capitella capitata leads us to modify our interpretation of electrophoretic results described earlier for two MDH loci (Grassle and Grassle 1974).

At the faster locus (MDHI) the three bands identified are monomorphic homozygotes characterizing type I (the band with the slowest migration), type II and type III (the band with the fastest migration) Capitella. Most of the field results and all of the field experiments described in Grassle and Grassle (1974) apply to type I Capitella (Table 2), the type normally most common in intertidal marsh environments. Reexamination of the MDH gels previously described indicates that 46% of the Wild Harbor population in April 1971, then classified as heterozygotes at MDHI, were type III Capitella. The December 1969 and July 1970 samples (from Stations II and IV respectively in Wild Harbor) were composed entirely of type I worms. Winter collections from Station IV in the years subsequent to 1971 indicate that type III Capitella reach peak population densities in the months of December and January, when they are also reproducing. The results of our sampling indicate that the oil spill prevented settlement and reproduction in the type III worms in 1969-70 and perhaps caused late settlement in 1970-71.

At the slow locus (MDH2), the gel pattern previously classified as Type 2 is characteristic of type III Capitella. That is, 46% of the April 1971 Wild Harbor population are type III Capitella. In December 1969 all the worms were type I and there were two gel patterns at the MDH2 locus: 38% of the individuals with a single main band (and two conforming bands) were classified as either homozygotes or heterozygotes for the active allele; 62% of the individuals, with

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1PHI, phosphohexose isomerase; XDH, xanthine dehydrogenase; PGM, phosphoglucomutase; IDH, isocitrate dehydrogenase; MDH, malate dehydrogenase; aGPDH, α-glycerophosphate dehydrogenase.
no activity at the MDH2 locus, belonged to the null homozygote class. In the July 1970 sample all individuals were type I and 100% were homozygous for the null allele. The August 1970 Sippewissett control samples had 77% of the type I individuals in the null homozygote class. In Wild Harbor, April 1971, 40% of the type I individuals were in this class. At the MDH2 locus the null allele was selected for by conditions associated with the oil spill. Our interpretation of the significance of the null allele in the type I worms needs to be confirmed by further breeding studies.

Samples of Capitella populations collected at different times of the year at seven different locations in Massachusetts have shown dramatic changes in the percent contribution of the six sibling species. For example, samples collected subtidally at the Woods Hole sewer outfall show five of the six species living sympatrically, although the contribution of a given species does not remain constant throughout the year. Temporal fluctuations in the percent composition of the different Capitella species have been found at all stations sampled for more than one year. A comparison of two subtidal samples collected on the same date at Gloucester at two localities separated by one mile, showed three species in one and two species in the other. In the first, 90% were type IIIa, in the second, 90% were type Ia, indicating that the proportions of the different species vary greatly over short distances.

Before the electrophoretic results conclusively demonstrated the existence of several species, we made many attempts (more than 200 crosses between individual males and females) to cross breed pairs of types I with Ia, II and III, and II with III, without success. This lack of success is hardly surprising considering the lack of common alleles between any two species (with the single exception of the PCM in types I and Ia). Table I shows that although these separate species in general lack differentiating morphological features, they exhibit marked differences in reproductive modes, particularly in the degree to which the larvae are dispersed. Species IIIa has only males and females (gonochoristic), species I, Ia, and II have males, females and protandrous hermaphrodites (which in type I can be selfing), and species III is an obligate outcrossing protandrous hermaphrodite. The length of planktonic larval life ranges from zero for the benthic larvae produced by type IIIa, to several weeks (or possibly longer) for type III.

TEMPORAL ADAPTATION AND DISPERAL

In unpredictable environments niche separation is likely to result from differences in length of life cycle relative to the period of environmental change (Hutchinson 1965, Southwood et al. 1974). Hutchinson (1965) indicated that such temporal adaptation is likely to be particularly important for terrestrial and freshwater invertebrates. In an environment of a given average predictability (Grassle 1972), length of life cycle relative to the period of environmental
change places each species in an environment of slightly different predictability—i.e., temporal adaptation renders the environment variously predictable to the species. Schoener's (1974) generalization about resource partitioning, that "Habitat dimensions are important more often than food-type dimensions which are important more often than temporal dimensions," may not apply in highly unpredictable environments. In such environments closely related, relatively opportunistic species such as the Capitella species will be separated by temporal adaptations based on life history differences.

Studies of temporal adaptation are scarce, in part, because the data are difficult to obtain. Where populations of closely related species have been intensively studied, life history adaptations to differing temporal regimes have been found. Among the best examples are the temporal adaptations occurring in a wide spectrum of species of Drosophila (Carson 1965; Dobzhansky 1965; Levins 1965). Perhaps the best example of a group of closely related species in which niche separation results from differences in temporal adaptation to environments are the nine species of the genus of water striders, Gerris, studied by Vepsäläinen (1974). In these species wing length determines dispersal ability, and dispersal ability is correlated with the degree of uncertainty and evanescence of the environment that the species are exposed to.

We believe the six species of Capitella represent several distinct temporal adaptations based partly on the dispersal capability of the larval stages. There are benthic larvae, larvae with a planktonic life of several days, and larvae that can remain in the plankton at least 14 days. Some of the species (e.g., Ia and III) seem to have relatively short breeding seasons limited to the winter or early spring, while others (e.g., I and II) breed throughout the year. Despite the enormous differences in life history features, all of the Capitella species may be considered to be relatively opportunistic. The differences in colonizing ability reflect differences in the environmental variability of their respective local habitats. Unlike the species of Gerris, the species of Capitella with the greatest powers of dispersal (types III and Ia) occur in the less variable, subtidal habitats. The species with the most rapid response to disturbed environments is type I. Although it has relatively limited dispersal ability, this is the species with the largest rate of increase, largest maximum population size, and highest mortality (Grassle and Grassle 1974).

The most opportunistic polychaetes brood their young (Grassle and Grassle 1974), and yet good dispersal ability is a requisite for colonization of the short-lived, unpredictable habitats where they become abundant. A distinction can be made between species which spend the greater part of their embryonic development in the plankton, and those which are brooded to a stage capable of either immediate settlement or dispersal over relatively short distances. Species with primarily planktonic development (e.g. Capitella species Ia and III), must adapt to local conditions through short-term selection
every generation. The heaviest mortality in these species (which in *Capitella* have the highest number of eggs per brood) occurs in the plankton chiefly from predation (Mileikovsky 1971; Thorson 1946), but their relatively wide dispersal allows the selection of potentially more favorable habitats. Consequently, the postlarval phase of their life history appears less opportunistic. The mussel, *Mytilus edulis*, is this kind of opportunistic species (Koehn and Mitton 1972). In species where the offspring may settle adjacent to the adult (e.g., *Capitella* species I and IIIa, adaptation to local environments can occur by selection through several generations.

The distinction between adaption in species with large outcrossing populations and in species divided into subpopulations is somewhat similar to the distinction between adaptation in central and peripheral populations (Frank 1974). In species with a number of separate subpopulations there is, in addition to differential response to selection, a high incidence of local extinction which may occur as a result of a variety of unpredictable events. However, the resultant interdemic selection probably will contribute only to long-term evolutionary changes in the species.

**LEVELS OF ORGANIZATION AND TIME SCALES OF TEMPORAL ADAPTATION**

A simple gradient of degree of opportunism is not sufficient to explain the subtle differences in life histories which may reflect differences in temporal adaptation (see Wilbur et al. 1974). Every species adapts to the environment at a combination of levels of organization, each being appropriate for a different time scale of environmental variation (Haldane 1956; Lewontin 1957; Thoday 1953). Each unique life history is adapted to the pattern of environmental change in a unique way e.g. a species which has a life cycle of one year and breeds once during a two-week period will interact differently with seasonal and other environmental changes than a species in which individuals have a life span of four months and breed continuously for three of those four months. To clarify this concept levels of organization are presented in Table 3 along with time scales of adaptation and significant life history features.

To illustrate how the Table might be used, we may consider the observation that body size and degree of opportunism are related (Fenchel 1974; Pianka 1970). Large animals, because they are generally better regulators than small animals, usually adapt at the level of the individual rather than the population. An environmental change not included in the range of tolerance of every individual is likely to have an unpredictable effect and adaptation will be at the ecological or genetic level. This argument may be applied to the observation of Selander and Kaufman (1973) that invertebrates have higher genetic variability than vertebrates. The vertebrates they studied were homeotherms except for a fish with relatively high genetic variability. Selander and Kaufman explained the differences in genetic variability by saying that the environment of vertebrates is
more fine grained because of their larger body size, greater mobility and greater homeostatic control. From Table 3 we would say that vertebrates are better physiological (and behavioral) regulators, so

<table>
<thead>
<tr>
<th>Level of organization:</th>
<th>behavioral and physiological individual</th>
<th>developmental individual life cycle</th>
<th>genetic populational</th>
<th>ecological spatial inter-populational</th>
<th>evolutionary temporal inter-populational</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unit of adaptation:</td>
<td>long</td>
<td>frequent</td>
<td>on same scale (usually seasonal) and infrequent</td>
<td>localized unpredictible and infrequent</td>
<td>gradual autorelated</td>
</tr>
<tr>
<td>Population size:</td>
<td>small</td>
<td>intermediate</td>
<td>large</td>
<td>spatially separated large</td>
<td>small</td>
</tr>
<tr>
<td>Genetic variability:</td>
<td>low</td>
<td>intermediate</td>
<td>high additive</td>
<td>high, not necessarily additive</td>
<td>small</td>
</tr>
<tr>
<td>Selection:</td>
<td>normalizing</td>
<td>normalizing</td>
<td>diversifying-temporal model</td>
<td>diversifying-spatial model and interdec</td>
<td>long term directional</td>
</tr>
</tbody>
</table>

that adaptation is more at the level of the individual than the population.

For consideration of temporal resource partitioning the important parts of Table 3 are labeled genetic and ecological to avoid coinage new terms. Benthic species with obligate planktonic dispersal have less of a spatial interpopulational component to the adaptation. Diversifying selection is important to these species but the temporal model, where different genotypes are selected at different times in an unpredictably varying environment, is more appropriate (Haldane and Jayakar 1963). The temporal model is somewhat less effective in maintaining genetic variation than the spatial model (Hedrick 1974), where different alleles are favored in each local environment and the genetic variability remains high as a result of limited gene flow between subpopulations (Levene 1953; Soulé 1971). Habitat selection and loss of alleles through founder effects would also contribute to genetic differentiation of local populations (see Levins 1970).

Spatial interpopulational adaptation is a significant component of adaptation in the most opportunistic species (Grasse and Grassle 1974). In benthic invertebrates, such as type I Capitella, the possibility for immediate settlement results in more spatial subdivision and allows the population in a local environment to respond to selection through several generations without being swamped by immigrants from surrounding populations. Short-term selection (see Williams 1975) is likely to be an important part of adaptation regardless of the degree of spatial subdivision. Marine benthic species with greatest powers of dispersal will undergo genetic differentiation only through intense selection from a large planktonic gene pool every generation. Perhaps equally important is the fact that species without planktonic larvae or with the possibility for almost immediate settlement will have the greatest rate of population increase since planktonic dispersal is always accompanied by heavy mortality. For example, most
of the type I, type II and type IIIa Capitella which can settle soon after hatching will form part of the rapid population increase in a local area (with only the occasional larva being widely dispersed). Every larva of types Ia and III Capitella colonizes a new environment so that rapid local population increases will be made up of larvae selected from a number of source populations each generation.

SPECIATION

Enormous differences in life history frequently occur in very closely related species. Species of the genus, Littorina (Heller 1975; Mileikovsky 1975), or Crepiedula (Coe 1949), are good examples in gastropods. Drosophila species can range from rare, narrow-habitat species of the tropical forest to very widely dispersed species adapted to the unpredictable habitats formed by man-made disturbance. Species with a large number of geographically separated subpopulations are more likely to speciate than those with larger breeding units (Carson 1960; Levins 1965).

In large genera that include opportunistic species the taxonomic unit that survives through evolutionary time may be a metaspecies in which species are continually becoming extinct and being formed. This is similar to the metapopulational equilibrium described by Levins (1970). In groups of asexually reproducing organisms it is frequently difficult to say whether the evolutionary unit represents a metaspecies or metapopulational equilibrium. Weeds, weevils (Suomalainen and Saura 1973), aphids (Hille Ris Lambers 1966) and brine shrimp (Barigozzi 1974) all provide good examples of opportunistic organisms where a large number of biotypes appear to form a complex that functions as an evolutionary unit (see Simpson 1961; Sokal 1974). Some members of nearly all the parthenogenetic groups maintain sexual reproduction (White 1973). The asexually reproducing lines may evolve repeatedly from sexually reproducing ancestors.

A complex of species may be the unit that survives through evolutionary time in sexually reproducing species where speciation may frequently occur through chromosomal events in isolated, founder populations (Mayr 1963). The very low allelic similarity in the Capitella species is not typical of groups of sibling species. About one-half to two-thirds of the loci among sibling species of Drosophila have alleles in common (Ayala et al. 1970; Zouros 1973). The extreme differences in Capitella electrophoretic patterns are more like those described for biotypes of weevils (Suomalainen and Saura 1973).

Opportunistic genera are often represented by groups of sibling species. In the well-known example of r-selection, one biotype of dandelion is favored over another biotype as a result of differences in temporal adaptation to habitats of different predictability (Gadgil and Solbrig 1972; Solbrig and Simpson 1974). The opportunistic marine species chosen for genetic studies because of short life histories and ease of culturing are representatives of sibling groups. The isopod species group, Jaera albifrons, includes five species, each with different chromosome numbers (Staiger and Bocquet 1956;
Bocquet 1972). The copepod genus, *Tisbe*, includes a number of sibling species each with somewhat different life histories (Volkmann-Rocco 1972; Volkmann-Rocco and Battaglia 1972). The situation most like that found in *Capitella* occurs in the polychaete genus, *Ophryotrocha*, studied by Åkesson (1973) and Bacci (1965). *O. labronica* may be similar in many ways to our type I *Capitella* since, although it is usually gonochoristic, selfing hermaphrodites have been found in one of the populations (Parenti 1960; Zunarelli 1962; Zunarelli-Vandini 1967). *O. puerilis* is like our type III *Capitella* in being a protandrous hermaphrodite. Both *O. labronica* and *O. puerilis* are considered pollution indicator species (Åkesson 1973). Some species of *Ophryotrocha* have brood protection and others do not. One species is viviparous. Twelve of the species may be put into three groups on the basis of chromosome number.

**SUMMARY**

Niche separation in the *Capitella* species results from temporal adaptations based on differences in dispersal ability. The various life history features of the *Capitella* species cannot be classified along a simple gradient of environmental predictability since dispersal ability and the extent of spatial division into subpopulations must be considered. The most opportunistic *Capitella* species, type I, has relatively limited dispersal ability, which is compensated for by the possibility of responding to selection through several generations in each local environment.

Sibling groups of opportunistic species show little tendency to exploit different habitats or foods and a variety of life history patterns are likely to evolve many times. The whole complex survives through evolutionary time as a unit with new adaptive modes continually being formed and becoming extinct.

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