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Trophic Polymorphisms, Plasticity, and Speciation in Vertebrates

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Abstract. Trophic polymorphisms are relatively common among vertebrates. In this chapter I review the occurrence of trophic polymorphisms among vertebrates, discuss what is known about the cause of these polymorphisms, enumerate the unifying ecological and morphological factors among the examples, and present a qualitative model of intraspecific trophic divergence where plasticity in combination with other factors can lead to sympatric reproductive isolation of the morphs. Trophic polymorphisms are found in all classes of vertebrates; however, they are most common among lacustrine fishes. Although little information is available about the relative contribution of genetic and environmental factors to the polymorphisms, data indicate that phenotypic plasticity alone could be responsible for the differences between morphs in many of the cases. The characteristics that unify the cases are as follows: (1) animals use only their mouths to subdue, capture, and process their prey; (2) there are two or more food types or suites of food items (e.g., zooplankton vs. benthic invertebrates) in different habitats that require different modes of capture or processing; (3) there is sufficient behavioral flexibility to take advantage of the multiple prey types; (4) the prey populations are temporally stable; and (5) the polymorphic species occur in relatively species-poor environments characterized by some empty niche(s).

In cases where the above five factors are satisfied, morphological divergence and, ultimately, speciation can occur via the following pathway. Behavioral plasticity can lead to foraging specialization. Foraging specialization can, in turn, lead to morphological differences as the result of morphological plasticity. These morphological differences reinforce the foraging specialization by changing the relative foraging efficiencies of the two morphs on the different food types. Induced morphological differences can affect mate choice or nesting habitat preference, or, if the polymorphism is habitat-based (e.g., the common limnetic/benthic polymorphism found in some temperate fishes), it can affect timing of spawning. When this sequence of events occurs, partial reproductive isolation can occur in a single generation solely as the result of behavioral and morphological plasticity. For the morphs to become significantly reproductively isolated, there also needs to be philopatry among the young to the parents' foraging ground or food type.

Introduction

Trophic polymorphisms (polymorphisms related to diet) and variation are intriguing because they provide the potential for intraspecific niche differentiation and, ultimately, speciation (Mayr 1963;

Rosenzweig 1978; Wilson 1989). In addition they provide an unparalleled opportunity to examine ecological phenomena such as competition and predation without the confounding effects of different phylogenetic histories. By polymorphism, I mean the occurrence of more than one discrete phenotype in a population (Mayr 1963, "old" definition), including both genetically and environmentally determined phenotypic differences, because for many instances the genetic and environmental contributions to the phenotypic differences are unknown. Some of the polymorphisms described below are discrete only when combinations of continuous morphometric characters are analyzed multivariately.

Polymorphisms can result from genetic influences, environmental influences, or a combination of both. For instance, flight polymorphisms in insects can be completely environmentally determined, under simple genetic control, or be the result of genotype-by-environment interaction (Harrison 1980; Roff 1986). Most characters are influenced by both genetic and environmental factors; different characters of an individual can vary in the amount of plasticity they express, and different genotypes can exhibit different amounts of plasticity in response to a range of environments.

In this chapter I first review the available literature on vertebrate trophic polymorphisms and the relative contributions of genetic and environmental factors to the polymorphisms. Next, the ecological correlates of the polymorphisms and the potential of trophic polymorphisms and variation, including that due to plasticity, to contribute to speciation are discussed. The evidence for the sympatric or allopatric origin of morphs where partial to virtually complete reproductive isolation has occurred is also discussed. For this reason some problematic examples of species complexes have been included where morphs in some populations may actually represent different biological species. This review is restricted to trophic characters and excludes color and meristic polymorphisms, and polymorphisms attributable to sex, age, or size differences because these have been previously reviewed and do not necessarily have the same causes or evolutionary implications (Barlow 1961; Selander 1966; Polis 1984; Werner and Gilliam 1985).

Trophic Polymorphisms and Variation in Vertebrates

The following section describes vertebrate trophic variation and polymorphisms. I have included a few examples of trophic variation that may not satisfy the requirements of discrete phenotypes within a population because the organisms illustrate trophic partitioning and correlated morphological and behavioral differences between morphs.

FISHES

Whitefishes

Coregonine fishes of the family Salmonidae provide a striking example of the problem that morphological polymorphism can present to systematists and ultimately to any biologist working on a polymorphic system. The whitefish genera (*Coregonus* and *Prosopium* spp.) are found in temperate lakes throughout the Holarctic. Scattered throughout their range are numerous lakes where two or

more forms of what appear to be a single species coexist. For instance, over 800 lakes in Sweden have more than one morph of whitefish living in sympatry (Svärdson 1979). Whitefish morphs are usually characterized by differences in gill raker number and length, often accompanied by differences in body shape and mouth position. Gill rakers enhance the capture of small food particles, such as zooplankton (Sanderson et al. 1991). Zooplanktivorous (limnetic) whitefish tend to have longer and more numerous gill rakers than those that feed on benthic organisms or insects. Of characters shown to vary between morphs, gill rakers are thought to be the morphological character most canalized (buffered) against environmental influence (Svärdson 1952, 1979; Kliewer 1970) although even gill rakers are somewhat susceptible to environmental modification (Koelz 1929; Kliewer 1970; Lindsey 1981). Other characters such as relative body size and shape dimensions are sensitive to both environmental and genetic influences (Svärdson 1949, 1970). For instance, Svärdson (1970) showed that dwarf morphs transplanted into fishless lakes grow larger and develop relatively different head and body dimensions than their dwarf counterparts. The directions of shape change parallel those expected from functional considerations. Fish feeding on more evasive prey, such as zooplankton, tend to have more fusiform bodies whereas fish feeding on stationary, benthic prey generally have deeper, rounder bodies (Webb 1984).

In North America the best known example of trophic polymorphism involves the lake whitefish, *Coregonus clupeaformis* (Mitchill). There are two forms in at least five lakes in Maine (Fenderson 1964), Opeongo Lake in the Ottawa-St. Lawrence drainage (Kennedy 1943), Squanga Lake and four others in the Yukon (Bodaly et al. 1988), and several lakes in British Columbia (McPhail and Lindsey 1970). The sympatric forms are a dwarf and a normal form. In four Maine lakes the dwarf has the higher gill raker count, and in the fifth lake the dwarf is bimodal with respect to gill raker count. However, in Opeongo Lake the dwarf morph has a lower gill raker count (Lindsey et al. 1970). In Squanga Lake and three other lakes in the Yukon, the dwarf form has more gill rakers (Bodaly et al. 1988) and is the zooplanktivore. Lindsey (1981) suggests that the high-rakered forms are usually dwarfed due to the relatively low abundance of zooplankton in northern lakes.

McCart (1970) documents the existence of two forms of the pygmy whitefish, *Prosopium coulteri* (Eigenmann & Eigenmann), in Alaska. One form is characterized by lower number of gill rakers, a subterminal mouth, concave head profile, deeper body and caudal peduncle, smaller orbit, and a less compressed body than the high-rakered form. Stomachs of the high-rakered form, as one might expect, were full of zooplankton whereas low-rakered forms fed primarily on bottom fauna. The two forms are spatially separated in lakes with the high-rakered fish found in depths <10 m and the low-rakered form found deeper. The two forms may spawn at slightly different times. The morphological differences found in two-morph lakes are not useful in identifying morphs when they exist in allopatry, suggesting that character displacement may be occurring in two-morph lakes.

Svärdson (1957, 1970, 1979) describes six to seven different forms of whitefish in Sweden. Many lakes contain two forms, and one lake contains five different morphs. Again, gill raker number in combination with size, spawning time, or color are the primary characters used to distinguish forms or species.

The differences between morphs usually involve a large suite of characters important in food capture, some of which are more or less canalized than other characters within the same organism. For instance, gill raker number in whitefish is more canalized than head and body shape measures (Svärdson 1979). So, for whitefish species, even where morphs within lakes are partially reproductively isolated, the relative influence of genotype and environment differs for every character examined.

Charr

Perhaps the best studied group of trophically polymorphic vertebrates, Arctic charr, *Salvelinus alpinus* (Linnaeus) (also in the family Salmonidae), comprise a complex of landlocked and anadromous populations found in lakes throughout the Holarctic. At least seven species have been described, but many, if not most, have been classified as morphs of a single polytypic species (Johnson 1980). Up to four morphs coexist in some lakes (e.g., Thingvallavatn Lake in Iceland), but usually only two forms—a dwarf and normal morph—coexist in a single lake (reviews in Balon 1980; Johnson 1980; Hindar and Johnsson 1982; Johnson and Burns 1984). These forms are characterized by differences in number of gill rakers, pyloric caecae, life history characters, color, body proportions, and diets. Usually the dwarf form is a midwater fish that feeds on zooplankton and is characterized by more gill rakers, a more pointed snout, and a larger eye, whereas the normal form feeds on benthic organisms (Johnson 1980). This pattern is reversed in some lakes and may be a function of the relative abundance of zooplankton and benthic organisms. Sometimes an additional anadromous morph is also present. Examples of polymorphism abound in lakes throughout northern North America, Europe and the CIS (formerly the Soviet Union) (Johnson 1980).

The most dramatic example of polymorphism is found in Thingvallavatn Lake, Iceland, where three or four forms of *S. alpinus* coexist (Hindar et al. 1986; Jonsson et al. 1988; Skulason et al. 1989): a small benthivore, large benthivore, a planktivore and a piscivore. Using detailed life history data, Jonsson et al. (1988) found evidence that all four morphs are partially reproductively isolated. In a breeding experiment, Skulason et al. (1989) found evidence for only three genetically distinct morphs; the piscivore appears to be a planktivore that has become big enough to eat sticklebacks.

The basis of morphological differences among charr morphs may be different in different drainages. In a breeding experiment using charr from the Salangen River, Norway, Nordeng (1983) found no evidence for genetic control of morph differentiation because each morph had offspring of all morphs.

Goodeids

In some rivers in Mexico, a narrow-mouthed fish originally described as *Ilyodon furcidens* (Jordan and Gilbert) is sympatric with a broad-mouthed fish originally described as *Ilyodon xantusi* (Hubbs and Turner 1939). Narrow-mouthed morphs possess rounded jaws, a narrow gape, and several rows of teeth whereas the broad-mouthed morphs possess squared jaws, a broad horizontal gape, and reduced or absent inner rows of teeth. Narrow-mouthed morphs also tend to have fewer teeth and gill rakers than broad-mouthed morphs (Turner and Grosse 1980). The dietary basis of the polymorphism is unknown. Turner and Grosse (1980) collected electrophoretic data indicating the two "species" were actually two morphs of a single species. Turner et al. (1983) did further electrophoresis and showed extensive differentiation among localities, but no differentiation between morphs from a single locality. Grudzien and Turner (1984) raised broods of fish for which the morphs of both parents were known and performed both heteromorphic crosses and homomorphic crosses. The young were fed a combination of brine shrimp nauplii and flake food. All but one homomorphic cross resulted in progeny of the opposite morph from the parents. None of the laboratory-raised young developed mouths as broad as field-collected, broad-mouthed fish. Also, a greater proportion of intermediate morphs occurred in the laboratory-reared fish than in the field-caught fish.

These results indicate a great deal of variation in trophic morphology in *Ilyodon*; however, they do not conclusively demonstrate plasticity. In order to show plasticity, sibs need to be raised on different diets. In addition to detailing the extent of plasticity, many questions still remain. On what do the different morphs feed? Why do some drainages contain monomorphic populations and others dimorphic ones? Does the absence or presence of other species "allow" the dimorphism to occur, or does it occur only in certain habitats? How stable is the dimorphism in a population over ecological and evolutionary time scales?

Sticklebacks

Threespine sticklebacks, *Gasterosteus aculeatus* Linnaeus, exhibit a limnetic/benthic polymorphism in some lakes in British Columbia, similar to the polymorphisms described for charr and whitefish. In Enos Lake, British Columbia, the limnetic (pelagic) morph is characterized by a relatively shallower body; longer and shallower head; longer snout, upper jaw, and gill rakers; and a bigger eye (McPhail 1984). Limnetics feed primarily on zooplankton, and benthics feed primarily on benthic invertebrates (Bentzen and McPhail 1984). The polymorphism in Enos Lake has a definite genetic basis. McPhail (1984) found that homomorphous crosses only resulted in offspring with parental phenotypes, whereas heteromorphous crosses resulted in F1s with intermediate morphology. The two morphs choose different habitat types (Bentzen et al. 1984), show almost perfect assortative mating, and build their nests in different places (Ridgway and McPhail, 1984). Studying a similar polymorphism in a different lake, Larson (1976) showed that benthics dominated limnetics in social interactions.

Schluter and McPhail (1992) reported that in all five two-morph lakes they examined the morphological and morphometric differences between morphs were bimodally distributed. Morphology and gut contents were highly correlated. Limnetic fish had zooplankton in their stomachs, and benthic fish were filled with benthic invertebrates. Mean morphological measurements of fish from one-morph lakes were intermediate to the means of benthics and limnetics from two-morph lakes. However, within single-morph lakes there was fairly good correspondence between the presence of zooplankton in a fish's stomach and its gill raker length. This observation indicates some ecological structuring even within single-morph lakes. Whether these differences are due to morphological plasticity in response to primary foraging mode, or are due to genetically determined morphology determining foraging mode is unknown.

Sunfish

Ehlinger and Wilson (1988) found that bluegill sunfish, *Lepomis macrochirus* Rafinesque, caught in the pelagic portion of Holcomb Lake, Michigan, had shallower bodies, shorter pectoral and pelvic fins, and pectoral fins placed more anteriorly than fish caught in the vegetation (limnetic and littoral, respectively). Bluegills caught in the two habitats forage differently: littoral bluegills feed on insects that are relatively cryptic, whereas limnetic bluegills feed on zooplankton that are relatively conspicuous. Littoral bluegills hover longer between movements than those from open water. When littoral bluegills are fed zooplankton in open aquaria, their hover rates decrease, but they still hover longer than limnetic bluegills. Maximum foraging rates in vegetation were positively correlated with

multivariate morphological scores (where higher scores indicated fish with more littoral-type morphology). Layzer and Clady (1987) observed that young-of-the-year bluegill sunfish collected in water <0.5 m deep had significantly deeper bodies and greater relative decrease in head length than those collected in water 0.5–3.1 m deep. Thus, habitat partitioning by juveniles could lead to the polymorphism observed by Ehlinger and Wilson (1988).

The pumpkinseed sunfish, *Lepomis gibbosus* (Linnaeus), is a benthic feeder that consumes primarily gastropods. Pharyngeal jaw (PJ) and muscle morphology were examined in fish from Wintergreen Lake, Michigan, a lake with few snails and Three Lakes, Michigan, a lake with an abundant snail population (Wainwright et al. 1991). Snails made up a large part of the diet in Three Lakes fish and little of the diet in Wintergreen fish. PJ elements weighed more and were wider in Three Lakes fish. Curiously, PJ teeth were no wider in Three Lakes fish than Wintergreen fish, although they were shorter, indicating greater wear. This observation contrasts with that made for cichlid pharyngeal teeth, where molluscivores appear to develop wider pharyngeal teeth (see *Cichlids* below). The pharyngeal muscles of snail-eating pumpkinseeds were also heavier, as was the cross-sectional area of the levator posterior muscle, a primary crushing muscle. The differences between these morphs do not appear to be as great as the differences between some of the PJ morphs in cichlids. Although this example does not represent a true polymorphism because the morphs do not coexist in the same population, it indicates the potential for polymorphism in this species.

Cichlids

Greenwood (1959) noted variability in *Astatoreochromis alluaudi* Pellegrin PJs and teeth: One morph possessed molariform pharyngeal teeth and enlarged PJ elements, whereas the other morph was characterized by papilliform pharyngeal teeth and a more delicate PJ. On the basis of this difference and a difference in caudal fin length, he assigned the morphs to different subspecies. He noted a correlation of the morphology with diet; the molariform morph occurred where hard-shelled snails were common.

Greenwood (1965) then raised the young of molariform parents of *A. alluaudi* on a snail-free diet and found a reduction in the size of the pharyngeal teeth, the size of the pharyngeal apophysis (the process of the neurocranium on which the upper PJ articulates), and smaller lower PJ elements. Following these results, Greenwood suggested that plasticity may be the cause of the PJ differences found in different *A. alluaudi* morphs.

Hoogerhoud (1986) is the only one to have thoroughly documented the environmental induction of different PJ morphs. He raised split broods of *A. alluaudi*; one half of the brood received soft pellets, and the other half received a diet of ostracods, chironomids, and the thick-shelled gastropod *Melanoides tuberculata*. The divergence in PJ morphology began to manifest itself at about 40 mm standard length (SL). The lower PJ was stoutest in fish fed *Melanoides* and more delicate in fish fed the soft pellets. In another experiment *A. alluaudi* were fed a soft-shelled gastropod, *Biomphalaria*, and PJ morphology was intermediate between that of fish fed *Melanoides* and those fed soft pellets (Hoogerhoud 1986). The differences in PJ were the presence of molariform teeth, deeper keel, wider posterior border, and shorter and stouter horns in the snail-fed fish. Fish raised on soft pellets in tanks with sand had stouter PJs than fish fed the same diet in bare tanks. It is not known if the two PJ morphs coexist in single populations.

In the Cuatros Cienegas basin, Mexico, there were what were considered to be three closely related species of *Heros minckleyi* (Kornfield and Taylor). Sage and Selander (1975) considered these to be a small species flock. One morph ate snails, possessed molariform pharyngeal teeth, and a short gut; another was a detritivore with papilliform teeth and a long gut; and the third was a piscivore with a fusiform body and tended to be larger than the first two morphs (Kornfield and Taylor 1983). Discriminant analysis perfectly classified the three morphs (Sage and Selander 1975). Pharyngeal tooth number was bimodal, with detritivores having the greater number. All individuals with snails in their stomachs had molariform teeth. Despite these morphological differences, an electrophoretic analysis supported the contention that the morphs were from a single population. Sage and Selander (1975) raised broods captured in the field and found that two of the three broods had young of both morphs. These results are confounded by the cross-fostering that sometimes occurs in cichlids (McKaye 1979). Sage and Selander (1975) argued that the morphs are one species undergoing speciation and that the morphological differences are the result of a polymorphic supergene controlling both PJ morphology and gut length. They postulated that the morphology of the fish is determined first and that this determines foraging mode.

Kornfield and Koehn (1975) found no electrophoretic differentiation among morphs of *H. minckleyi*; however, they argued for the existence of multiple species, citing LaBounty's (1974) data indicating that molariform and papilliform morphs of *H. minckleyi* did not change morphologically when fed a different diet and that only 18 of 2,500 wild-caught specimens displayed intermediate morphology. However, the observation that 57% of the observed mating pairs in Cuatros Cienegas were comprised of one molariform morph and one papilliform morph (Kornfield et al. 1982) was strong support for the conspecificity of the two morphs.

It is still unclear to what extent the differences in *H. minckleyi* are the result of plasticity or genetic differences. Some data indicate that the differences are indeed genetic (LaBounty's [1974] data cited above, Sage and Selander's [1975] observation of aquarium-raised fish being molariform in the absence of snails and Kornfield's cited, but unpublished data). However, a similar polymorphism has been shown to be the result of plasticity, making it important that the appropriate experiments be done before concluding that a given species' PJ polymorphism is the result of a genetic polymorphism or phenotypic plasticity.

Another case of PJ polymorphism is found in *Heros citrinellum* Günther (Meyer 1989) in Nicaragua. Molariform morphs are characterized by heavier PJs, molariform pharyngeal teeth, shorter and stouter PJ horns on the lower PJ, a larger neurocranial apophysis (Meyer 1990a), relatively shorter, blunter snouts, larger eyes, wider heads, and deeper bodies than papilliform morphs (Meyer 1990b). The genetic and environmental component of this polymorphism is unclear. In contrast to *H. minckleyi*, there were no differences in gut length. The smallest molariform fish were 40–50 mm SL, and large fish with intermediate morphologies were rare in the samples. Many more molariform fish had snails in their guts (94%) than did papilliform fish (17%). The relative abundance of morphs differed in the wet and dry seasons. Meyer (1990b) raised 12 papilliform fish on snails and, in 6 mo, two of the fish had developed molariform PJs. As a result, he attributed some of the differences between morphs to phenotypic plasticity.

How common are PJ polymorphisms in cichlids? Apparently, they may be very common. Hoogerhoud (1984, 1986) documents variability in the haplochromines *Haplochromis iris* Hoogerhoud and Witte, *H. hiatus* Hoogerhoud and Witte, and *H. ptistes* Greenwood and Barel. The Lake Victoria cichlids *H. pharyngomylus* Regan, *H. ishmaeli* Boulenger, *H. obtusidens* Trewavas, and *H. malacophagus* Poll and Damas may also have variable PJ morphology (Greenwood 1960). Other

African cichlids that display alternate PJ morphs are *Lethrinops mylodon* Eccles and Lewis (Eccles and Lewis 1979), *Labidochromis caeruleus* Fryer (Lewis 1982), *Hemichromis letourneuxi* Sauvage (Loiselle 1979), *Haplochromis flaviijosephi* (Lortet) (Spataru and Gophen 1985), and *Oreochromis aureus* (Steindachner) (Kornfield, 1991). In *H. flaviijosephi* only large males develop molariform PJs; thus, the polymorphism may be due to a sex-linked gene (but sex determination in cichlids is very malleable [Kornfield 1991]), a size-related phenomenon, or a combination of habitat segregation of males and females, in combination with size. Meyer (in press) has also documented alternate PJ morphs in the New World *Heros haitensis* (Tee-Van).

These PJ differences affect feeding performance. Hoogerhoud (1986) found that fish with stout, molariform PJs displayed shorter handling times than the papilliform morph when eating snails. However, when given a choice, all fish preferred insect prey to gastropods. Liem and Kaufman (1984) found a similar phenomenon in the papilliform and molariform morphs of *Heros minckleyi*. In their experiment, both morphs preferred all four other foods over snails, but molariform fish, which ate snails more efficiently, greatly increased their consumption of snails when food was scarce or in the presence of the other morph. Meyer (1989) found that papilliform *H. citrinellum* morphs fed more efficiently on soft gastropods (*Physa*) than hard-shelled gastropods (*Melanoides*), whereas molariform morphs fed more efficiently on *Melanoides*.

OTHER VERTEBRATES

Amphibians

Trophic polymorphisms have been described in *Ambystoma tigrinum* (Collins and Cheek 1983) and *Scaphiopus multiplicatus* (Pfennig 1990). In *A. tigrinum* the two morphs are a typical larva and a larger, "cannibalistic" morph (Rose and Armentrout 1976). The cannibalistic morph is characterized by a broader head, enlarged vomerine teeth, and a wider mouth (Pierce et al. 1983). Pierce et al. (1981) documented small significant differences in allele frequencies between cannibals and normal larvae at two electrophoretic loci. However, Collins and Cheek (1983) showed in container experiments that larval salamander density is positively correlated with the appearance of cannibal morphs. Food density does not seem to induce the appearance of the cannibalistic morph. The authors infer that the polymorphism is environmentally induced; however, the offspring used in the experiment were not the result of known matings, so a genetic component is not completely ruled out.

Polymorphisms have been reported in a number of *Scaphiopus* (spadefoot toad) species (Orton 1954; Pomeroy 1981; Newman 1989; Pfennig 1990). In *S. multiplicatus* one morph is "normal" and the other is a carnivore characterized by a broader head and larger orbitohyoideus muscle. Pfennig (1990) has shown that the ingestion of fairy shrimp or tadpoles induces carnivore morphology; thus, carnivore morphs are relatively more common in ephemeral pools in which fairy shrimp are more abundant. The development of carnivore morphology is positively correlated with the number of shrimp ingested in 4-day-old tadpoles, and this change is reversible (Pfennig 1992). Accelerated morphological development associated with carnivore morphology can be induced with thyroxine. Pfennig (1992) suggests that the ingestion of fairy shrimp or tadpoles, both of which contain thyroid hormone or its constituents, triggers development of the carnivore morphology.

Turtles

The only documented cases of possible trophic plasticity or polymorphism in "reptiles" of which I am aware occur in the malacophagous turtles of the genus *Emydura* (Legler 1981), the *Graptemys-Malaclemys* complex (Ernst and Barbour 1972), and in certain trionychids (Dalrymple 1977). Some *Emydura* species develop broadened heads and enlarged maxillary and palatine bones that form a secondary palate used for crushing that is opposed by a large dental symphysis. In most populations only some large females develop enlarged heads. Legler (1981) asserts that "megencephaly" occurs in some populations as the result of bone remodelling in response to the increased strains of mollusc crushing; however, in some populations all individuals are somewhat megencephalic, with the juveniles showing the characteristic megencephalic palatal patterns at hatching.

Birds

Smith and Temple (1982) suggested a bill polymorphism in the hook-billed kite (*Chondrohierax uncinatus*). Throughout their range from Central to South America, there are areas where bill morphs appear to be bimodally distributed. The large-billed morph possesses a deeper, more massive and more hooked bill than the small-billed morph. The size of the bill may be related to the size of snail that a kite can extract from its shell. Large-billed morph abundance was suggested to correlate with large snail abundance. However, the exact nature of this polymorphism is still not well documented.

The black-bellied seed cracker, *Pyrenestes estrinus*, an African estrildid finch, displays a bill-size polymorphism (Smith 1987). Large-billed morphs have deeper and wider bills than small-billed morphs. Lower mandible width is strikingly bimodal within populations. The polymorphism is not correlated with sex, size, age, or geography. The two morphs mate at random. Large-billed morphs are able to crack the hard seeds of one sedge species more efficiently than the small-billed morph, which appeared to rarely feed on the hard sedge seeds even in aviaries. Smith (1987) infers that the polymorphism is genetically based because the distribution of beak morphs in juveniles (<3 wk post-fledging) was already bimodal, and none of the birds remeasured up to 3 yr after first being measured showed evidence of switching morphs. However, the appropriate breeding experiments are needed.

Competition apparently occurs between morphs for seeds when resources are scarce (Smith 1990a). During this time of scarcity (the dry season), disruptive selection on juveniles appears to occur (Smith 1990b). Smith (1990c) suggests the possibility of the polymorphism initiating sympatric differentiation even though the morphs do not assortatively mate, because homomorphic large-billed pairs nest earlier than homomorphic small-billed pairs. This is due to earlier seed crops in the hard-seeded sedge species. This difference in mating time provides a possible mechanism for initiating divergence between morphs, similar to the situation seen in charrs and whitefishes.

Ford et al. (1973) reported that bill depth varied bimodally in male medium ground finches, *Geospiza fortis*. They suggested that the population may be undergoing disruptive selection and be in the process of splitting. Grant and Grant (1989) suggested that the apparent polymorphism may have arisen through hybridization of *G. fortis* with *G. magnirostris*, or immigration of *G. fortis* from another island combined with assortative mating.

Oystercatcher individuals, *Haematopus ostralegus*, specialize by feeding on different species of bivalves or even by feeding on the same species in different ways (Norton-Griffiths 1967; Durell and Goss-Custard 1984; review by Sutherland 1987). Bills reflect the particular specialization and

feeding mode; however, whether different bill morphologies increase feeding efficiency is unknown. These specializations are not temporally stable; they can change seasonally (Hulscher 1985), and diet and behavior can vary with age (Goss-Custard and Durell 1983).

Mammals

The research on bone remodelling discussed in the following section clearly demonstrates the plasticity of mammalian bone. Holbrook (1982) suggests that plasticity is the cause of mandibular shape differences between deermice, *Peromyscus maniculatus*, caught in areas comprised of a woodland and grassland mosaic. The anterior part of mandibles from woodland mice were slightly longer and deeper than those from grassland mice. Holbrook (1982) attributes this difference to woodland mice including more hard seeds in their diets (Jameson 1952).

Morphological Plasticity in Vertebrates

Although morphological plasticity is acknowledged to be common in plants (Bradshaw 1965; Schlichting 1986; Sultan 1987) and invertebrates (Dodson 1974; Havel 1986; Lively 1986), it is often thought to be rare in vertebrates (Bradshaw 1965; Schaal and Leverich 1984; West-Eberhard 1986). The plasticity of vertebrate bone and muscle is well established, and examples of environmentally induced differences in vertebrate trophic morphology are increasing in number. Even so, plasticity is often invoked only as a last resort to explain polymorphisms. For most of the trophic polymorphisms described in this chapter, the genetic or environmental basis for the morphological differences is unknown. To what extent could plasticity contribute to many of the morphological differences described herein?

Bone provides the framework for the vertebrate body and feeding apparatus. As a result, demonstrating the plasticity of bone is crucial to showing that trophic polymorphisms or variation can be the result of plasticity. Living bone is dynamic tissue that is constantly in flux by growing, undergoing remodelling, or serving as a calcium and phosphorus reservoir.

Bone consists of a collagenous matrix secreted by cells called osteoblasts that becomes mineralized with a calcium phosphate salt called hydroxyapatite. Osteoblasts that become trapped in the matrix maintain the bone and are classified as osteocytes. The outer surface of bone (periosteum) is where bone growth and bone shape change occurs. Internal remodelling occurs to mobilize minerals for metabolism and to rearrange the internal structure in response to changed mechanical loading regimes (El Haj 1990).

The shape of skeletal elements is both genetically and environmentally determined. Bone remodels adaptively in response to the mechanical loading regime it faces (Wolff 1892; Lanyon and Rubin 1985; Herring 1993). In muscle extirpation and paralysis experiments, where bones develop without the influence of the usual impinging muscular contractions, bone reaches a shape close to that expected when external environmental forces are present, but tuberosities and processes normally present are absent, and the affected bone lacks its typical curvature, internal structure, girth, and cross-sectional shape (see Herring 1993 for review). These differences are true of mammalian and avian long bones, mandibles, and temporal bones, the only skeletal elements for which these experiments have

been done. Changes in mechanical loading regime also cause shape differences in both mandibles and long bones (see Lanyon and Rubin 1985 for review). For example, differences have been induced in the mandibles of mice (Lavelle 1983), rats (Watt and Williams 1951; Moore 1965; Bouvier and Zimny 1987), rhesus monkeys (Bouvier and Hylander 1981) and squirrel monkeys (Beecher et al. 1983) by feeding them hard and soft diets. Such plasticity of bone and muscle morphology is well established in clinical settings, but its occurrence in nature is not commonly documented in vertebrates.

Among fishes, laboratory experiments have demonstrated morphological plasticity in oral jaws, PJs, and skulls, and in overall body shape (Hoogerhoud 1984; Witte 1984; Meyer 1987; Wimberger 1991, 1992). Oral jaws make up the mouth of a fish and consist of the premaxilla, maxilla, and lower jaw. Witte (1984) raised the young of wild-caught *Haplochromis squamipinnis* Regan on minced liver, *Tubifex*, and flake food. The tank-raised young developed shorter ascending premaxillary processes, a larger angle between the ascending and dentigerous arm of the premaxilla than wild-caught fish, and a symphyseal articulation facet, in contrast to the usual absence of the facet in wild-caught fish. Following functional models of Otten (1982) and Barel (1983), Witte hypothesized that these changes increase biting force.

To investigate osteological plasticity, I raised half of split broods of *Geophagus steindachneri* Eigenmann & Hildebrand and *G. brasiliensis* (Quoy & Gaimard) on brine shrimp (*Artemia*) nauplii and the other half on chironomid larvae. Fish raised on brine shrimp nauplii were relatively longer for almost all measures in the oral jaw region and had larger eyes (Wimberger 1991). The pattern was similar for both species, and the magnitudes of the differences induced between treatments for the two species was similar.

Meyer (1987) raised half of split broods of *Cichlasoma managuense* (Günther) on flake food and nematodes, and the other half on brine shrimp nauplii. Fish fed brine shrimp nauplii had relatively longer and more acute snouts, and relatively larger eye diameters. The diets of both groups were switched at 8.5 mo to a third diet (brine shrimp adults), and the fish measured again at 16 mo. The two groups converged on a single morphology suggesting that the responses were somewhat malleable.

Body shape has also been shown to vary as the result of differences in diet (Wimberger 1992). I examined body shape of *G. steindachneri* and *G. brasiliensis* raised on chironomid larvae or *Artemia* nauplii in a similar experiment as described above and found that fish raised on chironomid larvae had relatively shorter, deeper heads, longer and deeper bodies and deeper caudal peduncles than fish raised on *Artemia* nauplii (Wimberger 1992).

The amount that morphological measures differed between fish raised on different treatments was 2–4% of a given measure. This magnitude of difference is similar to the variation found between different morphs of the bluegill sunfish, *Lepomis macrochirus*, for which differences in foraging efficiency between the morphs has been documented (Ehlinger and Wilson 1988). Morphological differences as small as these are difficult to detect unless one is specifically looking for them. As a result, I expect that trophic variation of the order found by Ehlinger and Wilson (1988) in bluegills, and induced in *Geophagus*, is more common than presently realized.

The extent to which plasticity is variable among populations, species, or higher taxa is unknown. It would be interesting to compare the extent of morphological plasticity inducible in morphologically diverse and speciose groups, such as cichlids, with closely related but less diverse groups. We might ultimately find that the magnitude of morphological plasticity is linked to the extent of behavioral flexibility in a given taxon.

Because the distribution of phenotypes in trophic polymorphisms is bimodal, "developmental switches" have been proposed as a mechanism generating the vertebrate trophic polymorphisms (Sage

and Selander 1975; Collins and Cheek 1983; Meyer 1987; Pfennig 1990). Hypothetical developmental switch genes turn on alternative developmental pathways that are dependent on the environmental conditions encountered. Insect flight polymorphisms have been described as developmental switches (Harrison 1980; Roff 1986). For most examples of vertebrate polymorphism, the underlying developmental mechanisms are unknown; however, most, if not all, examples that result from morphological plasticity can be explained as the result of tissue response to biomechanical loading stimuli, where the underlying environmental stimulus is bimodal (for a potential exception, see Pfennig 1992). For example, in polymorphisms where one morph is feeding on some kind of armored prey, either snails or seeds, the force required to process the alternate diets is bimodal (e.g., Smith 1987; Meyer 1989). The characters that distinguish trophic morphs vary continuously within morphs and, at least in the case of *Scaphiopus* (Pfennig 1990), appear to vary as a direct function of the stimulus. If the response of the tissues involved (bone and muscle) is continuous and ontogenetic divergence appears to be gradual, why are there bimodal distributions of trophic morphology? The fundamental reason is that the underlying trophic niches are discontinuous (e.g., snails vs. no snails, hard vs. soft seeds, foraging for zooplankton vs. foraging for benthic organisms). Polymorphisms can thus be either the result of plasticity or disruptive selection on a continuously varying character. Until evidence is gathered to the contrary, it seems that the combination of tissue plasticity combined with a bimodal resource base is sufficient to explain the occurrence of polymorphisms, rather than resorting to a "developmental switch" hypothesis.

Ecological Correlates of Trophic Polymorphisms in Vertebrates

Trophic polymorphisms among vertebrates are mostly found in animals, such as fish, that subdue, handle, and process their prey using only their mouths. Other factors associated with the occurrence of trophic polymorphisms are the presence of alternative prey types that require different behavior and kinematics to capture and process, species-poor communities, and low dispersal of potential competitors and predators among populations.

In addition to all vertebrates with trophic polymorphisms using only their mouths or beaks to capture, handle, and process their food, they also lack appendages that can be used to subdue prey. Feeding specialization on different prey types that require mechanical differences in pursuit and handling has the potential to induce morphological differences as the result of morphological plasticity. Prey pursued in different situations require approaches different enough that the body shape differences such as those observed in whitefishes, charr, cichlids, and sticklebacks can result in either a single generation as the result of plasticity, over generations as the result of selection, or as a combination of both processes. Most aquatic vertebrates are limited to the use of their mouths for food capture, handling and processing and do not generally take bites out of their prey. It is striking that among amphibians and reptiles, the only documented cases of trophic plasticity or polymorphisms are found in the aquatic larval stages of anurans and urodeles, and in turtles, which are also largely aquatic. The lack of examples among mammals may be because many mammals have the potential to feed on different prey types in similar ways. Birds are more similar to aquatic vertebrates in that many birds also subdue, handle, and process their prey using only their beaks. One might predict

undetected trophic polymorphisms or variation in other vertebrates that use only their mouths for food capture, handling, and processing, such as snakes, if two prey types requiring different capture modes occur within the same population.

The second factor associated with trophic polymorphisms is the presence of alternate prey types that are captured using different kinematics. Trophic polymorphisms occur most often in lacustrine fishes. Lakes are characterized by limnetic (pelagic) and benthic (littoral) zones. These habitats are characterized by different suites of prey that require different modes of capture. Zooplankton populate the limnetic zone, while the benthic habitat harbors bottom-dwelling invertebrates. The presence of limnetic and benthic habitats is a stable feature of lakes. The relatively common occurrence of limnetic and benthic morphs in lake fishes is probably due to the temporal stability and ubiquity of these environments. The collapse of one prey species population will not make behavioral and morphological specializations useless.

An example of the ephemerality of a polymorphism based on a single prey species occurred in a Darwin's finch (*Geospiza conirostris*). Grant and Grant (1989) reported an unstable apparent polymorphism in this species. Beak shape differed between two groups of males that sang different songs. Type A males had longer, narrower and shallower bills than Type B males. Type A males fed from cactus fruits by drilling holes in the fruits and removing the seeds. Type B males tore open cactus pads with their beaks and fed on insect larvae and pupae. Cacti did not produce fruits for a couple of years and both the bimodal distribution of bill morphology and the association of bill morphology with song type disappeared in the following years.

In addition to limnetic/benthic polymorphisms, the other common kind of polymorphism occurs when a morph feeds on some type of armored prey such as snails or hard seeds. Vermeij (1987) has pointed out that armor reduces the vulnerability of prey, often making armored prey a relatively unexploited niche.

The presence or absence of other species can also influence the presence of polymorphisms. In general, species-rich communities provide fewer opportunities for niche expansion (Van Valen 1965); thus, polymorphisms generally occur in species-poor communities. All limnetic/benthic polymorphisms occur in northern temperate lakes, which are characteristically species poor. This may be the result of inadequate sampling in other areas. The absence of a species that is more efficient at exploiting certain prey provides the potential for the species that is present to expand its feeding niche. The absence of predators can also provide opportunities for niche expansion. For instance, Lindsey (1981) noted that lake whitefish, *Coregonus clupeaformis*, are only polymorphic in lakes where potentially competing ciscoes (more efficient zooplanktivores) are absent, and where their predators, pike (*Esox lucius* Linnaeus), are uncommon. In a number of descriptions of cichlid PJ variability, the presence or absence of other cichlid species may be correlated with the amount of PJ variation seen in the molluscivorous cichlids (Eccles and Lewis 1979).

Dispersal of lacustrine species is rare, so the absence of a species in a lake remains relatively constant and provides the potential for niche expansion of the species that are present. It is striking that very few instances of trophic polymorphisms occur in riverine environments, and none are known in marine environments. This difference may be because instances have not yet been documented, or because the same barriers to dispersal present in lakes are not found in marine and lotic systems. In environments where fewer barriers to dispersal exist, such as marine and riverine habitats, random differences in the type of species present may occur between communities, but may be less temporally stable than in lacustrine environments. As a result, long-term opportunities for niche expansion are

rarer than in lakes. Despite the presence of both pelagic and benthic habitats in marine systems, greater opportunity for dispersal prevents the formation of stable polymorphisms.

Riverine environments might provide "dimorphic" environments for fish, given the presence of a stable drift and benthic habitat. For instance, young-of-the-year brook charr, *Salvelinus fontinalis* (Mitchill), when inhabiting streams, specialize as either sit-and-wait foragers on drift, or actively forage on the benthos (Grant and Noakes 1987; also see Nielsen 1994). Unfortunately, morphology has not yet been examined. As is the case with marine fishes, the relative lack of dispersal barriers in riverine environments may prevent polymorphisms. Stream fishes are highly vagile (Grossman 1982). The importance of dispersal is illustrated by how the structure of stream fish communities is affected by the construction of barriers, such as dams, which restrict movement up and down rivers (Finger and Stewart 1987; Li et al. 1987). The dietary or habitat basis for the polymorphism seen in *Ilyodon* (Grudzien and Turner 1984) and the possible polymorphism in *Saccodon* (Roberts 1975), both stream fish, is unknown.

Plasticity, Polymorphisms, and Speciation

What role can plasticity play in trophic polymorphisms and subsequent reproductive divergence? The review above shows that variation in most aspects of trophic morphology can be environmentally induced. Greenwood (1974) speculated that morphological plasticity could contribute to speciation if it occurred with some other factor that enhanced reproductive isolation. Meyer (1990b) found that the PJ polymorphism in *Heros citrinellum* was correlated with a color polymorphism in that cichlid (McKaye 1980), fueling further speculation about the possible contribution of trophic polymorphisms to speciation. In previous work, I (Wimberger 1991, 1992) discussed the possibility of genetic assimilation (Waddington 1953, 1975) of character states originally expressed in response to certain environments. All of the above scenarios explicitly state that plasticity itself does not contribute to speciation, but if coupled with factors promoting reproductive isolation of morphs, it has the potential to contribute to the process. West-Eberhard (1986, 1989) summarizes evidence that both plasticity and polymorphisms may contribute to speciation.

Intraspecific polymorphisms suggest the possibility of sympatric speciation. However, sympatric speciation is considered by many to be highly improbable (Mayr 1963; Futuyma and Mayer 1980; Felsenstein 1981). Despite these theoretically based criticisms, some empirical observations of species suggest sympatric origin and have provided the impetus for disagreement (Bush 1969; Tauber and Tauber 1977, 1989; Diehl and Bush 1989). Models of sympatric speciation suggest that it could occur, but only under a very limited set of circumstances (Smith 1966; Felsenstein 1981). When examined in light of suggested examples of sympatric speciation, it becomes apparent that the models incorporate some assumptions that do not hold for the empirical examples, such as leaving the habitats for mating in a large common breeding pool (Diehl and Bush 1989).

The requirements for sympatric divergence include the following: fitness differences of morphs in the two habitats; habitat choice (philopatry) or assortative mating; mating within habitats; and temporal stability of different habitats. All of these conditions can occur as the result of behavioral and morphological plasticity. If all the requirements occurred as the result of plasticity, reproductive isolation could conceivably occur with no genetic differentiation between morphs! Some of the genetic models acknowledge that environmentally induced differences could contribute to reproduc-

tive divergence (Smith 1966; Diehl and Bush 1989; Wilson 1989), but this process needs to be modeled, and empirical data are needed for candidate groups.

I present below a simple conceptual model that illustrates how plasticity could contribute to reproductive divergence between morphs. This model borrows from the models and ideas of many people (Rosenzweig 1978; Felsenstein 1981; Smith and Todd 1984; Diehl and Bush 1989). It incorporates plasticity, and to begin with, is an explicitly nongenetic model. The environment consists of two habitats, each with a predominance of prey that require different foraging modes (e.g., a limnetic and benthic habitat). The organisms (fish) can feed on either prey type and can easily move between habitats. There are three stages to the life history: foraging, reproduction, and dispersal.

Initially the organisms begin to behaviorally specialize or develop a search image for a certain prey type that renders them more efficient at feeding on that prey type. Evidence for this type of behavioral specialization has been documented in many animals such as salmon (Nielsen 1994) and *Ambystoma tigrinum* larvae (Zerba and Collins 1991). This behavioral specialization exacts a small cost of switching.

As individuals become increasingly specialized and switch prey types less often, morphology begins to diverge as the result of morphological plasticity. As morphology diverges, the cost of switching increases. Differences in feeding efficiency of different morphs have been demonstrated in bluegill sunfish (Ehlinger and Wilson 1987), pumpkinseed sunfish (Wainwright et al. 1991), sticklebacks (Bentzen and McPhail 1984), guppies (*Poecilia* sp.) (B. Robinson, State Univ. New York, Binghamton, pers. comm.) and some of the different PJ morphs of cichlids (Hoogerhoud 1986; Meyer 1989).

After a season of foraging, reproduction occurs. One possibility is that both morphs will reproduce at exactly the same time, will not segregate by habitat, and will not choose mates based on some aspect of trophic differentiation. In this case reproductive divergence will not occur, as is apparent with *Heros minckleyi*, which exhibits random mating with respect to trophic morph (Kornfield et al. 1982).

However, other possibilities lead to positive assortative mating of morphs. For instance, if the temperature in the two habitats is different and spawning time is temperature dependent, the morphs will mate at different times, resulting in nonrandom mating (the allochrony hypothesis of Smith and Todd 1984). This mechanism of isolation may have occurred in whitefish. Another possibility is that after having spent much of their lives in different habitats, the morphs may choose nest sites more physically similar to their foraging grounds. Limnetic morphs may choose more open nest sites than benthic morphs. Body shape, size, or color differences induced by feeding on different foods may also form the basis for positive assortative mating. These phenomena occur in the Enos Lake stickleback (Ridgway and McPhail 1984). There is a positive association between PJ morph and color in *Heros citrinellum* that could lead to reproductive divergence (Meyer 1990b).

Now, there is some degree of nonrandom mating based solely on differences that have arisen as the result of plasticity. However, for reproductive divergence to occur, philopatry among the young to their parents' foraging grounds is needed. Philopatry to reproductive grounds occurs in many birds (Shields 1982) and insects (Bush 1975), and is known to occur in fishes such as charr (Johnson 1980), whitefish (Smith and Todd 1984), and salmon (Hasler and Scholz 1983); however, the extent to which "philopatry" to feeding grounds occurs is unknown. Possibly, it could result in fishes when one of the parents guards the young and is followed by the young to its feeding grounds. And then the cycle begins again.

If a genetic component is added to the model, selection would probably reinforce the initial divergence. If selection acts upon trophic morphology so that fish with the most extreme genetically based morphologies for the alternate foraging modes are the fittest (disruptive selection), homomorphic matings would produce offspring initially better adapted to foraging in the parental fashion. In contrast, offspring from heteromorphic matings would possess intermediate morphology and be, as a result, less efficient foragers. Once reproductive isolation occurs, the differences initially expressed as the result of plasticity will probably become genetically determined relatively rapidly. Thus, the contribution of morphological plasticity to morphological differentiation will be temporally transient under conditions where selection acts upon morphology and reproductive isolation ultimately occurs.

Clearly, simulations are needed to estimate the theoretical values at which reproductive divergence could occur. Also, empirical data are sorely needed that indicate the values for many of these variables in polymorphic populations.

The temporal stability of the selective agents (prey, competitors, predators) is the key factor in determining the evolutionary potential of the polymorphism (Roff 1986; Diehl and Bush 1989). If relative prey abundances of the different prey types or community membership fluctuate, the ability to exploit alternative niches may exist for a short time—but the potential for the polymorphism to contribute to reproductive isolation of the morphs is small.

Origin of Trophic Polymorphisms: Sympatric or Allopatric?

In part of the previous discussion, I assume that at least some of the trophic polymorphisms in which morphs are reproductively isolated arose sympatrically. However, for charr, whitefish, and stickleback trophic polymorphisms, both allopatric and sympatric origins have been suggested.

The allopatric hypotheses for charr and whitefishes are similar. Svärdson (1965, 1979, 1988) and others (Behnke 1980; Bernatchez and Dodson 1990) have proposed that whitefish and charr morphs evolved in separate glacial refugia, and that lakes currently containing multiple morphs are the result of secondary contact of the different morphs after the last glacial recession. Lakes with multiple morphs of charr and whitefish are common (Svärdson 1979). In the allopatric scenario, it is not clear why glacial refugium lakes did not contain more than a single morph given the present ubiquity of lakes containing multiple morphs. Support for the allopatric hypothesis derives from the fact that lakes containing multiple morphs are sometimes in clusters (e.g., Maine lakes in Allegash Basin), a pattern one would expect in zones of secondary contact between refugia. However, Lindsey et al. (1970) suggest that there may be many more lakes containing multiple morphs than have been documented. Smith and Todd (1984) and Klemetsen (1984) infer that both sympatric and allopatric speciation have occurred for whitefishes and charr, respectively.

McPhail (in press) argues that different stickleback morphs are allopatric in origin and derive from successive invasions of a marine ancestor when the sea level rose. He proposed that lakes were invaded by marine forms twice—12,500 and 11,500 yr ago—and that reproductive isolation between the marine and lake forms occurred between the invasions. However, Schlüter and McPhail (1992) acknowledge the possibility of sympatric differentiation.

Inferring process from pattern is a Sisyphean task. Molecular systematics and phylogenetic methodologies may provide a means by which the sympatric and allopatric origin of morphs can be better distinguished. The sympatric and allopatric hypotheses result in two distinct phylogenetic hypotheses. If morphs arose in sympatry, a phylogeny ideally will show that different morphs within a lake are more closely related to each other than they are to either morph in any other lake. If the allopatric hypothesis obtains, a phylogeny will show that similar morphs in different lakes are more closely related to each other than they are to other morphs, even within the same lake. Extensive ancestral polymorphism and introgression will unfortunately obscure these patterns. Hindar et al. (1986) and Bernatchez and Dodson (1990) have begun to profitably exploit these techniques, but the data are equivocal.

Bernatchez and Dodson (1990) attempted to distinguish between the hypothesized sympatric and allopatric origins of lake whitefish morphs in Maine using mitochondrial restriction site data, but their data are not conclusive. They sampled both morphs from one of the two-morph lakes and a single morph from two other two-morph lakes. In addition, they sampled single-morph lakes to the east and west of the Maine lakes. There were two major classes of mitochondrial types: one type characterized fish from a western refugium, and the other type characterized fish from an eastern refugium. In the one lake where both morphs were sampled, the morphs sorted out perfectly into the two major mtDNA haplotypes; however, in both of the one-morph lakes, that morph was characterized by both of the major mtDNA haplotypes.

Isozyme analysis of *C. clupeaformis* in western Canada indicates the presence of two different refugia (Bodaly et al. 1988), suggesting that the sympatric presence of different morphs is due to secondary contact after the last glacial recession. Dwarf and normal morphs have significantly different allele frequencies within lakes, but normals appear to derive from both refugia and dwarfs do not appear to be monophyletic in origin (Bodaly et al. 1988).

An extensive allozyme survey of charr morphs in Norway studies indicates that, in most, cases sympatric morphs are electrophoretically more similar to each other than they are to similar morphs in different lakes (Hindar et al. 1986; but see Nyman 1972; Klemetsen and Grotnes 1980). This observation suggests sympatric differentiation.

Questions and Future Directions

The examples of plasticity and trophic polymorphisms in vertebrates provide many avenues for further research. The following general questions and issues need to be addressed for many of the documented cases and any new ones. The relative contribution of genetics and environment for most of the polymorphisms still needs to be elucidated. The ecological factors associated with the presence or absence of polymorphisms in any given population need examination. For example, what other species (competitors, predators) are present, and how stable are alternative food resources? How stable are the polymorphisms over time? There is a need for empirical data addressing the extent of behavioral and morphological plasticity, the feeding efficiency or fitness costs associated with plasticity or intraspecific morphological variation (see Helfman 1994), and the extent to which philopatry and assortative mating occur in polymorphic populations. The issue of sympatric or allopatric origin of different charr, whitefish, and stickleback morphs needs further study. Finally, plasticity needs to be included in theoretical models of reproductive isolation.

Trophic polymorphisms provide us with one of the richest sources of ecomorphological data; one can look at ecological and morphological differences free of confounding different phylogenetic histories, and look directly at efficiency or fitness effects of the observed differences. Even though trophic polymorphisms are important for only a limited number of species, the insights into the development and maintenance of these polymorphisms will provide us with a greater understanding of ecological and evolutionary questions.

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