RESOURCE VARIATION AND THE EVOLUTION OF TROPHIC PLASTICITY IN FISHES

A Thesis

by

CLIFTON BENJAMIN RUEHL

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2004

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

Thomas J. DeWitt (Chair of Committee)	James L. Pinckney (Member)
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ABSTRACT

Resource Variation and the Evolution of Trophic Plasticity in Fishes.

(May 2004)

Clifton Benjamin Ruehl, B.S., Trinity University

Chair of Advisory Committee: Dr. Thomas J. DeWitt

Resource variation and species interactions require organisms to respond behaviorally, physiologically, and morphologically within and among generations to compensate for spatial and temporal environmental variation. One successful evolutionary strategy to mitigate environmental variation is phenotypic plasticity: the production of alternative phenotypes in response to environmental variation. Phenotypic plasticity yields multiple characters that may enable organisms to better optimize phenotypic responses across environmental gradients. In this thesis, I trace the development of thought on phenotypic plasticity and present two empirical studies that implicate phenotypic plasticity in producing morphological variation in response to resource variation.

The first empirical study addresses trophic plasticity, population divergence, and the effect of fine-scale environmental variation in western mosquitofish (*Gambusia affinis*). Offspring from two populations were fed either attached or unattached food items offered in three orientations: (1) water surface, (2) mid-water, (3) benthic, and (4) a daily rotation of the former three (fine-grained variation). Attached food induced wide heads, blunt snouts and rounded pectoral fins relative to morphology in the unattached treatment. Mid-water feeding induced elongated heads and deeper mid-bodies relative to benthic and surface feeding induced morphologies. The rotating treatment produced intermediate morphologies. Population divergence seemed related to both trophic and predation ecology. Ecomorphological consequences of induced morphologies and the need for inclusion of greater ecological complexity in studies of plasticity are discussed.

The second study examines induced morphological plasticity and performance in red drum (*Sciaenops ocellatus*). I fed hatchery fish either hard or soft food for two months. Performance trials were designed to measure their ability to manipulate and consume hard food items. External morphology and the mass of pharyngeal crushing muscles were assessed for variation among treatments. A hard food diet induced deeper bodies and larger heads, more massive pharyngeal muscles, and initially more efficient consumption of hard food than fish receiving soft food. The observed morphological variation is in accordance with variation among species. Determining evolutionary mechanisms operating within red drum populations should eventually aid in developing and optimizing conservation efforts and ease the transition from hatchery facilities to estuaries.

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As a child my brothers and I were encouraged by our parents to spend time outside camping, backpacking, canoeing, but most importantly fishing and messing about in boats. These weekend adventures and vacations had profound influence on my eventual career choice. Without them I would have never discovered my love for and curiosity about nature. I owe this discovery to my family and I am forever indebted.

My parents have instilled in me a faith in God and the qualities of a good work ethic, persistence, drive, and a thirst for knowledge. They have listened to my ramblings, taught me patience, and have had faith in me when I was in doubt. My brothers have provided me companionship, encouragement, and necessary diversions. The gratefulness of these gifts cannot be conveyed with words.

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CHAPTER I

INTRODUCTION

The phenotype can be an inner physiological change, a behavioral response, or a visible expression of morphology. All of these responses stem from the interface among genotypes and environmental influences for given traits. As environments are rarely stable for long periods the interaction between the environment and the genotype often produces a variety of phenotypes across time. The production of alternative phenotypes by a single genotype in response to environmental cues is known as phenotypic plasticity. Organisms often alter phenotypes in accord with temporal and spatial changes in environments to maintain relatively high fitness (Schmalhausen 1949, Bradshaw 1965, Stearns 1989, West-Eberhard 1989, Pigliucci 2001).

Massimo Pigliucci (2001) reviewed the development of thought on phenotypic plasticity in his book "Phenotypic plasticity beyond nature and nuture." He begins with Weismann, in eighteen-eighty three who acknowledged that the soma (body) was influenced by the environment while the germline (reproductive cells) seemed to be static. The influence of the environment on the body was well established by the early twentieth century although studying the environment's role in the production of phenotypes did not become conceptually meaningful to evolutionary biology until nearly a century later (Bradshaw 1965, Pigliucci 2001). In the interim, the concept that

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This thesis follows the style and format of Ecology.

environmentally induced phenotypic variation might be meaningful to evolution was often lost. Concurrently animal husbandry researchers and experimental biologists actively sought ways to eliminate and control phenotypic “noise” that only served to muddle results.

Evolutionary biology was a burgeoning field in the early twentieth century culminating in the nineteen thirties and forties with the modern synthesis on evolutionary thought (Huxley 1942). Plasticity was largely left out of the modern synthesis and did not take center stage in evolutionary biology until the mid nineteen eighties, despite Herculean efforts during the sixties (Bradshaw 1965, Pigliucci 2001). What prevented plasticity from being more intimately involved in the synthesis during the thirties and forties? What prompted its renaissance in the eighties and nineties? What is the current state of studies involving plasticity? What are potential directions for future studies of genotype-environment interactions?

I will begin by placing plasticity in a historical context through the development of modern evolutionary thought and offer insight into the previous questions. I then turn to a discussion of current trends in plasticity and offer suggestions for future studies in plasticity. The next two chapters are empirical tests designed to incorporate several of these suggestions.

Plasticity Revealed

Pigliucci (2001) begins the book with a quote from Darwin that was found in a letter to Karl Semper in eighteen-eighty one: “I speculated whether a species very liable to repeated and great changes of conditions might not assume a fluctuating condition ready to be adapted to either condition." Most certainly Darwin is alluding to what is now referred to as phenotypic plasticity, although it was some forty years later that Nilsson-Ehle used the term "plasticity" as it is meant today (Bradshaw 1965, Sarkar 2004). Sixteen years after Darwin's letter to Semper, Darwinian evolution was floundering as it lacked a mechanism for the inheritance of phenotypic change that Lamarkian and other evolutionary theories provided (Bowler 1983). However, in eighteen-ninety six James Baldwin proposed a new application for Darwin's theory of natural selection. He proposed, using learned behavior and consciousness in mammals, that in addition to possessing a variety of phenotypes, individuals varied in their response to changing environments (Baldwin 1896, Robinson and Dukas 1999). Those individuals most "plastic" in their "neurologic" response were able to thrive in the face of environmental variation and contributed more offspring possessing those characters to the next generation, thus improving (stabilizing) the condition of the species to the current environment. It should be noted that Baldwin used the term "plastic" in a very broad sense of learned behavior and consciousness that was passed between generations (Baldwin 1895, 1896, Schlichting and Pigliucci 1998). Baldwin's ideas caught on and led to a renaissance of Darwinian evolution that has persisted to the present. More importantly, for the purposes of this paper he introduced the idea that various responses to environmental variation are passed through generations (i.e. heritable plastic traits). However, these ideas were not seriously considered until nearly a century later.

Pigliucci (2001) continues his review by pointing to Wilhelm Johanssen's (1909) distinction between, the now commonly used terms, "genotype" and "phenotype," which formally discriminated the concepts established by August Weismann in eighteen-eighty three. These developments were independent of Gregor Mendel's discoveries in pea plants between eighteen-fifty six and eighteen-sixty five. Mendel used the term "hereditary factors" for genes and was largely silent concerning phenotypic variation. Weismann and Mendel are largely credited with the development of modern genetical study and laid the ground work for the modern evolutionary synthesis of the nineteen thirties and forties (Huxley 1942, Bowler 1983, Schlichting and Pigliucci 1998, Pigliucci 2001).

With the distinction between genotype and phenotype solidified, Johanssen and others directed their research towards identifying reasons why phenotypes were not identical to genotypes. Pigliucci (2001) continues with the development of Richard Woltereck's work who was a devout selectionist convinced the genotype was directly responsible for producing phenotypes. He set out to prove evolution through continuous change using daphnia. It was fortuitous he chose daphnia as it was later discovered his experiments were among the first documented cases of adaptive phenotypic plasticity. Through his culture experiments and field collections of daphnia he observed cyclical variation in helmet size ("cyclomorphosis") in several German lakes throughout the year (Schlichting and Pigliucci 1998, Pigliucci 2001). It was disturbing to him that progeny of these organisms did not always produce the same phenotypes despite controlled laboratory conditions. He concluded, most disappointingly, that variation in helmet sizes resulted from genotypical change instead of differential phenotypic production of a single genotype. He saw his results as a strike against continuous evolution because the heritable factor (genotype) was not static and did not translate directly to the phenotype (Johannsen 1911, Dodson 1989, Schlichting and Pigliucci 1998, Pigliucci 2001).

Johanssen and others reasoned another factor was involved in the production of the phenotype and implicated the environment as that factor. Johanssen saw the genotype as being static with environmental conditions determining the degree and nature of phenotypes (Johannsen 1911). Pigliucci (2001) points out that Johanssen interpreted Woltereck's results more correctly by building on his distinction of the phenotype and genotype. Johanssen reasons that the development of differential helmet sizes might be a phenotypical response to various environmental conditions, not a genotypical response. It seemed obvious to Johanssen:

> [T]he *reactions of the genotypical constituents*, may under different conditions exhibit all possible forms of transition or transgression—this has nothing at all to do with constancy or inconstancy of genotypical differences... temperature has great influence upon the intensity of color in flowers… Such pure white flowering individuals are—as to color—phenotypically not distinguishable from genotypically pure "white" varieties. Nobody will assume that there should be *genotypical* transitions here … (Johannsen 1911)! (his italics and punctuation)

Johanssen's interpretation did not negate continuous evolution. It proposed that the genotype remained static, while the phenotype was the product of an interaction between the environment and the static genotype. Johanssen's interpretation supported continuous evolution, which is rather ironic as he was in the camp, as most Medelians, that evolution occurred through saltationism (Mayr and Provine 1980).

Woltereck, while misinterpreting his results still made a considerable contribution to evolutionary biology through his elegant display of results from his daphnia experiments. He was the first to develop what is commonly referred to today as the reaction norm—a curved plot of the phenotype's response to an environmental gradient (Dodson 1989). He called them "phenotypic curves" or "reaktionsnorms" and argued they were the heritable factors with modifications of the norm indicating a hereditary change (Sarkar 2004). Thus, he suggested that the genes changed as a function of the environment. This interpretation confirmed his belief that a genotype maps directly to a phenotype with no variation. Johanssen adopted the term "reaktionsnorms" and likened it to his concept of the genotype (Johannsen 1911). Woltereck's reaction norms were immediately used in the Soviet Union to represent phenogenesis, forgotten in the west until nearly the seventies and applied elsewhere during the nineteen twenties (Sarkar 2004). Thus, the course was set for the conceptual development of phenotypic plasticity but the path was only traveled in fits and starts for another quarter century when major advances were made but not followed through.

Plasticity and the Modern Synthesis

Pigliucci (2001) continues his review on plasticity by discussing the very minor role it played during the modern evolutionary synthesis. T. Dobzhansky, G. G. Simpson, B. Rensch, J. Huxley, J. B. S. Haldane, R. A. Fisher, E. Mayr, and many others brought together disparate aspects of biological research between the years of nineteen-thirty six and nineteen-forty seven in a theory of evolutionary biology that Huxley called the "evolutionary synthesis" (Huxley 1942, Mayr and Provine 1980). The synthesis united rival factions of naturalists and geneticists under the premise that (1) gradual evolution occurs through small genetic changes, recombination, and natural selection. (2) The observed diversity of flora and fauna on earth results from these genetic mechanisms (Mayr and Provine 1980). The molders of the synthesis largely combined population genetics, cytology, zoology, and paleontology to develop theories of micro- and macroevolution. However, research conducted in embryology and morphology played lesser roles in the developing synthesis (Mayr and Provine 1980).

The modern synthesis concentrated on proximate causes of evolution to answer ultimate questions. The evidence used to determine the mechanisms of evolution was principally from the budding field of genetics. Although Dobzhansky and the others recognized the importance of the phenotype and environmental influences in the development of organisms, they regarded them as less important factors than the gene in understanding the basis of evolution. This might have resulted from a lack in understanding the importance of the environment in development. Because embryologists and morphologists read and published in different journals they could not keep up with the literature in other fields such as genetics or cytology and may not have been fully aware of the advancements surrounding the synthesis. Likewise, disparity within their respective fields concerning rivaling theories of evolution, whether it was Lamarkism, Darwinism, or Orthogenesis may have served to limit the contributions made by their respective fields (Mayr and Provine 1980). Thus, the organismal studies, but more precisely the phenotype (except as it related to specific mutations) and therefore plasticity, did not have a large influence on the modern synthesis.

Pigliucci (2001) takes special consideration of two individuals that incorporated embryology, morphology, and paleontology into their own theories of evolution during the critical time of the synthesis. Ivan I. Schmalhausen published his seminal work in Evolutionary Biology: *Factors of Evolution: The Theory of Stabilizing Selection* (1949) in Russia where it would have remained except Dobzhansky, his compatriot had it translated to English in nineteen-forty nine. In the United States however, Conrad Waddington set out to empirically prove the importance of development and environmental influence in evolution using *Drosophila*. He independently derived theories very similar to Schmalhausen's. They both made significant efforts to include studies of the organism, development, and the environment into evolutionary thought. But for a variety of reasons the synthesis was principally solidified without their influence.

Schmalhausen not only called for the incorporation of the organism (embryology and morphology) into the modern synthesis, he also implicated the importance of plasticity (external environmental influences). *Factors of Evolution* is divided into four sections that all have significant bearing on current theories of phenotypic plasticity (Pigliucci 2001). Schmalhausen clearly distinguishes between internal and external factors that lead to the development of characters in an individual organism. He points out that both are equally important and dependent on each other:

> Every organization, the typical as well as the variant (including mutants), does not pre-exist but develops on a specific hereditary foundation (genotype). This development is determined not only by the genotype but also by the environmental factors" (Schmalhausen 1949).

Schmalhausen goes on to introduce the concept of reaction norms, however he never mentioned Woltereck's work. This is surprising in light of Sarkar's (2004) statement that "reaktionsnorms" experienced popularity in the Soviet Union during the early part of the twentieth century. Schmalhausen expands earlier work on reaction norms by applying the concept to the theory of stabilizing selection, initially proposed by W. Bateson, J. B. S Haldane, and R. A. Fisher (Schlichting and Pigliucci 1998, Pigliucci 2001). The original theory predicts organisms with extreme characters in a population would be eliminated in favor of the population mean. Pigliucci (2001) points out that Schmalhausen applies the term in the traditional fashion but additionally uses it to interpret the development of new reaction norms through selection. In the section of the book entitled "Adaptogenesis," Schmalhausen ventured that organisms respond to environmental fluctuations through alteration of reaction norms. He quite ingeniously applied this process to a much broader scale as he implicated adoption of the new reaction norm as a process for speciation events. He theorized that drastic environmental change should cause aspects of the old reaction norm to be replaced and subsequently lost in lieu of a new reaction norm fit for current environmental challenges. Thus, the new reaction norm is *stabilized* and the phenotype produced becomes the *wild-*

type, these phenotypical change would eventually accumulate to produce new species (Schmalhausen 1949, Pigliucci 2001).

Schmalhausen recognized the importance of the phenotype and the environment in the process of both micro- and macroevolution but felt it was an addition to the modern synthesis—not an integral part (Mayr and Provine 1980). Waddington advocated the inclusion of the phenotype (morphology and development) into the modern synthesis and was adamant that the synthesis would not be complete without these additions (Gilbert 1994). In empirical tests he subjected *Drosophila* to extreme conditions for several generations and noted morphological and developmental changes. He then reared offspring of the eccentric individuals in normal conditions and discovered they retained the adaptations developed in the extreme environments. Waddington argued the extreme traits had become "canalized" and termed the process "genetic assimilation" (Waddington 1942, 1959). Waddington defined canalized traits as persisting despite changes in both internal and external environments. Schmalhausen would have claimed a new *wild-type* was created for the extreme environment through the adoption of an alternative reaction norm using his theory of stabilizing selection. Waddington's experimental results are considered today as a loss of plasticity (Schlichting and Pigliucci 1998). Gilbert (1994) points out that Schmalhausen's and Waddington's theories were so similar the translator of Schmalhausen's book, Isadore Dordick, used the term "canalized" where surely Schmalhausen would have used stabilizing: "Such reactions are canalized into a narrow channel of a more specific norm which is adapted to definite conditions of the external environment..." (Schmalhausen 1949, Gilbert 1994).

Pigliucci (2001) concludes that Schmalhausen's work was largely theoretical but tragically he was never able to disseminate his work or test his theories empirically as Lysenko's rise to power marked the end of evolutionary genetic work in the Soviet Union. His book was well received in America and elsewhere, however much of the synthesis was established before the book was seriously considered by scientists. Waddington's empirical work with fruit flies was criticized for describing rare and unnatural cases and his theories were discounted by Dobzhansky and others as being Lamarkian (Gilbert 1994). However, as Pigliucci (2001) states, and Waddington himself makes clear, he did not interpret his results as implicating Lamarkian evolution (Waddington 1959). Waddington might have been estranged as an evolutionary biologist because of his intense belief that the modern synthesis was incomplete without the addition of embryology and morphology (Gilbert 1994). Schmalhausen, on the other hand held the less extreme position that the two complimented the synthesis. These unfortunate circumstances were not the primary reason for the exclusion of plasticity and development from the synthesis. By the nineteen forties, biological research had largely taken a turn towards genetic evidence for evolution (Sultan 1992, Schlichting and Pigliucci 1998).

Sonia Sultan reviewed the impact of phenotypic plasticity in the modern synthesis and concluded that it was largely absent, as a result of the narrow view framers of the theory took concerning the transmission of genes (Sultan 1992). The scientists chose a reductionist approach to the synthesis that Provine (1988) has called an "evolutionary constriction" as it did not include studies of development or the environment. Sultan (1992) argues the values and intellectual preconceptions of the practitioners of the modern theory are largely responsible for the absence. She believes the answer lies in two aspects of the conceptual environment during the mid-nineteen hundreds. First, organisms were seen as a passively determined outcome of their genetic program and therefore independent of environmental influences. The second factor was the strict definition that selection could only act on discrete heritable variants. Those traits affected by the environment were seen as not truly heritable and therefore not subject to selection, thus plasticity was omitted (Sultan 1992). Both of these factors were in stark contrast to views held by Schmalhausen and Waddington who believed evolution occurred through the interaction of the environment and the genotype. However, as Sultan (1992) suggests, the genotype-phenotype mapping function is highly complex and makes experimental as well as mathematical theory of the phenomenon very difficult. It is also unrealistic to limit studies in scope or complexity so they will fit within an accepted research mantra. But, perhaps the scientists of the thirties and forties promoted a reductionist research program for evolution because of the overwhelming nature of including aspects of environmental variation. These rather unfortunate circumstances and interpretations combined with the shift in biological research towards cellular and molecular levels meant phenotypic plasticity was not seriously considered as a factor in evolution for another quarter century.

Plasticity Revisited - A. D. Bradshaw

Although plasticity was not at the forefront of evolutionary biology during the forties and fifties both empirical and theoretical research continued to develop and further define the genotype-phenotype mapping function. As Schlichting and Pigliucci (1998) point out, Waddington continued his work on genetic assimilation in *Drosophila*. He was joined by a trio of plant biologists, J. Clausen, D. Keck, and W. Hiesey that made significant strides in defining the response of the genotype to environmental fluctuations. They sought to connect genetic and environmental effects to the production of phenotypes and discover the genetic basis of observed morphological variation across environments. The trio observed that genetic variation among races mimicked variation observed among species potentially providing a link between micro- and macroevolution. This research along with other research in plants provided fodder for a synthesis of phenotypic plasticity implicating its importance, relevance, and role in evolution (Schlichting and Pigliucci 1998).

A. D. Bradshaw, in a single work entitled “Evolutionary Significance of Phenotypic Plasticity in Plants” (1965) provided this synthesis. Pigliucci (2001) reviews Bradshaw’s seminal work on the importance of phenotypic plasticity to evolutionary studies. Bradshaw’s paper thoroughly defines plasticity and discusses its genetic basis as well as its relevance to different forms of selection. In the opening pages of the paper Bradshaw keenly narrowed the concept of phenotypic plasticity to morphological and physiological manifestations of the genotype in response to the environment. He pointed out that plasticity is not necessarily adaptive but it is specific to a character, specific in direction, responds to specific environmental influences, is under genetic control, and is subject to selection (Bradshaw 1965).

In the next several sections of the paper Bradshaw discussed fitness consequences of plasticity, conditions favoring plasticity, and how disruptive, directional, and stabilizing selection can favor the evolution of plasticity. Bradshaw argues that, in many cases, plasticity is adaptive where flexibility in phenotypes allows the organism to survive in the midst of environmental fluctuation. He seemed intrigued with the thought that variation in phenotypes is not necessarily due to a lack of adaptation or a mark of genotypic instability as implicated by scientists and animal breeders at the time. The potential advantage for instability in some characters is exemplified in this quote: "…maximum fitness does not require the same degree of stability in all characters. As a result of natural selection those characters in which stability is paramount for survival are likely to show greater stability than those in which some plasticity is not a disadvantage" (Bradshaw 1965).

Bradshaw concluded the paper by reiterating that plasticity is genetically based, subject to selection, displays various degrees of control ranging from almost complete canalization to continuous plasticity, and most importantly he states that plasticity can be of adaptive value under disruptive, directional, or stabilizing selection. This last point is important as it implicates plasticity as an evolutionarily important mechanism. He contends that placing plasticity in an evolutionary framework will require knowledge of how much genetic variability is available in natural populations for plasticity, the extent of genetic control in plasticity, and the ease with which selection operates on plasticity.

These suggestions for future studies on plasticity are monumental for the time as well as critical to the eventual incorporation of plasticity into theories of evolution. However, few researchers adopted Bradshaw's ideas or incorporated them into their research programs for another two decades (Schlichting 1986, Sarkar 2004).

Plasticity to the Front

During the mid nineteen eighties researchers returned to studies of genotype-environment interactions. Empirical and theoretical studies served to spark a revitalization of plasticity and served to place concepts of phenotypic plasticity at the forefront of evolutionary research by the mid-nineties. As Pigliucci (2001) points out a plethora of empirical studies emerged during this time examining the evolutionary consequences of plasticity in a diverse number of taxa including plants, salamanders, fish, and insects (Petrov and Petrosov 1980, Matsuda 1982, Turkington 1983, Scheiner and Goodnight 1984, Via 1984a, b, Meyer 1987, Schlichting and Levin 1988). Many of these studies not only document plasticity in field and laboratory settings they discuss it in the context of genetic assimilation, speciation, or the adaptive value and functional ecology of plasticity. Studies of trophic plasticity in fishes are a prime example of the empirical research at the time. Meyer (1987) and Wimberger (1992) both induced morphological variation in cichlids by rearing fish fed different diets and discussed the implications of plasticity on speciation. Meyer (1990) examined field caught *Cichlasoma citrinellum* and found seasonal fluctuations among two trophic morphologies corresponding to the abundance of different types of prey implicating lability of traits. Several reviews now cover the research on plasticity in fishes (Robinson and Wilson 1994, Smith and Skulason 1996, Rundle et al. 2000, Robinson and Parsons 2002).

Likewise, a glut of theoretical papers seeking to model the evolution of phenotypic plasticity emerged during the eighties and persists to the present (Via and Lande 1985, Lively 1986, Stearns and Koella 1986, de Jong 1990a, b, Gomulkiewicz and Kirkpatrick 1992, Moran 1992, Kawecki and Stearns 1993, Zhivotovsky et al. 1996, Pigliucci 2001, Berrigan and Scheiner 2004). These were largely quantitative genetic models and gametic models seeking to clarify evolutionary dynamics of quantitative characters in spatially and or temporally heterogeneous environments (Sarkar 2004). In particular Via and Lande (Via and Lande 1985) developed models on the evolution of plasticity in two independent coarse-grained environments (intergenerational environmental variation) for both soft and hard selection. "Soft" selection assumes that population size at the time of migration is independent of selection as each sub-population is of constant size across generations, whereas "hard" selection assumes the sub-population varies in size according to differential survival occurring prior to migration (Wallace 1968, Christiansen 1975, Via and Lande 1985). Via and Lande modeled the evolution in four separate cases: (1 & 2) a panmictic population under soft and hard selection; and (3 & 4) a sub-divided population under soft and hard selection. They assumed weak selection, a large population size, intermediate trait optima and that selection was stronger than effects due to mutation, drift, epistasis, and recombination (Via and Lande 1985, Sarkar 2004). Via and Lande found that as long as the genetic correlation was not ± 1 and there was no cost of plasticity, then models one and two arrived at a joint optimum, and models three and four had similar conclusions if gene flow was allowed (Via and Lande 1985, Sarkar 2004). Their findings led to models incorporating greater complexity (Stearns and Koella 1986, Via et al. 1987, van Tienderen 1991, Gomulkiewicz and Kirkpatrick 1992) and a debate on whether phenotypic plasticity is a target of selection and thus a separate set of genes, or a by-product of selection where plasticity evolves due to selection toward different phenotypic optima in alternative environments (Via 1993). For a through discussion of this debate read (Sarkar 2004). Other researchers assumed plasticity evolved, and concentrated on defining the realm through which plasticity operates in organisms (DeWitt et al. 1998, West-Eberhard 2003).

Both empirical and theoretical models provided fodder for review articles in the late eighties and early nineties (Schlichting 1986, Sultan 1987, Stearns 1989, West-Eberhard 1989, Thompson 1991, Pigliucci 2001). Among the most influential was by West-Eberhard (1989). With very broad strokes she addresses the importance of plasticity in evolutionary studies. The article reiterates Bradshaw's points made concerning the genetic basis and availability for selection of plasticity, but additionally West-Eberhard defines terms important to plasticity and clearly describes the role of plasticity in the initiation and amplification of change in organisms.

West-Eberhard establishes the role of plasticity in creating adaptive changes in organisms and then implicates plasticity as a mechanism for speciation describing the role it might play in macroevolution. She reinforces both of these concepts with examples from the primary literature building a strong case for plasticity's role as an initiator of large scale patterns of diversity in form. West-Eberhard concludes by making a plea for

> [A] change in how many biologists currently view the evolution of phenotypes…it requires understanding the sense in which characters do not have to be "genetic" (immune to environmental effects) to be evolutionarily important; and the manner in which phenotype expression, especially when there is a switch or bimodal distribution of forms, can focus natural selection to produce extensive divergent specialization without reproductive isolation (West-Eberhard 1989).

She further comments that plasticity had long been considered as an evolutionary force and was not in conflict with current evolutionary theory. Quite the contrary, she argued that incorporation of plasticity into evolutionary theory should clarify issues regarding speciation, and the origins of major novelties, a view reminiscent of Waddington's (Waddington 1975, West-Eberhard 1989, Schlichting and Pigliucci 1998, Pigliucci 2001). Despite her plea, much of the research on plasticity continued to describe the functional significance and novelty of plasticity across taxa instead of examining it as a factor that may promote diversification.

Plasticity in the Present and Beyond

The current state of phenotypic plasticity studies has moved in several interesting directions. Descriptive work on the generality of plasticity continues with rearing studies and field collections. Researchers are currently testing the adaptive nature of plasticity through performance trials and testing for functional tradeoffs for induced morphologies (as reviewed in Agrawal 2001a, b, Agrawal et al. 2002, Michimae and Wakahara 2002, Johnson et al. 2003, Weinig et al. 2003).

When considering species interactions, reliability of cues, and trophic structure; studies of plasticity need to incorporate more complexity in order to more accurately mimic natural complexity (DeWitt and Langerhans 2003 for further discussion see chapter II). Community and evolutionary ecologists are incorporating plasticity into studies of interactions among species (Chase 1999, Relyea 2000, Agrawal 2001a, Relyea 2002, Relyea and Yurewicz 2002, Werner and Peacor 2003). Currently many studies of species interactions look at only one side of the equation, how species X affects species Y, instead of considering the possibility of reciprocal interactions in a continual fashion similar to coevolutionary change (e.g. an evolutionary arms race) (Agrawal 2001a).

Cross domain work, such as incorporating multiple aspects of species interactions are also emerging (Johnson et al. 2003, Luttbeg et al. 2003, Vanhooydonck and Van Damme 2003, Werner and Peacor 2003). Studies indicate that predators directly affect behavior and morphology of prey (Crowl and Covich 1990, Bronmark and Miner 1992, DeWitt et al. 1999, Turner et al. 2000, Langerhans and DeWitt 2002). However, behavioral and morphological accommodations such as reduced activity, or altered habitat use affects prey resources. Thus, the prey’s initial response to a predator eventually cascades throughout the food web (Beckerman et al. 1997, van Buskirk and McCollum 2000, Agrawal 2001a). Additionally, predators potentially affect prey behavior and morphology indirectly. For example, predators may directly affect prey behavior by relegating them to fringe habitats. The fringe habitats probably have a different resource base that requires prey organisms to respond morphologically through the induction of alternate trophic characters as a result of feeding on alternative resources (Chapter II). Thus, predators potentially have direct and indirect effects on trait expression in prey as well as affecting other links within the food web. Multiple selection pressures operating within communities make studies concerned with evolutionary mechanisms very challenging. But adding complexity (e.g. fine scaled variation and aspects of predation) to a well designed laboratory experiment should aid in understanding indirect effects in community ecology (Chapter II).

Plasticity studies have also considered the costs and limits of plasticity. DeWitt et al. (1998) reviewed existing data and outlined several areas of endeavor for students of plasticity to consider. They identified nine potential costs and limits of plasticity: maintenance costs, production costs, information acquisition costs, genetic costs- (1) epistasis (2) pleiotropy, developmental instability, information liability limit, lag-time limits, developmental range limit, and epiphenotype problems. Recently, many studies have examined the costs of plastic responses (Relyea 2002, Benard and Fordyce 2003, Cipollini et al. 2003, Loman and Claesson 2003, Steinger et al. 2003, Teplitsky et al. 2003). Limits of plasticity have also been examined and seem more plausible than costs (Weinig 2000, Donohue et al. 2001, Langerhans and DeWitt 2002, Piersma and Drent 2003). Reliability of cues, time lags in responding to environmental cues; or the range through which plastic traits can respond might be limited compared to canalized traits (i.e. the jack-of-all-trades is a master of none analogy). Many of these ideas have yet to be tested empirically.

The chemical, visual, or auditory cues that elicit plastic responses are another interesting direction studies of phenotypic plasticity have considered. Langerhans and DeWitt (2002) examined the specificity of a cue that induces anti-predator morphology in *Physid* snails. They found it was a very general cue occurring in both molluscivorus and non-mollusc crushing sunfish. Thus, snails developed anti-predator morphologies despite minor threats of predation. Likewise, morphological and behavioral plasticity in response to one set of cues in order to combat predation may make the individual more susceptible to predation by another individual. For example, snails respond to fish predators by developing rotund shells and spending greater time in crevices or under rocks (Langerhans and DeWitt 2002). While this might be ideal for the avoidance of fish predators, round shells with large apertures invite the pereiopods of preying crayfish hiding under rocks. The snail went from the proverbial frying pan to the fryer due to maladaptive plastic responses (Langerhans and DeWitt 2002). The example just given and the study presented in Chapter II are both clear examples of the need to include multiple aspects of the environment in plasticity studies instead of relying on pairwise comparisons.

Research on trophic characters in fish has continued with extensive studies in the North American sunfishes. Specifically, molluscvirous pumpkinseed sunfish (*Lepomis gibbosus*) occur in temperate lakes that vary in the abundance of snail prey. Those inhabiting lakes with high abundances of snails have hypertrophied crushing muscles (levator posterior) and are more efficient consumers of snails than fish living in lakes depauparate of snails (Mittelbach et al. 1992). Likewise, similar polymorphisms have been documented in a number of cichlid species (Meyer 1987, Wimberger 1991, Swanson et al. 2003, Trapani 2003). More recently researchers have explored trophic plasticity in estuarine species. Cutwa and Turingan (2000) analyzed muscle mass and oral jaw biomechanics of sheepshead (*Archosargus probnatocephalus*) from two Florida lagoons distinguished by differing substrates and food resources. Analysis of jaw muscles and bones revealed significantly more massive jaw muscles and bones in the fish from Mosquito Lagoon verses the Indian River Lagoon. Mosquito Lagoon is characterized by having larger densities of hard shelled molluscs than Indian River Lagoon. However, estuarine studies like this one are a minority. Even rarer are studies examining plasticity in commercially and recreationally important estuarine species such as the red drum or spotted seatrout (Chapter III).

Another potential avenue of phenotypic plasticity research is the study of mechanisms by which organisms process environmental cues as well as the physical nature of the inducer itself. Understanding how organisms interpret and process cues at the molecular level may shed light on the accuracy of plastic responses or the additive effects of inducers. For example, Relyea and Mills (2001) exposed gray tree frog (*Hyla versicolor*) tadpoles to low concentrations of the pesticide carbaryl for ten to 16 days and found significant mortality (10-60%) reduced growth and activity. Additionally, mortality increased (60-98%) with the addition of predator cues, a more realistic case than most studies conducted in the lab to determine dose rates. The pesticide stressor is as of yet, unknown, however if it were discovered, alternative pesticide agents might be incorporated with knowledge concerning cues that cause ill effects in organisms. Moreover, this study implicates the importance of plasticity and development in the fields of conservation, management, and restoration ecology. By considering environmental effects on development and fitness, conservation and management efforts might be maximized as discussed in Chapter III.

The development of gene libraries in already well studied organisms such as *Drosophila* will enable researchers to study gene expression through incorporating new technologies such as microarrays. This may provide molecular information regarding plasticity genes or the activity of genes in certain environments. Population comparisons where morphological or physiological variation is already known maybe enriched with the addition of gene expression data as it will provide evidence of genes that are interacting to produce the alternative phenotypes. New techniques such as microarrays might conclusively answer the question posed by Via et al. (1993): Is plasticity a target or by-product of selection?

In this thesis I expand on trophic plasticity studies in fish that began in the late eighties. I empirically test for shape variation resulting from intragenerational environmental variation, population divergence, and indirect community effects. I incorporate performance trials and muscle mass comparisons to add predictive power and examine causative agents of induced morphologies. I argue for the consideration of phenotypic plasticity in conservation and management efforts, specifically in fish supplementation as this will aid in the critical transition period from the hatchery to the wild.

CHAPTER II

TROPHIC PLASTICITY AND FINE-GRAINED RESOURCE VARIATION IN POPULATIONS OF WESTERN MOSQUITOFISH, *GAMBUSIA AFFINIS*

Introduction

Natural environments vary spatially and temporally at myriad scales (Schmalhausen 1949, Ford 1964, Levins 1968, Endler 1986a). Environmental variation negatively impacts organisms by producing trade-offs where trait values favored in a given environment become liabilities in other environments. Trade-offs, or divergent natural selection, can lead to the evolution of phenotypic plasticity, population differentiation, generalization or bethedging, depending on the spatial and temporal pattern of environmental variation (Huxley 1942, Schluter 2000, DeWitt and Langerhans 2004, DeWitt and Scheiner 2004). Phenotypic diversification is more likely to evolve when organisms face relatively coarse-grained variation. It is generally accepted that coarse spatial variation leads to genetic divergence among populations, whereas coarse temporal variation (e.g. between generations) favors the evolution of phenotypic plasticity (Bradshaw 1965, Endler 1986b, Scheiner 1993). Plasticity is also expected to evolve in response to finer scaled variation, such as seasonality, if development can keep pace with environmental changes (Bradshaw 1965, West-Eberhard 1989, 2003). The question remains as to the scale at which environmental variation becomes evolutionarily irrelevant.

Phenotypic plasticity has been implicated as an adaptive solution with respect to several environmental gradients, including type or quantity of resources, predation risk, competition, or abiotic stress (reviewed by Pigliucci 2001, West-Eberhard 2003, Doughty and Reznick 2004, Dudley 2004). Most of these gradients will typically vary on multiple scales. Moreover, cross-domain interactions seem inevitable for example, predation risk can intensify resource competition (Werner et al. 1983). Among the gradients mentioned above, resource variation is particularly apt for studies of evolutionary diversification because resources typically vary on many spatial and temporal scales (e.g. Keast and Webb 1966). Additionally, patterns of resource use are vulnerable to influence by extrinsic factors, particularly biotic interactions such as competition and predation or abiotic factors such as oxygen or chemical gradients (e.g. Werner and Hall 1979, Mittelbach et al. 1992, Olson et al. 1995, Turner et al. 1999, Chapman et al. 2000, Relyea 2000, Turner et al. 2000, Relyea and Mills 2001).

Resource polymorphism has been well studied in fishes (reviewed in Robinson and Wilson 1994, Reznick 1996, Schluter 1996, Smith and Skulason 1996, Rundle et al. 2000). Documented cases of polymorphism are due in some cases to phenotypic plasticity (Smith and Skulason 1996, Svanback and Eklov 2002, Langerhans et al. 2003), while in other cases polymorphism stems from genetic differentiation (Day et al. 1994, Robinson and Wilson 1996, Schluter 1996, Svanback and Eklov 2003). More likely though, combinations of plastic and genetic factors lead to diversification (Day et al. 1994, Robinson and Wilson 1996, Schluter 1996, Svanback and Eklov 2003).

Furthermore, strong paradigms exist for the functional consequences of ecophenotypic variation in fishes (Keast and Webb 1966, Barel 1983, Winemiller 1990, 1991). Thus, I selected resource polymorphism in fishes as it is an ideal model organism to address questions concerning environmental complexity in plasticity.

In this paper I examined trophic plasticity and population differentiation in western mosquitofish, *Gambusia affinis*. As usual for trophic plasticity studies I created alternative foraging treatments (food type and orientation) in which subsets of offspring were raised exclusively in a single treatment. Additionally, I raised a subset of offspring on a daily rotation of foraging treatments to simulate fine-grained environmental variation. Two populations were used to address spatial variation in trophic characters and to address, in at least a preliminary way, the intersection of predation and trophic ecology in a plasticity study.

Study System

I selected *Gambusia affinis* for these studies because they occur in a diversity of habitats, have simple husbandry and a wealth of data exists regarding the ecology and evolutionary biology of the family Poeciliidae (e.g. Endler 1980Langerhans et al. unpublished data, Meffe and Snelson 1989b, Reznick et al. 1990, Johnson 2001). In south-central Texas *G. affinis* typically produce three generations per year (Krumholz 1948, Harrington and Harrington 1961, Haynes and Cashner 1995). They feed on a remarkably diverse number of food items, including zooplankton, epilithic films, insects, exuviae and at some times and locations snails and ostracods (Sokolov and Chvaliova

1936, Harrington and Harrington 1961, Garcia-Berthou 1999). These resources typically vary spatially and temporally within and among generations for natural mosquitofish populations.

Two populations in Brazos County, Texas, USA were chosen *a priori* because they differed in predator regime. Krenak Tap (30º36.6'N, 96º17.6'W) is a pond containing predatory sunfishes such as the largemouth bass, *Micropterus salmoides* and green sunfish, *Lepomis cyanellus*. Hensel (30º37.5'N, 96º20.8'W) is a drainage canal with no piscivorous fish. The flow rate in the Hensel drainage canal is only significant during rare and unpredictable flooding events, thus there is probably little selection for flowing verses non-flowing morphologies as found in constantly flowing rivers verses lagoons or lakes (Langerhans et al. 2003). As is typical for small fishes, mosquitofish avoid open water when sympatric with predators (Meffe and Snelson 1989a). My general hypothesis is that fish predators are major agents of selection acting in at least two ways on prey morphology. First, predators exert direct selection for body shapes that enhance escape swimming (Langerhans and DeWitt unpublished ms, Langerhans et al. unpublished ms). Second, habitat shifts induced by predators lead to altered resource use and hence altered selection on trophic characters. Therefore I expected morphological differences between *G. affinis* from contrasting predation regimes to reflect both direct effects of predators (e.g. exaggerated caudal peduncles) and indirect effects of altered habitat use induced by predators (e.g. trophic morphology).

Methods

Rearing experiment

In March 2002 I collected gravid female *G. affinis* from each population using dip nets. Females were rotated through breeding traps mounted on either side of a large (284-l) aquarium. The large tank was divided in half with a mesh panel that kept offspring from the two populations separate but allowed water exchange. Thus, all offspring experienced similar water conditions. Offspring, once delivered by females fell into the large tank volume where they remained until sufficient numbers were produced for the experiment. During brood production, hatchlings were fed twice daily on a rotation of live brine shrimp (*Artemia salina*; Order Decapoda), live microworms (*Panagrellus redivivus*; Order Nemata), live springtails (*Hypogastrura* sp.; Order Collembola), or spirulina flakes. Brooding females were fed brine shrimp and spirulina flakes. Over the course of 21 days 310 offspring were produced in this manner: 23 Krenek Tap females delivered approximately 150 young, while 33 Hensel females delivered approximately 160 young.

I conducted the rearing experiment in a 2,350-L recirculating system composed of twenty four 75-l aquaria, a 100-l settling tank, a 300-l biological filtration chamber and a sand filter through which water was circulated by a 1 hp pump. All tanks had a gravel substrate (5 mm mean particle diameter) to a depth of 15 mm. The experiment was conducted under a 12h light/ 12h dark cycle and water temperature was maintained at ~27° C. Each 75-l tank was divided with a mesh panel, yielding a total of 48, 35.5-l sectors for holding fish. Tanks were assigned to one of three food orientations (benthos, midwater, or water surface) or a rotation among orientations. One sector per tank was assigned to live food and the other attached food. Live foods were chosen to reflect prey typical to each orientation—insects (springtails) at the surface; crustacean zooplankton (brine shrimp) in the water column; and nematodes (microworms) in the benthos.

Feeding took place twice daily as follows. Springtails were dropped onto the water surface where they floated until eaten. Brine shrimp were loaded into a 60cc syringe and delivered through a long dispensing tube into the middle of the water column. Microworms were prepared in a similar manner as brine shrimp, but were delivered into the substrate. The live-rotation treatment was fed one live food each day with the type of food alternating between days. Fish were fed live food twice daily and within a single day the rotation treatment received the same live food. Attached food was made by mixing gelatin and ground commercial food (Rangen Corp.) in hot water to produce a paste. This paste was extruded onto plastic discs with a template to standardize the amount and distribution of food on every disc. Discs were allowed to cool and then placed in tanks according to treatment. Surface discs were allowed to float, while mid-water and benthic discs were attached to the side and bottom of tanks respectively via suction cups. Discs were replaced daily to ensure fresh food was available *ad libitum*.

Due to an error in tank assignment, there were two additional tanks for the following treatments: *bkp, bhl, mkp, mhl, rkp, rhl, tkp, thl* and two fewer tanks for *bkl, bhp, mkl, mhp, rkl, rhp, tkl, thp* where the first letter indicates the orientation, the second letter is the population, and the third letter is the type (live verses prepared food) assigned to each tank. No excess of phenotypic variance was noted for underrepresented tanks, and all main effects were consistent across both groups.

Six F_1 individuals from each population were randomly assigned to each tank sector. Due to initial mortality associated with handling larval fishes, replacements were made after eleven days to bring the density in each tank to five fish. Mortality was unbiased by treatment. Nine days later, further replacements were made with non-experimental albino mosquitofish to maintain sector densities while allowing for easy distinction and subsequent exclusion from analysis of the late replacements. Mortality after the addition of albinos was low (6%) but was biased toward the surface feeding treatment ($F_{3,\,32} = 8.02$; $P < 0.001$) and the prepared food type ($F_{1,\,32} = 10.7$; $P = 0.002$). After 60 days of rearing, fish were fixed in 10% formalin, rinsed with tap water overnight, and transferred to individual vials containing 70% ethanol for storage. Fish reaching sexual maturity (20 male, 1 female) by the conclusion of the experiments were excluded from analysis. This yielded a final sample size of 142 (for whole body morphology) or 148 (for pectoral fin analysis), or 3.2 ± 0.2 (mean ± se) fish per tank sector.

Morphometrics

After rearing, images of all specimens were captured from the lateral and dorsal perspective. MorphoSys Version 1.29 software was used to digitize eleven landmarks on the lateral images and six landmarks on the dorsal images (Fig 1a, b). Additionally, images of pectoral fins were captured by lowering fish tail-first through a gap between two horizontal glass plates and resting their pectoral fins flat against the glass. The

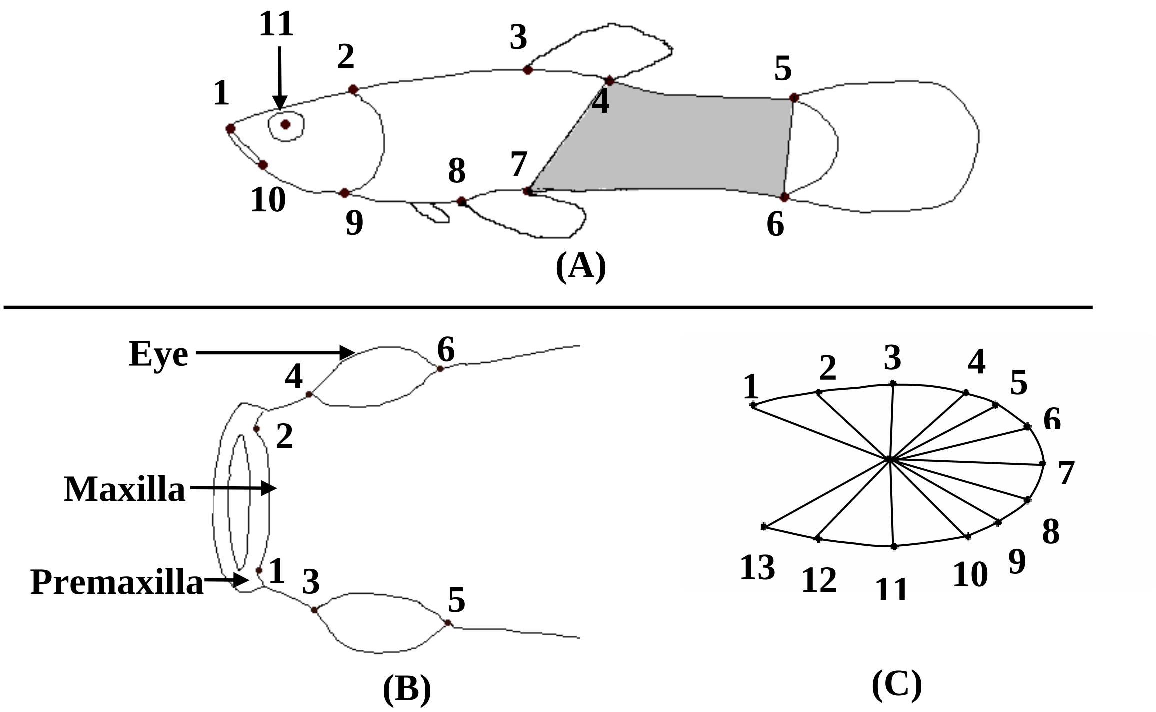

Fig 1. Juvenile *G. affinis* with landmarks used in geometric morphometric analysis. Illustration of lateral view (A.). Shaded area is the caudal peduncle region. Illustration of dorsal view (B.). Illustration of pectoral fin (C.). Points 1 and 13 are landmarks while, points 2-12 are semi-landmarks.

camera was oriented perpendicular to the glass allowing for capture of both fin images simultaneously. Two landmarks were digitized on the pectoral fin insertions. The remaining points were located by projecting from the centroid of the fin at regular angles (as per Fig 1c) onto the fin outline. I used both fins if they were intact by reflecting them into one aspect and averaging the landmark coordinates (N=85). If one fin was damaged the intact fin was used (right only, N = 40; left only, N = 23). No difference in shape was noted between left and right fins (approx. $F_{44, 156} = 1.17$; $P = 0.24$). All landmarks were digitized at a resolution of 0.03 mm/pixel.

Raw coordinates were aligned using least-squares superimposition and used to calculate shape variables (partial warps, including uniform components) using tpsRegr (Rohlf 2000a). Such geometric morphometric techniques are powerful new tools that are increasingly common in studies of fish body shape (Cadrin 2000, Douglas et al. 2001, Hjelm et al. 2001, Svanback and Eklov 2002, Langerhans et al. 2003). Geometric methods differ from traditional morphometrics as they retain information about the spatial covariation between landmarks allowing the geometry of shape variation to be conserved throughout the analysis and reconstructed during visualization (Rohlf and Marcus 1993).

Analysis

I performed nested multivariate analyses of covariance (MANCOVA) for each aspect of shape (Tabachnick and Fidell 2001). Lateral, dorsal, and pectoral landmark constellations yielded 18, 8, and 22 partial warps, respectively. Partial warps served as dependent variables in each MANCOVA and were tested for effects due to centroid size (covariate); food type (unattached or attached); food orientation (surface, mid-water, benthic, or rotation); population; all interactions among type, orientation, and population; and tank nested within the type, orientation, population interaction (e.g. as in Table 1). Canonical axes from MANCOVA were visualized using TpsRegr (Rohlf 2000a). Visual inspection of transformation grids and examination of canonical loadings were used to determine the nature of morphological change on each canonical axis. For each multivariate axis representing trophic plasticity I interpreted the observations with respect to the functional ecological literature on foraging, and addressed the additivity and uniqueness of inducibility when resources fluctuated rapidly (i.e. the rotating treatment). Additivity was assessed by an a posteriori contrast designed to distinguish fine-grained resource variation from coarse grained variation.

For the axis representing population differentiation I posed two specific questions: (1) Does the population effect in lab-reared fish resemble that found among fish in the field? (2) Is the population effect related to both direct and indirect effects of predation regime? Both questions required comparison of my lab-reared fish with fish from a previous study (Langerhans et al., unpublished ms). For consistency with the other study, landmark 10 was removed from the lateral configurations of my lab-reared fish, and partial warps were regenerated for pooled data. Combining datasets allowed us to create a single morphospace wherein I performed two tests. (1) I conducted a discriminant analysis to see if functions created to discriminate wild fish could successfully predict the population of origin for lab-reared fish. If shape variation across populations were similar for lab and wild fish, then a discriminant function for one class of fish should correctly classify a significant proportion of fish from the other group. Similarly, values between lab-reared and field-observed diversity would then suggest a genetic basis for differences observed in the wild. (2) I performed multiple regression of canonical scores from the population and foraging (food type and orientation) effects of this study with canonical scores assigned from a burst-swimming axis from the previous study. That is, for each of my focal fish, based on their morphology, I could assign a predicted burst performance score from the prior study. I could then ask if the population differentiation observed simultaneously reflected elements of trophic and predation ecology.

All statistical procedures were conducted with JMP software (Version 4.04, SAS Institute Inc., Cary, NC). Polynomials were centered for interaction terms involving continuous independent variables (Tabachnick and Fidell 2001).

Results

Growth rate

Centroid size did not differ for fish raised on alternative food types (i.e. live free versus attached foods, $F_{1, 98} = 2.88$, $P = 0.1$), except indirectly through an interaction between food type and orientation ($F_{3, 98} = 3.54$, $P = 0.02$). This interaction was due to elevated growth in the live/mid-water treatment, implying that brine shrimp is a superior food to either microworms, springtails, or prepared foods. Size was also influenced by orientation ($F_{3, 98} = 21.2$, $P < 0.0001$). Fish fed on the surface grew 18% slower than fish raised in other treatments (Tukey HSD test, $\alpha = 0.05$). Finally, growth rate was 9% greater for fish from the predator population (Krenak Tap) relative to those from the no-predator population (Hensel) ($F_{1, 98} = 8.22$, $P = 0.005$). Yet, despite some significant differences in mean size by treatment, substantial overlap was typical between categories. Thus, in subsequent analyses I used centroid size as a covariate in assessing shape variation.

Induced responses

Fish body shape significantly differed according to *how* (food type) and *where* (orientation) they fed (Table 1). Shape also differed between populations (Table 1). Multivariate allometry was evident, but there was no evidence of change in allometry by treatment (i.e. no heterogeneity of slopes for the covariate; $P \geq 0.4$ in all cases). Each effect is discussed in turn below.

Food Type— Fish fed foods that were live verses attached foods were morphologically distinct in all three aspects of shape (lateral, dorsal, and pectoral fin, all $P \leq 0.003$; Table 1). The food-type effect explained 43.7%, 21.9% and 48.8% of morphological variation along their canonical axes for lateral, dorsal, and pectoral fin models respectively. These axes are illustrated in Figure 2. Feeding on attached food items induced a short, deep head, and an increase in the downward angle of the caudal peduncle in fish (Table 2; Fig 2a). Attached foods also induced wider heads (Table 3; Fig 2b), and wider paddle shaped pectoral fins (Fig 2c).

Table 1. MANCOVA results for morphological variation in *G. affinis*. Dorsal and lateral body perspectives and shape variation in the pectoral fin is depicted.

Lateral (N=142)	Effects	F	df	P
	Type (T)	3.45	18, 80	< 0.001
	Orientation* (O)	1.85	54, 239.2	< 0.001
	Population (P)	1.91	18, 80	0.03
	O x P*	1.22	54, 239.2	0.17
	O x T*	1.04	54, 239.2	0.41
	PxT	1.13	18, 80	0.34
	O x P x T*	1.39	54, 239.2	0.05
	Tank(O x P x T)*	1.32	504, 1239.3	< 0.001
	Centroid size	4.73	18, 80	< 0.001
Dorsal (N= 142)				
	Type (T)	3.15	8, 90	0.003
	Orientation* (O)	1.2	24, 261.6	0.24
	Population (P)	0.73	8, 90	0.67
	O x P*	1.00	24, 261.6	0.47
	O x T*	1.38	24, 261.6	0.12
	PxT	0.62	8, 90	0.76
	O x P x T*	1.05	24, 261.6	0.40
	Tank(O x P x T)*	1.16	224, 710.6	0.08
	Centroid size	2.48	8, 90	0.02
Pectoral fin (N= 148)				
	Type (T)	3.46	22, 80	< 0.001
	Orientation* (O)	1.06	66, 239.8	0.37
	Population (P)	1.35	22, 80	0.17
	O x P*	1.18	66, 239.8	0.19
	O x T*	0.98	66, 239.8	0.52
	PxT	2.08	22, 80	0.01
	O x P x T*	0.81	66, 239.8	0.85
	Tank(O x P x T)*	1.57	660, 1528.3	< 0.001
	Centroid size	3.98	22, 80	< 0.001

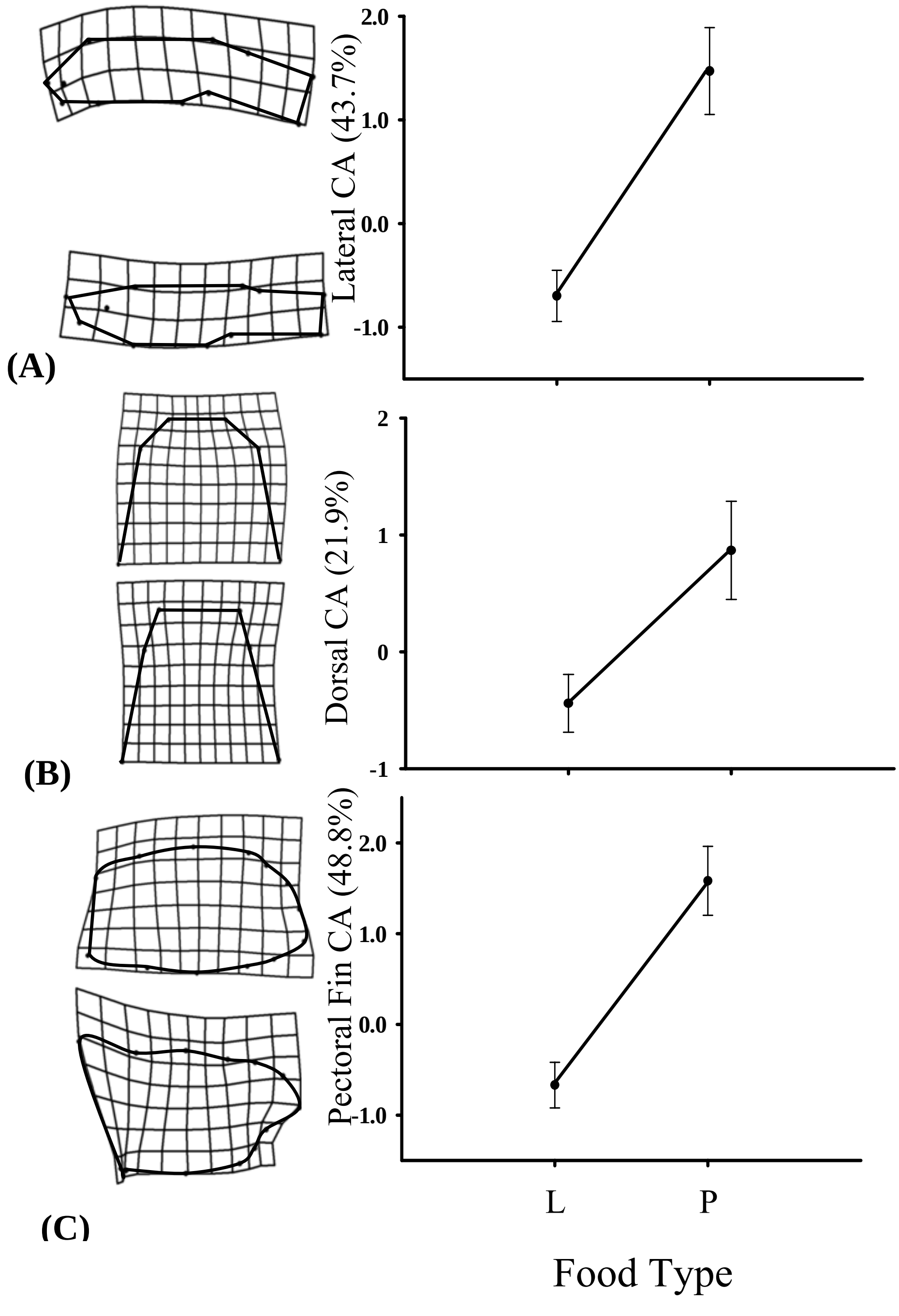

Fig 2. Reaction norms and thin-plate spline transformation grids of the food type effect in *G. affinis*. Unattached (L) vs. attached prepared (P) warped grids are depicted for lateral view (A.), dorsal view (B.), and pectoral fins (C.) from top to bottom respectively. Transformation grids are magnified 2X. Notice the live vs. attached variation harkens to Barels epilithic scraper and pursuit predator distinction (p. 388), and the blunt snout to his sucker/planktivore-biter/scraper distinctions (p. 384-5) (Barel 1983).

Table 2. Canonical loadings and interpretations for the MANCOVA of lateral shape in *G. affinis*. Loadings ≥ |0.2| are set in bold.

Dependent Variable	Interpretation	Orientation CA 1	Orientation CA 2	Orientation CA 3	Food type CA	Population CA
PW1X	eye position, mouth angle and size	-0.05	-0.09	**0.25**	**0.24**	**-0.30**
PW1Y	eye position, mouth size	-0.05	-0.04	-0.08	-0.08	-0.17
PW2X	Ratio of dorsal:anal fin length	-0.05	**0.58**	**0.21**	0.01	-0.11
PW2Y	angle of dorsal:anal fin insertions	0.09	**0.23**	-0.03	-0.03	-0.00
PW3X	dorsal and anal fin length	-0.16	0.02	**0.22**	0.07	-0.07
PW3Y	dorsal fin insertion angle	**-0.34**	**0.24**	-0.12	-0.15	**0.36**
PW4X	snout length	-0.04	-0.09	0.19	0.06	-0.02
PW4Y	eye position, mouth angle and size	0.18	-0.16	**-0.31**	-0.06	0.05
PW5X	caudal insertion angle	**0.32**	**0.36**	-0.19	**0.30**	-0.10
PW5Y	caudal insertion length	-0.13	-0.02	**-0.30**	0.02	-0.07
PW6X	Head angle	-0.12	**0.21**	-0.08	-0.01	**0.59**
PW6Y	**Head depth**	**0.21**	**-0.23**	**-0.20**	**-0.20**	**0.20**
PW7X	Head length	**0.22**	**0.23**	-0.13	**0.27**	**0.29**
PW7Y	sinusoidal axial bending	**0.24**	-0.00	**0.36**	**0.31**	-0.05
PW8X	Head and caudal peduncle length	**-0.27**	-0.12	**0.23**	0.08	0.19
PW8Y	Back-bending	0.11	-0.06	-0.01	**0.49**	0.19
Uni X	Shearing	0.09	**0.26**	-0.05	0.09	**-0.34**
Uni Y	aspect ratio	**-0.44**	-0.02	-0.00	0.16	**-0.46**

Table 3. Canonical loadings and interpretations for the MANCOVA of dorsal shape in *G. affinis*. Non-significant effects are not displayed. Loadings ≥ |0.2| are set in bold.

Dependent Variable	Interpretation	Food type CA
PW1X	Head width	**0.52**
PW1Y	Eye to maxilla distance	**-0.13**
PW2X	Uninterpretable	0.24
PW2Y	Eye length	**0.23**
PW3X	Head width	0.06
PW3Y	Uninterpretable	0.07
Uni X	Shearing	0.04
Uni Y	aspect ratio	**-0.47**

Orientation— Fish also varied according to whether they were fed at the surface, mid-water, or benthic orientations regardless of type (P = 0.001; Table 1). The multivariate shape axes of the orientation effect explained 29.2% of the morphological variance of the lateral MANCOVA. Within the twenty-nine percent, each of the three orientation canonical axes explained 15.4%, 7.6%, and 6.2% of the variance specific to the orientation effect. The three canonical axes are depicted with thin plate spline transformation grids (Fig 3), while canonical loadings with verbal explanations are also reported (Table 2). Fish fed in the mid-water were distinguished on the first shape axis from those in the surface and benthic orientations. The rotating treatment was largely intermediate in shape with no single treatment having significantly more influence on shape in the rotating treatment than others ($F_{18, 80} = 1.42$; P = 1.47). However, the third morphological shape axis separated the rotating treatment from the static treatments (Fig 3). The mid-water treatment exhibited a shortening of the caudal peduncle (Fig 3; Table 2), lengthening of the dorsal fin base, deepening of the body (UniY), and narrowing and lengthening of the head (Fig 3; Table 2).

The second multivariate shape axis separated surface fed fish from all other orientations (Fig 3). Shape variation on this axis involved a decrease in dorsal fin base length (Table 2), narrowing and shortening of the mouth and head, a shift to an up-turned head orientation, and a down-turned caudal peduncle (Fig. 3; Table 2).
Finally, the third food orientation axis captured aspects of shape variation peculiar to fish fed the rotating diet (Fig 3). This axis describes a shortening of the head and caudal region (Table 2) and lengthening of the posterior insertion of the anal fin (Fig. 3; Table

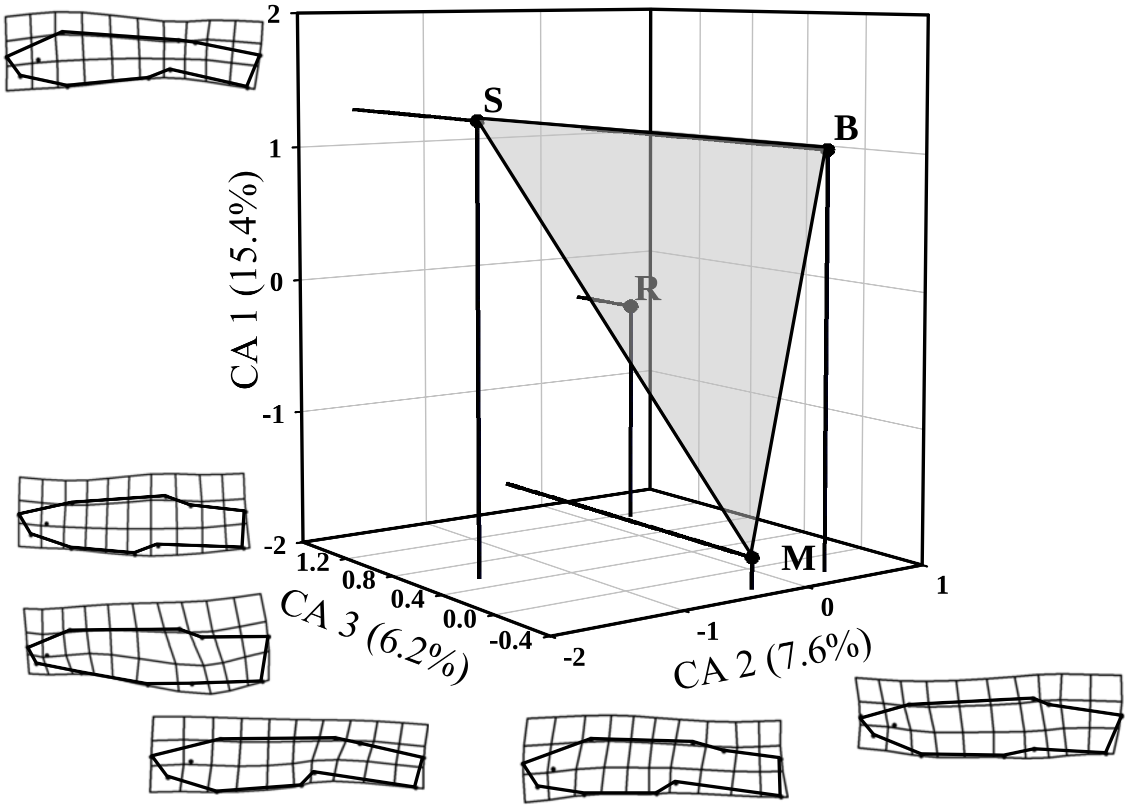

Fig 3. Induced morphological variation in *G. affinis* resulting from the orientation in which the fish fed. Orientations included: surface (S), mid-water (M), benthic (B), and a rotation (R) of the three. The first multivariate canonical axis (CA 1) describes 15% of the variation along the orientation axis and explains differences between mid-water and the surface/benthic orientations. The second canonical axis (CA 2) explains 8% of the remaining variation along that axis and describes differences between the surface and benthic feeding orientations. The third multivariate axis (CA 3) explains 6% of the remaining variation along that axis. This axis set the rotation treatment (test of intra-generational variation) a part from the other single orientation diets.

2). The significance of the rotating diet inducing unique morphologies may indicate the development of morphologies to cope with intra-generational environmental variation, not merely the production of a generalized morphology.

Population differentiation— The population main effect was significant with respect to lateral shape ($P < 0.03$; Table 1), while the population multivariate axis explained 2.4% of the total morphological variation in the MANCOVA of lateral shape ($P < 0.03$; Table 1). The population axis describes a morphological shift in the angle and depth of the head, a change in mouth length, and a change in the length of the dorsal fin (Table 2). Hensel, the no-predator population, exhibited a shallow head and short caudal peduncle, whereas Krenek Tap, the predator population, had a deep head and long caudal peduncle similar to a field study with and without predators involving multiple populations including the two in this study. I now compare this result with the field study (Langerhans et al. in prep). Using the pooled data set and the newly derived partial warps as described above (see methods) I performed the standard MANCOVA model resulting in a similar significance structure and derived nearly identical canonical axes as the primary analysis. With these results I performed two tests designed to answer the questions posed concerning population differentiation and direct/indirect effects of predation. (1) I performed a discriminant analysis using wild caught mosquitofish to classify fish in the present study. The discriminate function correctly classified 74.6% of lab reared fish to their respective population ($P < 0.0001$). (2) I derived a surrogate canonical axis for predator avoidance shape using results from fast start performance in mosquitofish. Fish body shape (canonical axis derived from the

MANCOVA on shape) and fast start performance were correlated in fish from the two populations validating my assumption that speed depends, at least in part, on shape (R^2 = 0.12; Partial r = 0.35). Langerhans et al. found a similar relationship among six populations. Next, I performed a multiple regression of the population canonical axis using the four trophic axes and the newly derived predator avoidance shape axis as regressors (R^2 = 0.45). I found the population axis was correlated with the three orientation axes ($P < 0.001$, $P = 0.11$, $P < 0.001$; Partial $r > 0.35$ in all cases), negatively correlated with the type axis ($P = 0.91$; Partial r = 0.04), but was also correlated with the surrogate predator avoidance shape axis (Partial r = 0.42). Thus, the population axis differed in response to both trophic and burst swimming aspects of shape.

Discussion

Induced morphology and functional implications

We found extensive induced morphology among mosquitofish from two populations when fed unattached or attached food at different orientations. The most pervasive influence on morphology, was due to *how* (unattached vs. attached food) fish fed. Foraging mechanisms for acquiring unattached involve picking, suction or ram feeding. These differ substantially from methods used for obtaining attached foods, which involves biting and scraping (Barel 1983, Webb 1984, Meyer 1987, Winemiller 1991). Mosquitofish reared on attached foods (those biting/scraping) had wider heads, blunt snouts, and lower aspect ratio pectoral fins (Fig. 2). Blunt snouts are typically associated with scraping modes of foraging (Barel 1983, Meyer 1987, Winemiller 1991, Winemiller et al. 1995, Kassam et al. 2003) and lower aspect ratio pectoral fins indicate the ability to generate thrust over short distances, often necessary when scraping against and biting into epilithic biofilms (Keast and Webb 1966, Barel 1983, Webb 1984). Narrow, long heads and narrow pectoral fins were evident in fish from the unattached treatment. These morphological traits facilitate fine-scale targeting of suction streams steadied by maneuvering (trimming) fins (Keast and Webb 1966, Webb 1982, Barel 1983, Webb 1984, Schluter 1993). Thus, my findings for mosquitofish reflect classically observed morphological variation among taxa, like that of coral scraping butterflyfishes (Motta 1988) and epilithic algae scraping cichlids (Barel 1983), although the variation was as extreme as interspecific differences. This may indicate an adaptive response to enhanced feeding efficiency.

Other axes of variation emerged among fish fed at different orientations (Fig. 3). The most pronounced effect was the development of short heads, terminal mouths, straight bodies, and increased body depth between the dorsal and anal fins in the fish from the mid-water treatment compared to alternative orientations (Fig 3). Deep bodies are typical for fish species that hover in the water column and pick at unattached items (Keast and Webb 1966, Barel 1983, Motta 1988). Likewise, a narrow head and deep mid-body characterizes limnetic sticklebacks relative to benthic stickleback species (Schluter and Mcphail 1992, Schluter 2000). This axis of variation in sticklebacks is also reflected in phenotypic plasticity within species where limnetic forms pick plankton from the water column and benthic forms eat prey found in the benthos (Day et al. 1994). Thus, trophic polymorphisms found in other species such as the sticklebacks is partly analogous to this system, and the functional ecology correlates of shape are similar (midwater prey vs. other).

The shape of fish fed at the surface differed from those fed in the benthos along a second shape axis. This morphological shift involved a characteristically more tapered snout with a small mouth, and slender body for surface fed fish, relative to those fed benthic prey (Fig 2). This finding was similar to that described in guppies by Robinson and Wilson (1995) and may indicate accommodations for feeding at the air water interface. Thus, for my several pure (invariant) environments, phenotypic plasticity was common and reflected *a priori* ecomorphological expectations.

In addition to corroborating plasticity results from this species with those of other poeciliids and fish from other families, I wanted to preliminarily address two relatively unexplored aspects of plasticity evolution: (1) responses of plasticity to fine-grained environmental variation that is potentially unpredictable for the organism and (2) exploring the intersection of resource-based plasticity with other ecological domains (i.e. E × E interactions), such as predation.

Fine grained environmental variation

Resources often vary on time scales much less than the generation time of an organism. Such fine-grained variation imposes developmental challenges to organisms (Schmalhausen 1949, Hutchinson 1959, Bradshaw 1965, Levins 1968, Tufto 2000). Phenotypic plasticity is often cited as a strategy to mitigate divergent selection across generations, but is rarely considered for fine-grained environmental variation with the exception of predictable variation (Gosler 1986, Meyer 1990, Weinig and Delph 2001).

Theory suggests that generalist strategies (Levins 1968) should evolve when developmental responses cannot keep pace with the rate of environmental change (Levins 1968, Lively 1986, Moran 1992, Tufto 2000, DeWitt and Scheiner 2004). However, my thesis is that plasticity may produce generalist phenotypes in addition to its classic role of producing specialist morphologies across coarse-grained environmental gradients. Under fine-grained environmental fluctuation, morphologies might develop to reflect the weighted sum of environmental experiences (i.e. a dynamic generalist). These weighted-average phenotypes may not sum evenly among environments and thus should be more flexible than generalist phenotypes thereby achieving adaptive compromises unique to mixtures of environments. Finally, plasticity could produce a unique phenotype under fine-grained environmental variation embodying emergent elements unobservable in any pure environment. Metaphorically, the plastic jack-of-all-trades may have unique adaptations.

Few empirical studies of plasticity include treatments that change during the course of rearing (Wimberger 1991, Day et al. 1994, Hegrenes 2001, Johnson 2001, Johnson et al. 2003). Studies are typically designed to asses whether a single switch-point results in a reversal of developmental trajectories (Meyer 1987) or assess seasonal variation in phenotype that is related to a progressive change in environment (Gosler 1986, Meyer 1990). Recently, Weinig (2001) demonstrated that plastic responses early in life can compromise responsiveness later in life indicating a constraint to plasticity. My goal in the present study was to examine the effects of rapid resource variation (rotating treatment). Mosquitofish thrive in particularly harsh and variable environments making the species a good candidate for studies of fine-grained resource variation (Meffe and Snelson 1989b). Morphology of mosquitofish reared under daily resource variation was largely intermediate (generalized) on all three orientation axes indicating the rotating treatment was in fact similar to a weighted sum of environmental experiences. However, the third morphological axis separated the rotating treatment (fine-grained variation) from the static environments, indicating some unique aspects of morphology (a possible unique phenotype) due to resource variation (Fig 3; Table 2). Although I cannot remark on the adaptive value of generalist phenotypes or unique phenotypes achieved through plasticity in response to fine grained environmental fluctuation observed in this study, it is reasonable to expect that in many systems these results could represent adaptive solutions for specific challenges.

Population differentiation

Mosquitofish from the two populations differed in growth rate and shape but not in the magnitude or nature of trophic plasticity. This suggests genetic differentiation in the traits, but no differentiation in levels of plasticity among traits (i.e. no gene × environment interaction(sensu Via and Lande 1985). Fish originating from the Krenak Tap (predator) population grew 9% faster than fish from Hensel population; which suggests a possible life history shift in the predator population. Faster growth in predator populations has also been observed in guppies (Reznick 1996) and is a general prediction from life-history theory (Roff 1991, Kawecki and Stearns 1993).

Morphological variation among populations most likely reflects genetic differentiation arising through divergent natural selection. Examination of shape variation among populations indicated that it was similar to variation found in a field survey of six populations with and without predators (Langerhans & DeWitt, unpublished ms; Langerhans et al., unpublished ms). Fish from predator populations developed longer caudal peduncles and were generally more elongate than those from predator free sites. Thus, I prepared a pooled data set of the studies to (1) rigorously test how closely fish from the two studies resemble each other and (2) examine potential direct and indirect effects of predation.

The discriminat function correctly classified 74% of the fish indicating morphology was analogous between the field and lab studies. These results not only indicate genetic differentiation between populations but also implicate predation as the primary agent of divergent selection. However, predation may have indirect effects on a number of traits including trophic morphologies by restricting resource acquisition or limiting habitat use (Abrams 1995, Relyea 2000, Schmitz and Suttle 2001, Luttbeg et al. 2003, Persson and De Roos 2003). In the present study, resources are similar between the two populations (i.e. food in all orientations), but predators likely restrict prey fish from using open water habitats and force them to forage in shallow areas that potentially have a different resource base (Crowl and Covich 1990, Turner et al. 2000, Bernot and Turner 2001). Thus, I expected shape differences between populations to reflect selection on both anti-predator morphology (direct effect) and trophic morphology (indirect effects).

We examined trait-mediated interactions of predators on prey through the multiple regression of trophic and predator avoidance shape axes derived from the pooled data. The results indicated significant portions of variation were attributable to both swimming performance and trophic aspects of shape. Thus, predators seemingly affect prey initially through the development of morphologies affecting predator avoidance and secondarily through trophic characters resulting from altered habitat and resource use. Morphologically, fish from the predator-free population (presumably with greater access to open mid-water habitats) developed short caudal peduncle and were shaped more like fish fed in the mid-water, whereas fish from the predator population developed long caudal peduncles. This result is consistent with the hypothesis that predators (e.g. *Micropterus salmoides*) exclude fish from feeding in the mid-water, forcing them to feed on alternative food items found in shallow habitats. Studies examining species interactions need to consider the cascading nature of species interactions as they are likely to be ecologically meaningful.

Summary

I sought to create a well-controlled environment where variations in phenotype were those induced by the experimenter as a test for effects due to both coarse- and fine-grained environmental variation and genetic differentiation among populations. I found extensive divergence in morphology among treatments and populations in both static (coarse-grained) and changing (fine-grained) environments indicating the value of including naturalistic complexity (i.e. environmental variation) in plasticity studies. The nature of divergence in shape suggests functionally important trophic variation, predator-induced variation, and possible interactions among the two. Interactions require subsequent experimentation to assess the importance of altered habitat use in trophic morphology. The presence of strong variation across all experimental levels suggests that phenotypic flexibility and population differentiation is perhaps a key to the wide habitat breadth and colonization ability of mosquitofish.

CHAPTER III

TROPHIC SPECIALIZATION AND PERFORMANCE IN RED DRUM, *SCIAENOPS OCELLATUS*

Introduction

Ecomorphological studies often seek correlations among morphologies that determine function and environments that determine functional needs (Keast and Webb 1966, Barel 1983, Findley and Black 1983, Motta 1988, Losos 1990, Winemiller 1991, Garland and Janis 1993, Motta et al. 1995, Wainwright and Richard 1995). A common approach is to study multiple, functionally distinct species and their performance in alternative resource environments (Keast and Webb 1966, Barel 1983, Webb 1984, Wainwright and Richard 1995, Winemiller et al. 1995, Grubich 2003). Similarly, many studies consider the effects of intraspecific morphological variation in light of resource use (Meyer 1987, Ehlinger and Wilson 1988, Meyer 1989, Ehlinger 1990, Mittelbach et al. 1992, Skulason and Smith 1995). A considerable amount of the morphological variation occurring within species arises through phenotypic plasticity, the production alternative phenotypes in response to environmental cues (Bradshaw 1965, Schlichting 1986, Stearns 1989, West-Eberhard 1989, Scheiner 1993, Robinson and Wilson 1995). Plasticity is thought to evolve in response to fluctuating environments where phenotypic optima change spatially and temporally within and among generations necessitating the need for organisms to sense and respond to fluctuating conditions (Schmalhausen 1949, Bradshaw 1965, Levins 1968, West-Eberhard 1989).

Environmental cues elicit phenotypic responses ranging from alternative behaviors and color patterns (Trexler and Travis 1990, Trexler et al. 1990), to variation in life histories (Reznick et al. 1990, Johnson and Belk 2001), and the rearrangement of bone and tissue (Bronmark and Miner 1992, Robinson and Wilson 1994, Chapman et al. 2000, Langerhans et al. 2003). Phenotypic diversity in response to resource variation has been particularly well studied in fishes (Day et al. 1994, Robinson and Wilson 1994, Smith and Skulason 1996, Hjelm et al. 2001). Phenotypic polymorphisms often arise through plasticity (Kornfield et al. 1982, Ehlinger and Wilson 1988, Meyer 1989, Ehlinger 1990, Skulason and Smith 1995, Smith and Skulason 1996), however others have a genetic basis (Lavin and Mcphail 1987, Schluter 1996). Regardless of the source, phenotypic polymorphism is quite common in fishes. Therefore, studies examining polymorphisms are important for understanding how organisms successfully acquire food items in the midst of environmental fluctuation.

Study System

Estuaries, like most ecosystems, vary in both abiotic and biotic factors at multiple scales. Temperatures, salinities, and dissolved oxygen can fluctuate quite substantially both temporally and spatially throughout estuaries (Stickney 1984, Day et al. 1989, Mann 2000). Likewise, many estuaries contain extensive variation in habitat complexity, predation risk, and quality, quantity and types of resources within and among generations (Stickney 1984, Mann 2000). Thus, estuarine inhabitants such as juvenile fishes may be highly dependent upon phenotypic plasticity as a means to maximize fitness in an ever changing environment.

Red drum (*Sciaenops ocellatus*) are an estuarine inhabitant for the first six years of life. They exploit the productive interface of fresh and salt waters, which afford a degree of protection from predators due to the shallowness and inherent habitat complexity of estuaries (Pearson 1929, Miles 1950, Holt et al. 1985, Day et al. 1989, Matlock 1990). Larval red drum are transported into bays and estuaries and subsequently settle in a variety of habitats including seagrass, sand, salt marshes (*Spartina* sp.), and oyster beds (Minello 1999, Stunz et al. 2002a, b). Settling in these different habitats might select for a generalist morphology or require alternative behavioral and morphological accommodations in order to exploit resources and avoid predation.

Red drum are generalist foragers that reveal two notable niche shifts during juvenile growth. As very small juveniles (0-29 mm), red drum primarily consume copepods and mysid shrimp, but after reaching about 30 mm their diet switches to fish, crustaceans, and eventually crabs (Boothby and Avault 1971, Bass and Avault 1975, Overstreet and Heard 1978, Scharf and Schlicht 2000). Therefore, red drum may be model organisms for the study of plasticity, because they are generalists that develop in habitats that fluctuate temporally and spatially within and among generations.

In addition to being a good model species for studying the evolution of phenotypic plasticity red drum are a recreationally and commercially important species along the Gulf and Atlantic coasts of the United States (Pattillo et al. 1997). As a result the species has suffered from over harvest since the early twentieth century (Pearson 1929, Swingle 1990). Supplementation efforts as well as recreational and commercial limits were implemented over twenty years ago in the hope of reviving the fishery (Swingle 1990). The decline in red drum stocks due to overharvest led to extensive research concerning their life history in an attempt to optimize conservation and supplementation efforts (Pearson 1929, Holt et al. 1981, Holt et al. 1985, Rooker et al. 1998a, Minello 1999, Stunz et al. 2002a, b). More recent work has sought to establish genetic population structure for the same purpose (Gold et al. 2001, Gold and Turner 2002). Evolutionary aspects of red drum ecology should improve our ability to predict how the species will respond to conservation or stock enhancement efforts (Templeton et al. 2001, Schlaepfer et al. 2002, Stockwell et al. 2003).

It is my purpose in this chapter to use an ecomorphological construct developed mainly for interspecific comparisons of fishes (Keast and Webb 1966, Barel 1983, Motta 1988, Wainwright and Richard 1995, Wainwright et al. 2002) to examine intraspecific morphological variation in red drum. Evidence of morphological variation within red drum may aid in understanding the evolutionary mechanisms operating in this estuarine species and to optimize conservation and supplementation efforts. I addressed these aims preliminarily by conducting a rearing experiment using hatchery-born red drum and fed them either hard or soft food for two months.

Methods

Rearing

Red drum (~ 28mm) were obtained from the Sea Center Texas hatchery (Lake Jackson, Texas) and brought to College Station, TX. These fish were housed for two weeks in a recirculating circular tank with biological filtration and treated with a copper solution (Cutrine) at 0.15 ppt to guard against parasitic infection (Gaylord and Gatlin 1996). Fish were transferred to a 2,350-L recirculating system composed of 24, 75-L aquaria, a settling tank, a biological filtration chamber, a sand filter, and a 1hp pump and kept at a 12h light/ 12h dark cycle with a water temperature of 27º C (± 3). Each tank was divided in half with a partition yielding a hard food and soft food sector for each tank (48 tanks, 36-L/sector). Three fish were randomly assigned to each sector. Fish were fed their treatments diets in the morning and received a maintenance diet of commercially prepared food in the evening (Rangen Corp. starter diet #2, 1.70 mm^3). The hard food treatment consisted of crayfish limb segments, while the soft food treatment received crayfish meat minus the weight of the crayfish limb exoskeleton in the afternoon. Mortality during the first 30 days of rearing probably resulted from aggressive behavior (28% H and 36% S fish). As a result, I randomly reduced the number of fish in each tank to one (28 H and 22 S fish were removed). The remaining fish (24 H and 24 S fish) were reared for another 30 days. The random removal of almost half of the fish at the mid-point of the experiment allows for the examination of induced morphologies at two points during ontogeny.

Performance

At the end of the sixty-day rearing experiment fish underwent feeding trials to assess performance on hard-bodied food. I hypothesized that fish reared on hard food items would manipulate and consume hard food more efficiently than fish reared with soft food. Two trials were conducted on the first and third day of a three day period. The fish received the usual maintenance diet of commercial food on the interim day.

During the trials fish were fed one hard food item (72 mm^3 ± 21mm^3) per trial. Trials were considered successful if the food item was picked up and manipulated at least once. If seven minutes passed without any response the trial was terminated. One researcher observed the fish while another recorded time intervals. I measured performance three ways: 1) time to first contact with food. 2) handling time, 3) time to consumption. Time was recorded from the presentation of the food until the fish either consumed, or rejected the item. Time was noted if a fish stopped manipulating the item; however the watch was left running in case the fish did not swallow the item and began manipulating it again. Additionally, time was recorded if the fish rejected the food item and subsequently picked it back up. After the fish rejected the food item and did not pick it up again for two minutes the trial was terminated. Time between bouts was subtracted from total feeding time to arrive at a processing time.

Morphometrics

Upon the conclusion of the performance trials, fish were sacrificed, preserved in 10% formalin for two weeks, washed with water, and stored in 70% ethanol. Lateral and dorsal images were captured for each experimental fish using a video imaging system with a telecentric lens. MorphoSys (V. 1.29) software was used to digitize twelve landmarks on lateral images and seven landmarks on dorsal images (Fig 4 a, b). All measurements were made at a resolution of 0.002 mm/pixel for all images. Variation in shape among the digitized images was measured using geometric morphometrics. This is a powerful tool that retains information on the spatial covariation between landmarks, thus landmarks are relative to each other and geometry of shape variation is conserved throughout the analysis (Rohlf and Marcus 1993). TpsRegr software (Rohlf 2000a) was used to obtain superimposed landmark coordinate configurations for images. This software uses generalized least squares superimposition to align data by rotating, translating and scaling, the landmark coordinate information. Superimposed landmark coordinates were then used to calculate shape variation by parsing it into affine and non-affine components of shape (partial warps) (Bookstein 2001). Affine components are homogenous aspects of shape covariation in the X (shearing, uniX) and Y (stretching, uniY) planes. Shearing of an object is parallel movement of landmarks in the X plane similar to forcing a square into a parallelogram. Likewise, stretching is parallel movement of landmarks in the Y plane such as stretching a square into a rectangle.

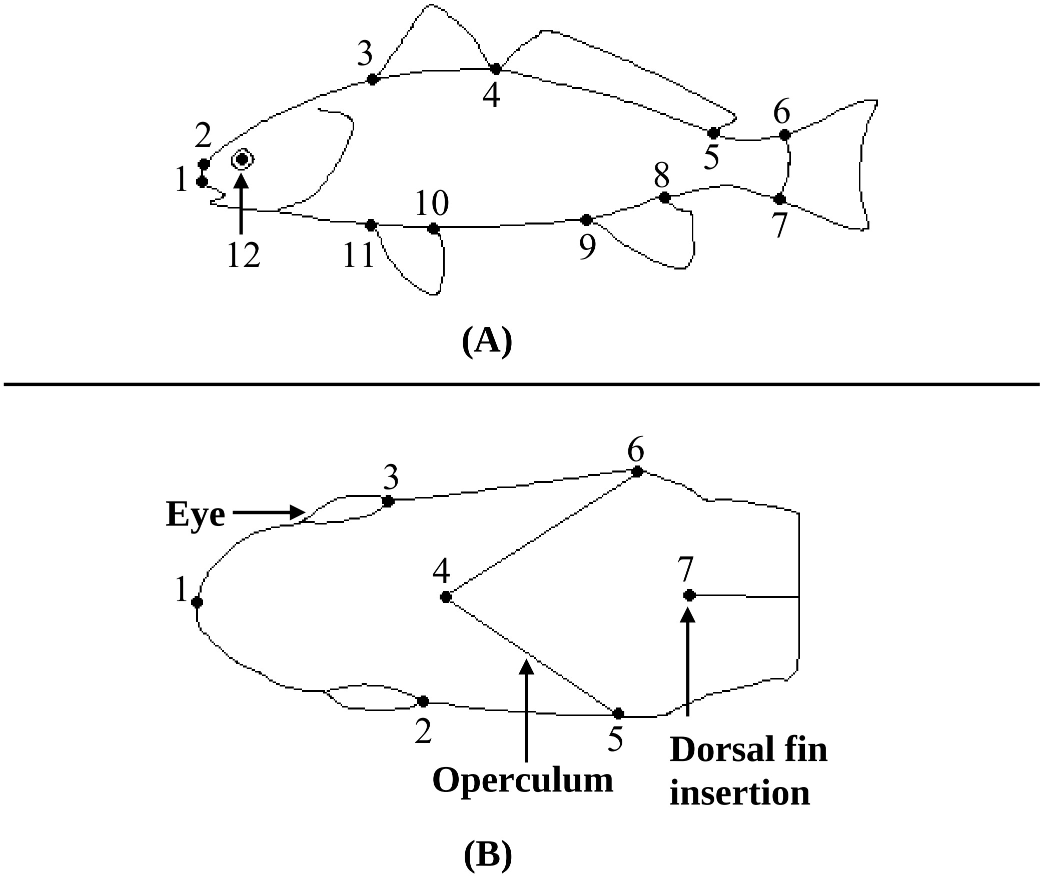

Fig 4. Juvenile *S. ocellatus* with landmarks used in geometric morphometric analysis. Illustration of lateral view (A) and dorsal view (B).

Non-affine components of shape are the remaining partial warps, which are inhomogenous aspects of shape describing spatial covariation in the X and Y plane.

Muscle Mass

In order to compare muscle masses among treatments I dissected the levator posterior (LP) and the levator externus 3 and 4 complex (LE). These muscles were chosen because they are actively involved in the operation of the pharyngeal jaws during mastication of food (Sasaki 1989, Wainwright 1989, Mittelbach et al. 1999, Grubich 2000). The LP muscle orginates on the neurocranium and inserts onto epibranchial 4 (EP4), while the LE complex originates on the nuerocranium anterior to LP and inserts on EP4 superior to the LP (Sasaki 1989; Grubich 2000). EP4 serves as a lever in force production during the mastication of food as described by Wainwright's model of pharyngeal jaw function (Wainwright 1989). Muscles were dissected from three month old fish, stored in 95% ethanol, blotted dry and weighed three times. The log transformed mean muscle masses were used in analysis. The LE complex was weighed together following Grubich (2003).

Analysis

MANCOVA was used to test for diet-induced morphology in both lateral and dorsal aspects of shape (e.g. Table 4). Additionally, a discriminat function analysis was designed to classify fish according diet based on shape. Landmark constellations from

Table 4. MANCOVA results for morphological variation in *S. ocellatus*. Dorsal and lateral aspects of shape are depicted for two month and three month old fish. DFA results display the percent correctly classified to their respective treatment.

		Dorsal				Lateral			
Age	Effects	F	df	P	DFA	F	df	P	DFA
2 months	F. Type	0.78	10, 35	0.64	74%	1.07	20, 25	0.43	77%
(N = 47)	C. size	1.38	10, 35	<0.001		3.78	20, 25	0.001	
3 months	F. Type	0.61	10, 33	0.79	65%	2.27	20, 23	0.03*	96%
(N = 45)	C. size	2.10	10, 33	0.05		2.90	20, 23	0.007	

lateral and dorsal images yielded 20 and 10 partial warps respectively which served as dependent variables in each model. TpsRegr software (Rohlf 2000a) was used to visualize shape variations by producing thin-plate spline transformation grids illustrating shape change along canonical axes of the MANCOVA. The transformation grids were magnified 2× in order to aid in the identification of key morphological differences. Muscle masses were analyzed using one-tailed t-tests where I expected fish from the hard food diet to have more massive muscles than the soft food treatment. I analyzed performance using an ANCOVA for each trial with a sequential Bonferroni correction to maintain a low (5% chance) type one error rate. All statistical procedures were conducted with JMP software (Version 4.04, SAS Institute Inc., Cary, NC).

Results

Morphology

Results indicated fish morphology was significantly influenced by diet. However, there was evidence of multivariate allometry as centroid size, a multivariate measure of size, was significant for food type ($F_{1,34} = 0.046$, $P = 0.832$). But, there was no heterogeneity of slopes ($P > 0.3$ in all cases) that would signify interactions among size and treatment effects. Therefore, in all subsequent investigations of shape I included centroid size as a covariate (Table 4).

To determine the nature of shape variation MANCOVA's for both aspects of shape within groups were performed. Red drum significantly differed in their lateral body morphology for 3 month old fish (Table 4, Fig 5), however they did not differ in two month old fish or dorsal aspects of shape (Table 4). The food type effect for lateral shape in three month old fish explained 66% of the morphological variation along the multivariate axis of shape. The axis indicated fish fed hard food developed deeper and longer heads (Table 5; Fig 5). The discriminant function (DFA) provides an intuitive metric for how well shape variables classify fish to their respective treatment. The DFA correctly classified 95.6% of the 3 month old fish from the lateral view into their respective diets (Wilk's Lambda approx. $F_{20, 24} = 0.34$; $P = 0.02$).

Muscle Mass

The mean mass of LE muscles indicated fish from the hard diet had significantly more massive LE (mean = 2.65, range = 2.7) muscles than fish receiving the soft diet (mean = 2.60, range = 3.5), ($F_{1, 38} = 3.45$, $P = 0.036$; Table 6; Fig 5). However, there was no significant difference among hard (0.79, 0.63) and soft (0.82, 0.77) food treatments in the LP muscle ($F_{1, 38} = 0.619$, $P = 0.218$; Table 6).

Performance

Handling time among food types was significant for the first trial after Bonferroni correction ($F_{1, 12} = 8.9$, $P= 0.011$; Fig 6). The other three trials were non-significant and converged to have virtually the same mean by trial four ($P > 0.15$ in all cases; Fig 6). In the fourth trial the log of mean performance times were very similar (H = 0.94 ± 0.47, S = 0.92 ± 0.43).

Table 5. Canonical loadings and interpretations from the MANCOVA of lateral shape in three-month-old *S. ocellatus*. Levator posterior (LP) and the Levator externus complex (LE).

Partial Warp	Interpretation	3 months
PW1X	snout angle	**0.24**
PW1Y	snout height	0.03
PW2X	uninterpretable	-0.05
PW2Y	caudal peduncle width	**0.21**
PW3X	head length	**0.21**
PW3Y	uninterpretable	0.08
PW4X	uninterpretable	0.07
PW4Y	uninterpretable	0.16
PW5X	caudal fin length	0.08
PW5Y	uninterpretable	**-0.27**
PW6X	dorsal body length	0.04
PW6Y	uninterpretable	-0.06
PW7X	uninterpretable	-0.17
PW7Y	caudal and head width	0.01
PW8X	ventral body length	0.10
PW8Y	uninterpretable	-0.03
PW9X	center of mass shift	0.11
PW9Y	Bendiness	**0.31**
Uniform X	Shearing	-0.13
Uniform Y	aspect ratio	-0.09

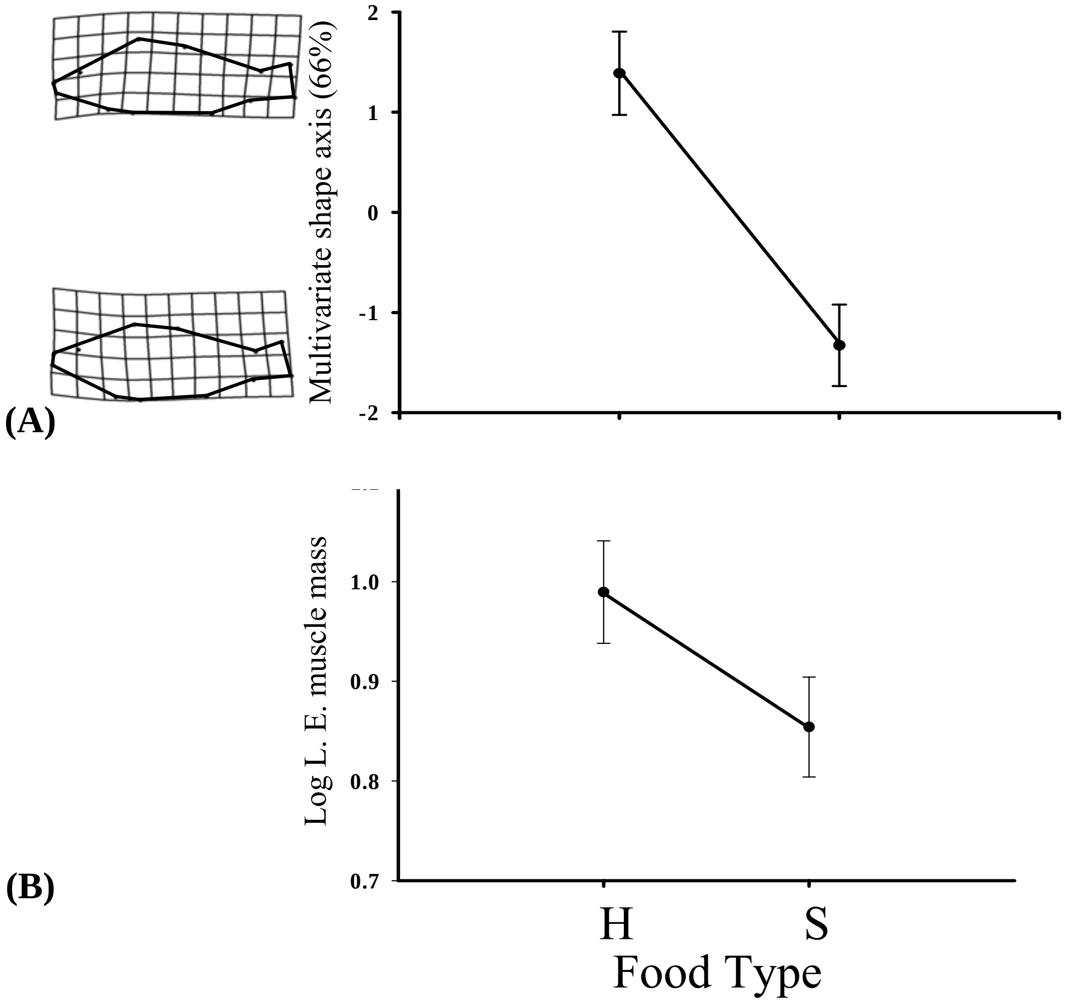

Fig 5. Reaction norms for morphology (lateral view) and muscle mass of the levator externus complex (LE) for *S. ocellatus*. (A) Warped grids of the lateral perspective magnified 2 × to key in on morphological variation.

Table 6. One-way ANCOVA results of pharyngeal muscle mass in three-month-old *S. ocellatus*. Interpretations reflect morphological variation from food type in each partial warp and were made by analyzing animations using tpsRelw (Rohlf 2000b). Loadings ≥ |0.2| are displayed in bold.

	Muscle Mass 3 months (N= 40)					
	L. P.			L. E.		
Effects	F	df	P	F	df	P
Food Type	0.62	1, 38	0.44	3.45	1, 38	0.034
Centroid size	34.8	1, 38	< 0.001	35.9	1, 38	< 0.001

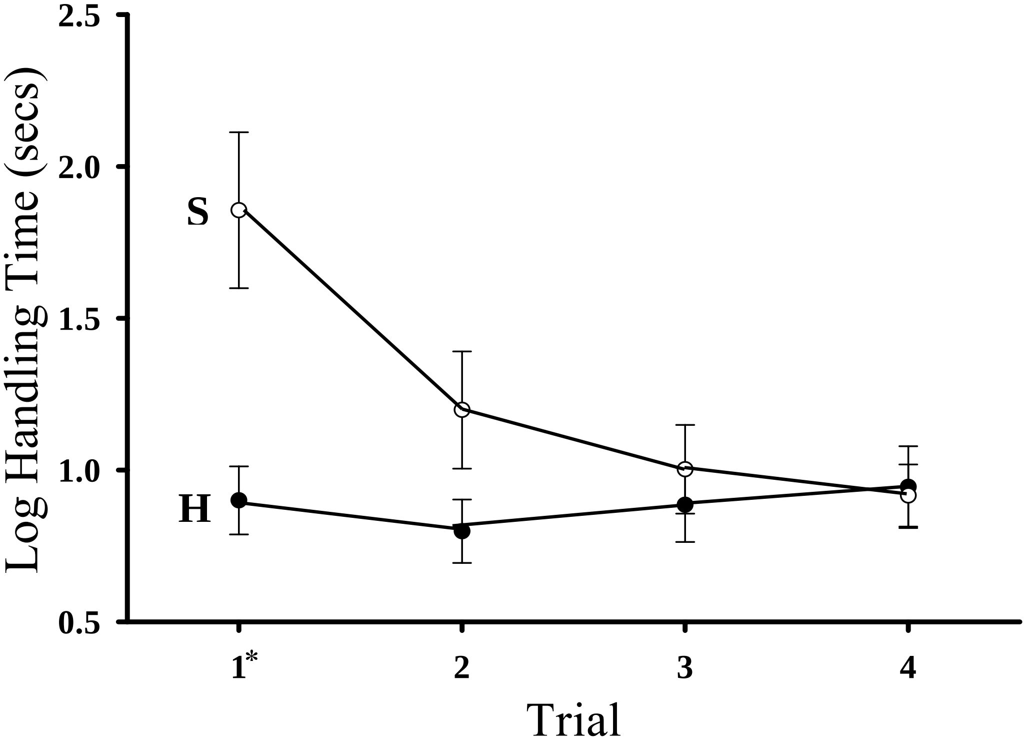

Fig 6. Log transformed treatment means for food type (S = soft, H = hard) of each performance trial. Univariate tests using a sequential Bonferroni correction indicates soft food handling time was significantly longer than hard food handling time for the first trial (P= 0.011).

Discussion

We found behavioral, physiological, and morphological plasticity in three month old red drum as a result of rearing them on a diet supplemented with hard food items (Table 4). Fish receiving hard food items developed deeper and longer heads, more massive pharyngeal muscles, and initially were more efficient consumers of hard food items than those reared on soft foods (Fig 4).

Applying ecomorphological principles to intraspecific morphological variation provides an opportunity to compare my results to variation known among species. Typical ecomorphological studies make comparisons among multiple species relating morphology to resource use (Keast and Webb 1966, Barel 1983, Findley and Black 1983, Motta 1988, Losos 1990, Winemiller 1991, Garland and Janis 1993, Motta et al. 1995, Wainwright and Richard 1995). Likewise, many studies also compare intraspecific morphological variation (Meyer 1987, Ehlinger and Wilson 1988, Meyer 1989, Ehlinger 1990, Skulason and Smith 1995). Specifically, molluscvirous pumpkinseed sunfish (*Lepomis gibbosus*) occur in temperate lakes that vary in the abundance of snail prey. Those inhabiting lakes with a high abundance of snails have hypertrophied (overdeveloped) crushing muscles (levator posterior) and are more efficient consumers of snails than fish with populations depauparate of snails (Mittelbach et al. 1992). A similar morphological polymorphism has been documented in *Herichthys minckleyi*, a cichlid occurring in the Cuatro Cienegas region of Mexico (Kornfield and Koehn 1973, Kornfield et al. 1982, Swanson et al. 2003, Trapani 2003).

Additionally, ecomorphological studies incorporating performance trials (Motta et al. 1995, Koehl 1996, Vanhooydonck and Van Damme 2003), lever ratios among bones (Wainwright 1989, Mittelbach et al. 1992, Grubich 2000, Wainwright et al. 2002), variations in bone shape and mass (Wainwright et al. 1991, Cutwa and Turingan 2000), and muscle mass/activity (Wainwright 1989, Mittelbach et al. 1999, Grubich 2000, Wainwright et al. 2002) increase predictive power as they provide evidence of performance trade-offs and implicate mechanisms behind external morphological variation. For example, performance trials were used to demonstrate that bluegill sunfish display differential foraging behavior based on size and experience in Michigan lakes indicating learning as well as resource specialization are important in determining an individuals resource use (Werner et al. 1981). Likewise, Cutwa and Turingan (2000) analyzed muscle mass and oral jaw biomechanics of sheepshead (*Archosargus probnatocephalus*) from two Florida lagoons distinguished by differing substrates and food resources. Analysis of jaw muscles and bones revealed significantly more massive jaw muscles and bones in the fish from the lagoon with greater densities of hard shelled molluscs. Like these studies, my research included performance trials and muscle development along with morphology to make predictions about the effects of morphological variation on feeding performance.

Morphologies induced in my rearing experiment are characteristic of morphological shifts observed among the genus *Cynoscion* and the black drum (*Pogonias cromis*). Red drum fed hard food items developed sub-terminal mouths and deeper, longer heads similar to black drum, while those fed soft food items developed terminal mouths and more streamlined bodies, characteristics found in *Cynoscion* species (Fig 5).

The family Sciaenidae includes a variety of species with morphological adaptations for utilizing specific food types among an array of food resources. The genus *Cynoscion* is primarily piscivorous and includes species such as the silver weakfish (*Cynoscion nothus*), sand weakfish (*Cynoscion arenarius*) and spotted seatrout (*Cynoscion nebulosus*). In contrast the black drum (*Pogonias cromis*) are durophagous sciaenids feeding on hard shelled molluscs and therefore lies at the opposite extreme of the feeding axis. The red drum is a generalist forager eating a wide range of prey including shrimp, blue crabs and fish. Morphologies of these two groups are disparate with the *Cynoscion* species having a streamlined body, long narrow head, and terminal mouth, while the black drum has a deep body and a large deep head with a sub-terminal mouth. Red drum is intermediate in morphology having a relatively deep head, terminal mouth, and streamlined body. Internal feeding structures follow a similar pattern with black drum having modified the pharyngobranchial 3 (PB3) into a robust toothplate covered with molariform teeth and very robust pharyngeal muscles (Sasaki 1989, Grubich 2000, 2003). The *Cynoscion* condition is a reduced PB3 with a field of conical teeth (Sasaki 1989). Again, the red drum is intermediate in form having a large PB3 with conical teeth (Sasaki 1989, Grubich 2000, 2003). Rearing red drum on an exclusive diet of hard food items induced the development of morphologies analogous to the black drum, while feeding them soft food items induced *Cynoscion* characteristics. However, the morphological shift observed in red drum is small compared to observed morphological variation among species.

Analysis of internal morphology provided evidence of a causative agent for the variation in external morphology. Eating hard food items would be expected to induce the development of larger muscle mass due to increased use of pharyngeal muscles. The increase in mass usually coincides with an increase in muscle size potentially requiring a larger origin and insertion site as well as space accommodations within the skull (Wainwright et al. 1991, Cutwa and Turingan 2000).

The levator externus 3 and 4 muscle complex (LE) and the levator posterior (LP) originate on the nuerocranium but have different insertion points along the fourth epibranchial (EP4). According to Wainwright's (Wainwright 1989) model of pharyngeal jaw function both muscles are integral in the processing of prey. Synergistic contractions of these muscles cause EP4 to pivot ventromedially, depressing PB3 and inducing a ventral biting movement of the upper toothplates. LE and LP have been used as a correlate for all of the pharyngeal muscles and I did the same(Grubich 2000). LE was significantly more massive in fish receiving hard food (Fig 5; Table 6). This finding might be evidence that red drum develop larger, deeper heads to accommodate more massive pharyngeal muscles in response to eating hard food items.

Performance trials provide a test of whether induced morphological and physiological traits confer advantages for consuming hard food items. In light of the heavier musculature induced from feeding fish hard food items I expected enhanced performance. The first trial indicated fish eating soft foods could not manipulate hard food items as well as those having exclusive experience with hard food. However, there was no significant difference between treatments in the three remaining trials (Fig 6). The fourth trial performance was very similar indicating fish in the soft food treatment had learned how to consume hard food items, despite their morphological disadvantage.

The hypothesis for this project was that induced traits are likely to be vital to survivorship and performance of fish in natural environments. Thus, such knowledge could be used to improve supplementation efforts by identifying traits labile to habitat variation and subsequently exposing hatchery fish to variations that would confer higher survival for post-release fish. Red drum has long been sought commercially and recreationally along the Atlantic and Gulf Coasts of the United States (Pearson 1929, Swingle 1990, Pattillo et al. 1997). Popularity has resulted in their exploitation and over harvest (Swingle 1990) with the commercial fishery being closed in 1990 due to reduced catches (GMFMC 1996). However, the species still supports a thriving sport fishery in bays and estuaries (Pattillo et al. 1997). Length requirements and limits were implemented during the early eighties to rejuvenate offshore breeding stocks (Swingle 1990, Pattillo et al. 1997). Additionally, supplementation efforts began in the early eighties and have grown into a 1.3 million dollar industry (Swingle 1990).

However, the effect of supplementation on red drum recruitment to the breeding population is unknown. There has been substantial research on understanding the life history of red drum in order to optimize commercial production and release of red drum. Such studies have concentrated on settlement patterns of larvae (Rooker and Holt 1997, Rooker et al. 1998b, Stunz et al. 2002a), sensory capabilities (Fuiman and Delbos 1998, Poling and Fuiman 1998), population genetic structure (Gold et al. 2001, Gold and Turner 2002), and resource use (Boothby and Avault 1971, Bass and Avault 1975, Overstreet and Heard 1978, Scharf and Schlicht 2000). However, little research has been done to understand evolutionary mechanisms such as phenotypic plasticity or resource polymorphism working within populations of red drum to create local adaptation and increase survival. Studies designed to test mechanisms of evolution in fishes may be important in conservation efforts, as they might provide insight on effects of habitat fragmentation, pollution, and, more pertinent to this study, effects of supplementation on populations of red drum.

Summary

My study indicates red drum are capable of morphologically responding to variation in resources through phenotypic plasticity. Variations in morphology are similar to observed variations existing among species indicating the potential for a narrow axis of morphological diversification in respect to resource acquisition. These results have implications for supplementation efforts as hatchery red drum may benefit from pre-adaptation to feeding resources likely encountered in the wild. This would ease the transition between hatchery facilities and estuaries for red drum and thus increase the number of hatchery fish surviving to be harvested or to breed.

CHAPTER IV

CONCLUSION

In many habitats, resources vary across space and time. In order to survive and reproduce organisms must compensate for resource variation as well as avoid predation and react to competition. Phenotypic plasticity is an evolved mechanism that organisms use to cope with resource variation. Plasticity allows them to respond behaviorally, physiologically, and morphologically to habitat heterogeneity. Conservation and supplementation efforts rarely consider factors of evolution (sensu Schmalhausen 1949), such as phenotypic plasticity, that affect success after release. In this thesis, I placed phenotypic plasticity in a historical context, examined phenotypic plasticity as it relates to trophic characters in two disparate species, and considered the utility of phenotypic plasticity for applied goals.

In both the mosquitofish and red drum experiments, I sought to create a well-controlled environment where variations in phenotype were those induced by the experimenter as a test for effects due to the intended treatments. In the mosquitofish experiment, I examined both inter- and intra-generational environmental variation, genetic differentiation among populations, and indirect aspects of shape between populations. I argued that the extensive divergence in morphology resulted from functionally related trophic variation across static (inter-generational) and rotating (intra-generational) environments as well as predator related variation among populations. The presence of strong variation across all experimental levels suggests that phenotypic flexibility and population differentiation in poecilids is widespread and that incorporating complexity (e.g. intragenerational variation and aspects of predation) into plasticity studies will aid in understanding indirect effects in community ecology.

In the red drum experiment, I examined trophic plasticity in light of conservation and supplementation efforts. The red drum is a commercially and recreationally important species. There has been substantial research to understand the species life history, but little research has been done on evolutionary mechanisms, such as phenotypic plasticity or polymorphism. This study indicated that red drum is capable of morphologically responding to variation in resources through phenotypic plasticity. I argued that morphological variations are similar to observed variations existing among species, an indication that red drum might adaptively respond to feeding regimes. These results have implications for supplementation efforts as hatchery red drum may benefit from pre-adaptation to feeding resources likely encountered in the wild. This would ease the transition between hatchery facilities and estuaries for red drum.

Phenotypic plasticity is experiencing a renaissance that began in the nineteen eighties with empirical and theoretical studies examining the nature and extent of plasticity across taxa, the evolution of plasticity, as well as the costs and limits of plasticity. As we progress into the twenty-first century, evolutionary ecology will benefit greatly from the insight gained from knowledge concerning the interface between the environment and the genotype. Integration of ecological complexity should reveal interesting aspects of plasticity not fully realized by testing one environment verses another. Likewise, environmental factors affecting the development and phenotypes of organisms should be considered in conservation and supplementation efforts as plasticity probably bears on the relative success of such efforts.

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