Chapter 2
Predator Diversity Changes the World: From Gene to Ecosystem

Abstract Trophic polymorphism, defined as the state in which two or more clearly different feeding functional traits exist within the same population of a species, is general in fishes. In aquatic ecosystems, the fishes often have strong impacts on prey communities as keystone predators, so that phenotypic divergence of their feeding traits can alter biotic and abiotic attributes of environments through changes in the form of trophic interactions. The predator-induced environmental alterations may, in turn, drive evolutionary changes in adaptive traits of themselves as well as of other members in the communities. This process, in which ecology and evolution reciprocally interplay over contemporary time-scales, is termed "eco-evolutionary feedback." In this chapter, we review how and when trophic polymorphism has been generated in fish populations and then discuss what consequences it has in ecological and evolutionary aspect. Special references are made to the case in the ancient Lake Biwa, which has a geological history long enough for divergent fish populations to come to ecological speciation and thus provides a good opportunity to understand how such an evolutionary process diversifies biological communities and consequently ecosystem properties in lakes.

Keywords Biodiversity • Eco-evolutionary feedback • Ecological speciation • Ecosystem functioning • Keystone predator • Mesocosm • Species pair • Trophic polymorphism

2.1 Why is Biodiversity Important?

What is the ecological significance of conserving biological diversity within a species? In the context of conservation biology, it could be argued that maintenance of intraspecific phenotypic variation has the advantage of increasing population viability because it provides the population with the adaptability to respond to changing environments. However, such a traditional view has been replaced by recent

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ecological findings that the intraspecific diversity of a keystone species impacts substantially on biological communities and their ecosystem functioning. In this chapter, we first focus on phenotypic polymorphism in fishes as keystone predators of aquatic ecosystems, referring to genetic mechanisms underlying their polymorphism. We also introduce some of the latest studies, which demonstrate that intraspecific functional diversity of fish predators alters aquatic community structure and ecosystem processes. Finally, we show that environments modified by a predator's functional diversity can serve as a driver for the evolutionary diversification of aquatic biota through eco-evolutionary feedbacks.

2.2 Biodiversity at Three Levels

According to the Convention on Biological Diversity (CBD), biological diversity includes diversity within species, between species and of ecosystems, being viewed at different levels of biological organization from genes to ecosystems. In terms of conservation biology, the maintenance of intraspecific diversity is of ecological importance because a population with a variety of phenotypes, which have the potential for adaptation against unpredictable environmental changes in the future, such as global warming, habitat alteration and prevalence of emerging pathogens, may be able to prevent extinction. Furthermore, recent developments in community genetics have provided a new insight into the ecological and evolutionary consequences of intraspecific diversity. In a population of terrestrial plant, for example, cottonwood *Populus*, individual phenotypes can harbor different arthropod communities according to their anti-herbivore defense capacity, which is based on genotypes (Whitham et al. 2006). The genotypic difference among individuals further causes intraspecific variation in condensed tannin production in leaves, which in turn affects litter decomposition processes attributable to forest floor microbes. Since this finding, an increasing number of studies have looked at the cascading effects of intraspecific biodiversity on community structure and ecosystem processes, attracting much attention from both community and evolutionary ecologists.

2.3 What is Phenotypic Polymorphism?

Phenotypic polymorphism, defined as the state in which two or more clearly different phenotypic traits exist within the same population of a species, is a common phenomenon found in a variety of taxonomic groups from prokaryotes to higher vertebrates. The polymorphic phenotypes include behavioral, morphological, physiological and life history traits (Gross 1996). In a narrower sense, phenotypic polymorphism is confined to discontinuous phenotypic variation within a Mendelian population in which interbreeding individuals share a common gene pool. In a broad sense, however, it is applicable to the case in which intraspecific phenotypic variation results from secondary contact between multiple populations under different selection regimes and/or undergoing different genetic drifts in different locations. In addition, some studies have recently reported that the polymorphic state is attained by phenotypic plasticity within a genetically monomorphic population (Agrawal 2001; Miner et al. 2005). To understand the evolution of phenotypic polymorphism, it is essential to elucidate the origins of polymorphic phenotypes and the underlying mechanisms for polymorphic expression. But yet, such a subject is at the state of the art. In this chapter, when treating with cases in which there exists discontinuous phenotypic variation within a given population at a given time, we regard all of them as phenotypic polymorphism without referring to the processes and mechanisms for generating it.

2.4 Phenotypic Polymorphism in Aquatic Ecosystems

In aquatic organisms, phenotypic polymorphism is often observed in traits related to predator–prey interactions. Prey organisms often show a polymorphic pattern of traits in relation to inedibility, termed anti-predator defensive traits. For example, phytoplankton can avoid zooplankton predation by means of colony formation, while zooplankton under high predation pressure express their sharp helmet and extended tail spine, which functions to deter fish and invertebrate predation (Lass and Spaak 2003). In contrast, fish predators show polymorphism in behavioral and morphological traits associated with feeding habits, which is referred to as trophic polymorphism (Smith and Skulason 1996). Intraspecific variation in feeding traits leads to discrete variation in species trophic niche through functional differences in prey size selectivity or prey species-specific foraging efficiency (Robinson 2000).

2.4.1 Trophic Polymorphism and Adaptive Divergence

In the East African Great Lakes, which have a long geological history spanning hundreds of thousands to tens of millions of years, cichlid fishes are well known to be a group showing adaptive radiation. In this group, it has been believed that a small number of ancestral species evolved to the diversity of existing species through specialization of their habitat and food resource utilization (Seehausen 2006). The ancestral species, which was the first to colonize these lakes, would have intensified intraspecific competition for food resources and habitats in the process of its population expansion under environments in which there existed few or no predators and competitors. As an efficient way to reduce intraspecific competition, the fish might have partitioned their resources to occupy alternative empty niches as the population became saturated. Individual variation in plastic foraging behavior may have been the first step of niche specialization (Bolnick et al. 2003). When the foraging behavior is partly inherited in the progeny, behavioral specialization can facilitate the subsequent physiological and morphological adaptations to specific resource utilization (Sacotte and Magnan 2006). Such a phenotypic adaptation, which enables each individual to utilize different resources more efficiently, will favor disruptive selection within the population (Knudsen et al. 2010). If it is accompanied by reproductive isolation due to sexual selection, then the adaptive divergence can lead to ecological speciation (Seehausen et al. 2008). Marked interspecific diversity of trophic niches and morphology found in African cichlids may be an evolutionary consequence of resource partitioning among individuals derived from a colonized population (Bootsma et al. 1996; Genner et al. 1999).

There is excellent evidence supporting the evolutionary scenario of adaptive radiation in cichlids, in which colonized populations of ancestral species partitioned resources among individuals and subsequently diversified their morphology, leading to ecological speciation. In a Nicaraguan crater lake, which was formed by volcanic activity less than 23,000 years ago, two cichlid species coexist and form a monophyletic assemblage (Barluenga et al. 2006). One species, which is widespread among adjacent lakes, lives in the littoral habitat and another endemic species lives in the limnetic habitat of the deep crater lake. The two species also differ greatly in their feeding habits and morphology, with the limnetic species possessing a more slender body. Molecular data revealed that these two species were reproductively isolated less than 10,000 years ago, suggesting that morphological divergence through habitat/food preference and subsequent reproductive isolation through assortative mating led to sympatric speciation. This finding seems to reconfirm assumptions of adaptive radiation of cichlids in African Great Lakes in which morphologically diverse species have derived from a few ancestors. In the case of Nicaraguan cichlids, colonization to newly created environments, where competitors are originally absent, would have facilitated phenotypic divergence of trophic morphology and the subsequent ecological speciation, which provides unique opportunities to understand the evolutionary process of adaptive diversification within a lake environment.

Although trophic polymorphism has been found in phylogenetically different groups of fishes, some of its features are shared among them. One of the most remarkable, in this respect, is that the evolutionary pattern of morphological divergence associated with feeding specialization is similar across species. For example, individuals with a deeper body, a shorter snout and a wider mouth feed on benthic prey preferentially, while those with a slenderer body and an elongated snout frequently feed on plankton in pelagic waters. In the former case, the wider mouth has the advantage of readily consuming benthic prey on the lake bottom (Robinson 2000) and the deeper body allows the development of larger pharyngeal muscles, which are advantageous in the crushing of the hard shells of benthic invertebrates, such as gastropods and decapods (Wainwright et al. 1991; Osenberg et al. 2004). By contrast, in the latter case, the slender body is suited to optimize swimming performance, which would be required to extensively search for planktonic prey (Hendry et al. 2011). In addition, these individuals have a greater gill raker number and narrower gill raker spacing, which are both effective in the filtration of small particles such as plankton (Robinson 2000). Such a morphological divergence is closely associated with habitat-specific food resource distribution, characterized by typical lake food webs, i.e., plankton prey derived from a pelagic food chain in the limnetic habitat and benthos prey from a benthic food chain in the littoral habitat. For many fish species with phenotypic polymorphism, even if there are interspecific variations, their morphological divergence is usually associated with two different trophic niches, planktivory and benthivory.

2.4.2 Ecological Speciation and Species Pair

Trophic polymorphism has also been frequently observed in freshwater fish species inhabiting postglacial lakes in northern temperate environments: e.g., salmonids, sticklebacks and osmerids (Taylor 1999). The reason for this is associated with the geological history of these lakes. In high latitudes of the Northern Hemisphere, the land surface was extensively covered by ice during the last glaciation, which extended from approximately 110,000 to 10,000 years ago. According to the most predominant hypothesis, fish species that were the first to colonize in postglacial lakes would have undergone morphological divergence in order to utilize unused food resources in the absence of competitors. If that is true, the evolution of trophic polymorphism in high latitudes must have occurred during the last 10,000 years. This time scale is too short for the fish population to diverge into different biological species with complete reproductive isolation (i.e., speciation) but it may be long enough for the population to undergo adaptive divergence (Hendry et al. 2009).

The above situation reported for freshwater fishes in high latitudes is often regarded as a species pair. A species pair is defined as a pair of populations that are typically distinguished from each other by differences in ecology, behavior and/or morphology, but are taxonomically classified as the same species because of their incomplete reproductive isolation (Taylor 1999). However, sexual selection following divergent natural selection will lead to the evolution of reproductive isolation through assortative mating based on ecologically selected traits, which can be the principal mechanism of ecological speciation (McKinnon and Rundle 2002). Recent molecular studies also provide strong support for the hypothesis that adaptive divergence contributing to reduction of gene flows will cause genetic incompatibility responsible for reproductive isolation and promote ecological speciation between members of a sympatric species pair (Rogers and Bernatchez 2007).

In traditional systematics based on morphological taxonomy, it does not matter if the species pair accords with the entity of biological species. For freshwater fishes whose local populations have experienced isolation and reorganization repeatedly through geological events such as river and lake capture, it is not easy to define a boundary for a biological species. Whether discrete variation in feeding traits found in a focal taxa is regarded as intraspecific or interspecific variation relies on how a researcher classifies a biological entity into "single species" or "different species". However, "species" is just an operational taxonomic unit and its definition is not an important issue for understanding how a diversity of feeding functions has evolved from an ancestral lineage. It is more important to recognize that polymorphic populations observed in nature can be arrayed somewhere along a continuum from panmixia to complete reproductive isolation (Hendry 2009).

2.4.3 The Ancient Lake Biwa as an Evolutionary Hot Spot

The ancient Lake Biwa, which has a geological history longer than postglacial lakes (tens of thousands years) and shorter than the oldest African Great Lakes (tens of millions years), provides a good opportunity to observe how the process of ecological speciation leads to species diversification. This lake was formed south far from its current location ca. four million years ago (see Chap. 1). It is a tectonic lake, i.e., the lake formed as a result of tectonic movement, having gradually moved northwards. The lake deepened through faulting at the current location ca. 400 thousand years ago and then has stood still there. At present, it shows a high biodiversity with 1,769 aquatic species recorded, including 61 endemics (Timoshkin et al. 2011). Similar to other ancient lakes created by tectonic movements, Lake Biwa is characterized by the development of deep pelagic habitats, which support many pelagic fishes (Okuda et al. 2012). Recent molecular techniques have revealed that some endemic fishes, which have adapted to pelagic environments, are derived from littoral or fluvial ancestral species (see Chap. 1). Many of these pelagic species share adaptive traits, such as a slender body and narrow gill raker spacing, which are advantageous to inhabiting pelagic waters. Because such an evolutionary divergence is found among phylogenetically distant groups, it is suggested that convergent evolution of phenotypes adaptive to the pelagic habitats has occurred following the appearance of newly created deep water environments in Lake Biwa.

Even if divergent evolution progressed over geological time scales in this lake, reproductive isolation may remain incomplete. This is the case in sister species of a minnow, *Gnathopogon*, living in Lake Biwa (Fig. 2.1). *Gnathopogon elongatus elongatus* is a common freshwater fish inhabiting rivers and ponds in western Japan, while *G. caerulescens* is endemic to Lake Biwa. In Lake Biwa, these two species coexist but segregate their habitats: i.e., *G. elongatus elongatus* lives in littoral and fluvial habitats, whereas *G. caerulescens* lives in limnetic habitats. The former is typical of benthivores and the latter of planktivores. The planktivorous *G. caerulescens* has a slender body and narrower gill raker spacing, which is advantageous to feeding on plankton in pelagic waters. An advanced molecular technique, with a next generation sequencer, elucidated the genetic basis of such a morphological adaptation (Kakioka 2013; also see Sect. 2.4.6). Although there are remarkable morphological differences between these coexisting fishes, their phylogenetic relationship is closer than that of allopatric populations within the species *G. elongatus elongates* (Kakioka et al. 2013a; Fig. 2.1). More interestingly, they are reproductively compatible to each other in captive conditions and their hybrids sometimes occur in nature (Nakamura 1969; T. Kokita, unpublished data), suggesting that discrete variation in their feeding morphology stands for

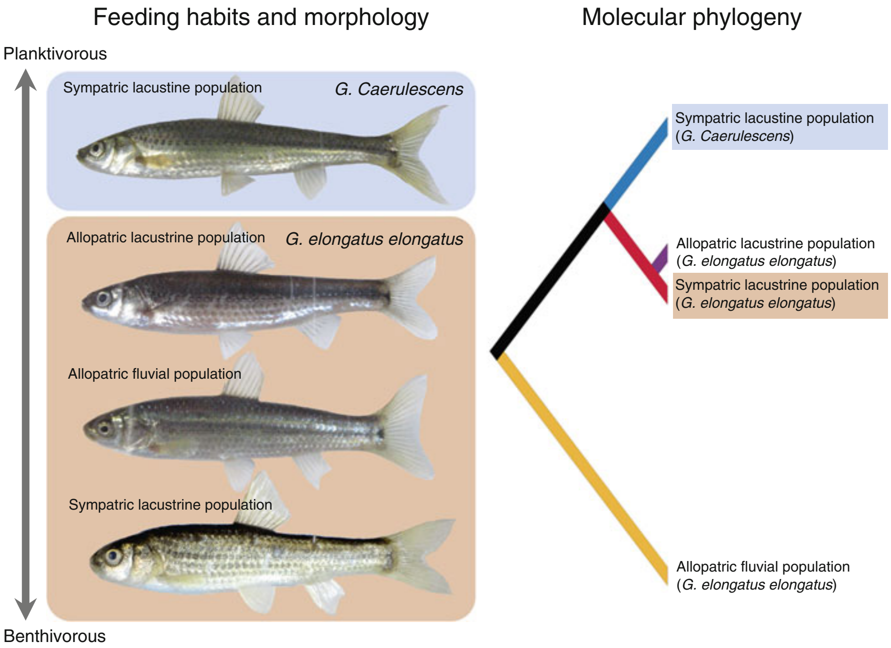

Fig. 2.1 Feeding habits, morphology and molecular phylogeny of a genus *Gnathopogon* in Japan. The phylogenetic tree was modified after Kakioka et al. (2013a)

trophic polymorphism within a species pair rather than interspecific variation between sister species. This phenomena may also be true for sister species of some other fish groups in Lake Biwa.

2.4.4 *Life History Polymorphism*

In freshwater fishes, another example of phenotypic polymorphism is often found in life history traits. In many species of salmon and sticklebacks in which trophic polymorphism is well known, two different life history forms coexist within a population, i.e., a diadromous form, which migrates between freshwater and marine habitats, and a non-diadromous (or landlocked) form, which occurs in freshwater environments throughout its entire life (Taylor 1999). In these polymorphic populations the non-diadromous form generally has a smaller body size at maturity and more gill rakers or narrower gill raker spacing than those in the anadromous form (Foote et al. 1999; McKinnon and Rundle 2002). For migratory threespine sticklebacks with a marine origin, molecular phylogenetic evidence suggests that the migration-related morphological traits (e.g., the pattern, number, and size of the bony lateral plates) have evolved repeatedly in populations from different locations (Colosimo et al. 2004).

An alewife *Alosa pseudoharengus* (Clupeidae) is one example where relationships between life history, trophic morphology and feeding habits have been intensively investigated (Palkovacs and Post 2008). In this species, anadromous fish migrate from the ocean to freshwater lakes for breeding in spring. Their young-of-the-year (YOY) fish spend several months in nursery lakes to preferentially prey upon large bodied zooplankton before migrating to the ocean in autumn. However, if there are any physical barriers to their migration route, the migratory populations become landlocked, completing their entire life in the nursery lakes. While migratory populations are sometimes landlocked by natural barriers such as beaver dams and wind throws for years to decades, some of them have been completely isolated by artificial barriers such as man-made dams, resulting in the prevention of gene flows.

In alewives, non-migratory landlocked populations have smaller gape width and narrower gill raker spacing than anadromous populations. In lakes with landlocked alewives, zooplankton size is small all year round, as compared to lakes with anadromous alewives, because of constant fish predation of large bodied zooplankton. In a situation where intra- and/or inter-specific food competition is intense and constant among planktivores coexisting in lakes, evolution might favor the landlocked morph with the smaller gape width and narrower gill raker spacing, which are more adept at foraging on small-bodied prey items. Estimations based on molecular data suggest that such a divergent evolution occurred between 5000 and 270 years ago, during which time dams were built in this region (Palkovacs et al. 2008).

For migratory fishes, geographic barriers temporarily isolate local populations in terms of geological time scales, while their high mobility promotes the reorganization of different populations under different selection regimes, creating spatio-temporal heterogeneity in trait distribution within and/or among populations. As a consequence, a multimodal distribution of phenotypes may be observed at a given time and space in relation to trophic morphology as well as life history traits. This may explain why polymorphic phenomena, such as trophic polymorphism or a species pair, have often been reported for freshwater fishes with a diadromous origin.

2.4.5 Rapid Evolution of Trophic Polymorphism

How rapidly can trophic polymorphism emerge within a population after colonization of a new environment? Human introductions of non-native species, which have been considered a serious conservation issue worldwide, can provide unexpected opportunities to study the evolutionary process of trophic polymorphism. The bluegill sunfish *Lepomis macrochirus* was introduced into Japan from the United States in 1960 and, thereafter, rapidly spread throughout the country. Surprisingly, all of the introduced fish are derived from only 18 individuals collected from the Mississippi River at Guttenberg, Iowa, and genetic diversity is very low in the respective introduced populations, probably due to a founder effect arising from introduction of a small number of individuals with subsequent genetic drift (Kawamura et al. 2006). In the original population there are two feeding morphs. The littoral or benthic morph has an enlarged body depth and long pectoral fins, indicating a feeding specialization towards benthic prey, while the limnetic or pelagic morph has a slender body and short pectoral fins, which give an advantage in searching for zooplankton in pelagic waters (Ehlinger 1990, 1991; Wilson 1998).

In Lake Biwa, there are records indicating that introduced bluegills mainly fed on shrimp in the early phase of their colonization during the 1970s (Terashima 1980), suggesting that their founders were originally the littoral morph. More than half a century after the colonization, however, Yonekura et al. (2002) found that the introduced population showed specialization of feeding habits, i.e., individual food preferences for zooplankton, zoobenthos or submerged plants, and that they individually differed in morphology corresponding to their feeding specialization. Their trophic morph-specific feeding habits were also consistent through the time, as suggested by their stable isotopic signatures, which revealed that each of the morphs occupied a different trophic niche (Uchii et al. 2007). Such a feeding specialization might have been promoted by food resource partitioning among introduced bluegills because their habitats are confined to a narrow zone of shallow waters in this deep lake. Yonekura et al. (2007b) demonstrated that the smaller gill raker spacing characteristic of the pelagic morph increases foraging efficiency for zooplankton prey, whereas the wider mouth characteristic of the benthic morph increases foraging efficiency for zoobenthos prey. More interestingly, submerged plant feeders have developed an intermediate morph between benthic and limnetic morphs. Uchii (2007) revealed that bluegills in captive conditions could not compensate for their growth by feeding on submerged plants exclusively, suggesting that the submerged plant feeders found naturally adopt “the best of a bad situation” strategy, because their intermediate morph is not specialized for either benthos or plankton feeding.

The example of introduced bluegills implies that newly colonized populations can achieve phenotypic divergence much faster than expected from the evolutionary time required for a species pair, which is estimated as ten thousand years. Unfortunately, it remains untested whether trophic polymorphism of introduced bluegills is attributed to genetic divergence during their colonization, which gives direct evidence for the rapid evolution. However, recent molecular data suggests the possibility that polymorphic variation in feeding traits is under the control of phenotypic plasticity (see Sect. 2.4.6). Another excellent example of the rapid evolution, if not of trophic polymorphism, in fishes is the case of sockeye salmon, in which introduced populations derived from a common ancestry colonized adjacent river and lake habitats separately, resulting in phenotypic divergence. In these introduced populations, Hendry et al. (2000) demonstrated that reproductive isolation rapidly evolved between two divergent populations within fewer than 13 generations of their colonization. Therefore, it is possible for newly colonized populations to evolve trophic polymorphism followed by assortative mating between the same morphs on an ecological time-scale, sometimes even within decades.

2.4.6 Genetic Mechanisms of Trophic Polymorphism

Although it remains unknown how phenotypic polymorphism is maintained within a population, there are two mechanisms for generating it. One is genetic variation, with the other being phenotypic plasticity, defined as ontogenetic phenotypic changes in response to changes in the environment. Some studies have reported that trophic polymorphism in fishes has at least partly a genetic basis. For example, Proulx and Magnan (2004) conducted common garden experiments with a lacustrine brook charr, in which both pelagic and littoral morphs coexisted. Young-of-the-year (YOY) fish of each morph were transplanted to a tank, either simulating a pelagic or a littoral habitat, and fed pelagic or benthic food respectively. Some variation in feeding morphology was accounted for by genetic effects, whereas some was environmental. More interestingly, additional experiments, under which fish habitats were alternated between each other during their growth, indicated that some of the morphological traits were plastically changed to adjust to a new habitat, suggesting the ecological significance of phenotypic plasticity during ontogenetic habitat shifts. For many species showing trophic polymorphism, phenotypic plasticity plays an important role in intraspecific phenotypic variation, as discussed later.

Recent advances in molecular techniques have stimulated studies to elucidate the genetic mechanisms of phenotypic polymorphism in fishes: the techniques include comparative genomics, genetic mapping, candidate gene approaches, transcriptomics and so on (Ellegren and Sheldon 2008). Quantitative trait loci (QTL) analysis, one of the linkage mapping, is a powerful approach for identifying genome regions that contain genes responsible for variation in quantitative traits. Since the QTL analysis requires intercross and backcross between different populations, which have divergent phenotypic traits but are reproductively compatible to each other, species pairs are considered a promising subject for this analysis. Threespine sticklebacks are among the best understood species in fishes in relation to the genetic basis on life history and trophic polymorphisms with the application of the QTL (Peichel et al. 2001; Colosimo et al. 2004; Cresko et al. 2004; Shapiro et al. 2004; Kimmel et al. 2005). Although we have difficulty in applying this technique to wild populations of non-model organisms because of the labor intensive and time consuming work required to get their genomic resources, the development of high throughput next generation sequencers will enable us to efficiently perform it with wild fish populations (Baird et al. 2008; Kakioka et al. 2013b).

Because the QTL can only detect genome regions containing or linked to target genes, positional cloning and nomination of candidate genes are required to find causative genetic variants. Colosimo et al. (2005) is the first to identify a particular gene involved in the expression of divergent phenotypes in wild fish populations. In threespine sticklebacks, landlocked populations evolved from fully armored anadromous ancestors and experienced armor reduction repeatedly in different locations (Barrett 2010). Colosimo et al. (2005) demonstrated that the ectodysplasin gene, which is involved in proper development of a number of ectodermal derivatives and dermal bones in mammals, was responsible for the armor reduction in landlocked threespine sticklebacks by means of genetic mapping, sequencing and transgenic techniques. Surprisingly, the causative alleles were shared among widely separated populations, suggesting a molecular genetic basis of the rapid parallel evolution of phenotypes adaptive to freshwater habitats.

Transcriptome profiling is also a promising tool for unraveling complex molecular genetic basis of phenotypic divergence between closely relatives by examining their differential gene expression on the microarray. Using this technique, for example, Derome and others demonstrated in polymorphic populations of lake whitefish *Coregonus clupeaformis* that two sympatric morphs, a dwarf morph adaptive to limnetic habitats and a normal morph to benthic habitats, showed differential expression of genes involved in energetic metabolism and regulation of muscle contraction, both of which are associated with swimming activity, and that their differential gene expression was parallel among different lakes (Derome and Bernatchez 2006; Derome et al. 2006). This is reasonable when considering that the dwarf morphs are selected for high swimming performance in the limnetic habitats. More interestingly, the expression of the same genes involved in modulating swimming activity were upregulated for a sympatric congener *Coregonus artedi*, a specialist competitor for the limnetic trophic niche, providing the molecular evidence of parallel phenotypic evolution.

While an increasing number of studies have reported evidence for the molecular genetic basis of phenotypic polymorphism in fishes, they do not usually reject the possibility of its environmental determination, i.e., phenotypic plasticity. Many researchers have used common garden experiments to demonstrate that phenotypic plasticity of feeding morphology is induced by diet and/or habitat manipulation in fish populations with polymorphic phenotypes (Hegrenes 2001; Andersson 2003; Andersson et al. 2005; Olsson and Eklöv 2005). In introduced populations, which have been recently colonized by a small number of individuals and, therefore, possess low genetic variation, trophic polymorphism may be substantially controlled by phenotypic plasticity, as in the case of bluegills introduced into Japan (Yonekura et al. 2007a; also see Sect. 2.4.5). Although it is hypothesized that the phenotypic plasticity can be controlled by epigenetics (i.e., heritable changes in gene expression or cellular phenotype caused by mechanisms other than changes in the underlying DNA sequence), its molecular mechanisms are poorly understood. In particular there is little published information regarding which key genes are involved in phenotypic plasticity of polymorphic traits and how they control developmental plasticity through a gene regulatory network (Sibthorpe et al. 2006). Without understanding the molecular mechanisms for phenotypic plasticity, difficulties remain in discriminating between genetic and environmental effects on trophic polymorphism. Further advances in molecular techniques and their application to wild fish populations are needed to elucidate the genetic mechanisms underlying life history and trophic polymorphisms.

2.5 Niche Construction

A member of a biological community embedded within an ecosystem has a number of effects on other individuals simply by utilizing the space and energy provided by the ecosystem. These effects can sometimes alter ecosystem structure and functioning through ecological interactions between individuals or between biotic and abiotic components. In such an interaction network, species that have strong impacts on community and ecosystem processes are termed “keystone species” or “ecosystem engineers.” When “environment” is defined as “physical, chemical and biological properties outside the organism under consideration,” phenotypes of the keystone species can shape their environments. The environments altered by the keystone species may, in turn, act as a driver for the evolution of both itself and other members of the community. The process by which phenotypes expressed by a given species shapes the adaptive landscape of phenotypic evolution for itself or other species through alteration of biotic and abiotic attributes of their environments is termed “niche construction” (Odling-Smee et al. 2003).[1]

In aquatic ecosystems, although there are a large number of examples of niche construction by fish acting as keystone predators, two key mechanisms of trophic cascade and nutrient transportation can be recognized (Fig. 2.2). Trophic cascade is defined as a food web consequence in which predators have indirect effects on non-prey organisms at trophic levels lower than those of their prey, through trophic interactions within a food web (Carpenter et al. 1985). For example, in the presence of planktivorous fish, large-bodied zooplankton are preferentially eliminated from the plankton community through fish predation (Brooks and Dodson 1965). This predation effect can alter microbial communities including microalgae, bacteria and protozoa. Since large-bodied zooplankton such as *Daphnia* have higher grazing rates, they depress growth of their microbial prey to a greater extent. Despite their microscopic size, microalgae and bacteria have large impacts on ecosystem processes, including production and decomposition rates, because of their large biomass and high metabolic turnover. When the abundance of planktivorous fish increases, microbial communities enhance their production and decomposition through alleviation of predation by large-bodied zooplankton, resulting in an alteration of aquatic environments.

The mechanism of nutrient transportation is more effective in a situation where predator fish move from productive to less productive habitats (Vanni 2002). For example, when a large shoal of anadoromous fish migrate from the ocean to oligotrophic streams and lakes, or when benthic fish exhibit vertical feeding migration from the lake bottom to surface waters in which nutrients are prone to be depleted, a supply of nutrients is transported to the less productive habitat as their excreta or their body mass themselves. The transported nutrients are quickly consumed by microalgae and bacteria, increasing their production and decomposition rates. This fish-driven nutrient transportation can have a substantial effect on material cycling within an ecosystem.

In this way, fishes that are considered keystone predators of aquatic ecosystems have the potential to drastically alter community structure and ecosystem processes

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[1] Post and Palkovacs (2009) recommended restricting the use of the term “niche construction” to the process by which organisms shape environments in order to separate it from the process by which biologically constructed environments shape selection regimes for the evolution of organismal traits.

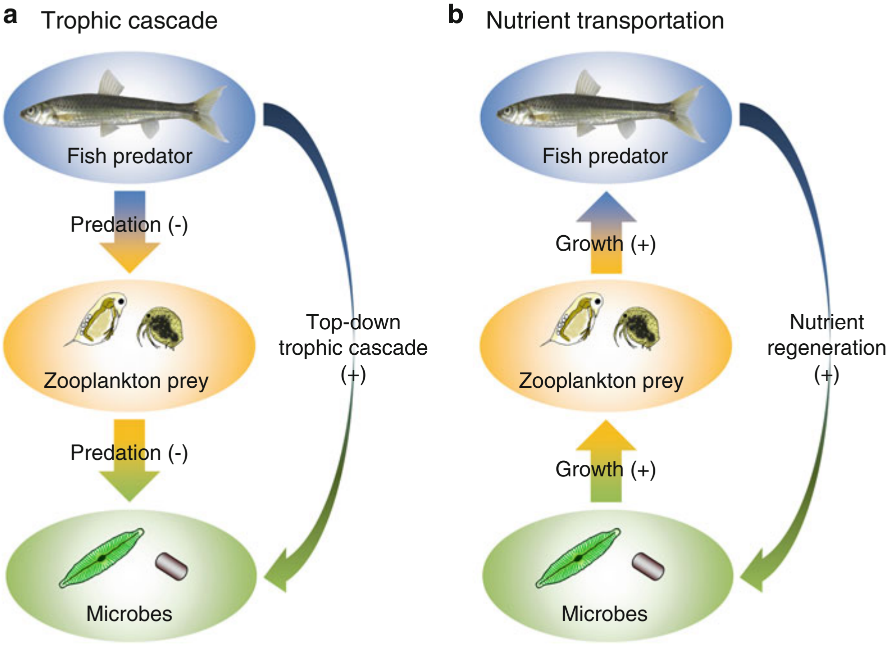


Fig. 2.2 Ecological impacts of keystone fish predators on plankton communities through top-down trophic cascade (**a**) and nutrient transportation (**b**). (+) and (−) indicate positive and negative effects on prey or predator biomass, respectively

through trophic cascade and nutrient transportation. If mutation occurs on loci involved in the expression of traits affecting trophic interactions and nutrient transportation or if gene flows occur through outbreeding with such variants from different populations, a new niche might be constructed within the naive population. In the next section, we will introduce some empirical studies demonstrating that intraspecific phenotypic variation in predator fish creates new environments in aquatic ecosystems.

2.6 Predator Diversity and Ecosystem Functioning

It has been a great challenge for ecologists to answer the question of why biodiversity is important for us. A plant ecologist David Tilman tried to answer this question by elucidating relationships between biodiversity and ecosystem functioning (Kinzig et al. 2001). He is the first to experimentally demonstrate that plant species diversity positively correlates with their biomass as an index of primary productivity in terrestrial ecosystems. Considering that terrestrial plants provide a variety of ecosystem services, (i.e., humankind benefits from a multitude of resources and processes supplied by natural ecosystems, such as, supporting, provisioning, regulation and cultural services; see Millennium Ecosystem Assessment 2005 for definition), it is obvious that we profit from the conservation of plant species diversity, which results in increased primary production. Inspired by his work, several theoretical models have been proposed and subsequently an increasing number of empirical studies have been conducted, for both animal and plant communities, to test the hypothesis that biodiversity enhances ecosystem functioning (Waide et al. 1999).

What about the role of predators? Unfortunately, very few studies have examined how the species diversity of predators affects community composition and ecosystem processes (Straub and Snyder 2006; Schmitz 2009). There are various reasons why studies on predator diversity effects are so limited. First, we have difficulty in experimentally manipulating the species composition of predators, which have an extensive home range associated with their high mobility. Secondly, it is not easy to theoretically predict how a combination of different predator species, which feed on prey at different trophic levels and from different trophic pathways, will impact on an ecosystem. Even if predator diversity effects are detected, we cannot easily interpret their mechanisms using theoretical models. Furthermore, even when effects on community composition and ecosystem processes can be quantified for each predator species, it is impossible to conclude what traits actually lead to such community and ecosystem consequences because the species are different from each other in traits other than those related to feeding (Chalcraft and Resetarits Jr. 2003; Wesner 2012). However, there is a measure to overcome such difficulties in demonstrating predator functional diversity effects on community structure and ecosystem processes, which is, to manipulate a diversity of trophic morphs or a species pair of fish predators.

As mentioned previously, trophic morphs are usually different only in trophic and/or life history traits and, otherwise, share all other ecological characteristics. By comparing different morphs or by manipulating a combination of these morphs within a predator population, we can examine how phenotypic diversity of a focal trait affects community and ecosystem properties. Based on this idea, Post et al. (2008) tried to demonstrate that intraspecific phenotypic variation among predator fish populations can alter prey community structure under natural conditions.

Post et al. (2008) focused on geographic variation in migration behavior and feeding morphology among alewife populations from 19 lakes in Connecticut, USA. They compared body size and biomass of zooplankton prey among lakes either with anadromous or landlocked alewives or entirely without alewives. As stated in Sect. 2.4.4, since the anadromous alewives have larger gape width and gill raker spacing than the landlocked alewives, the former preferentially feed on large-bodied zooplankton prey. In the anadromous lakes, alewives were absent during the winter season, so that large-bodied zooplankton dominated in the absence of strong zooplankton predators. However, spring breeding migration by the anadromous alewives and the subsequent recruitment of their YOY facilitated selective predation on large-bodied zooplankton, seasonally eliminating larger individuals from the zooplankton communities. By contrast, in landlocked lakes in which alewives reside through the year, zooplankton communities are always exposed to intense and indiscriminate predation by landlocked YOY with smaller gape and gill raker spacing, perpetually skewing the zooplankton community size towards a smaller distribution.

Intraspecific geographic variation over their life history and trophic polymorphisms of alewives can also alter lake environments through top-down trophic cascades (Post et al. 2008). In the anadromous lakes, phytoplankton biomass increases during the seasonal reduction in zooplankton body size and biomass, suggesting that the anadromous YOY have positive, indirect effects on phytoplankton by depressing the grazing intensity of large-bodied zooplankton. The work of Post et al. (2008) is noteworthy as a milestone study demonstrating that intraspecific variation in predator feeding functions affects ecosystem processes such as primary productivity.

2.6.1 Mesocosm Experiments

Even though variations in prey community structure and ecosystem processes were found between lakes with different feeding functions within a predator species, they might be attributed to geographic variation in limno-physical and -chemical characteristics or to the density of other planktivorous fish. In order to reveal the ecosystem consequence of intraspecific predator functional diversity, experiments are required in which environmental factors, with the exception of predator feeding functions, are controlled. One promising approach is that of mesocosm experiments.

Since Forbes (1887) proposed the idea of "The Lake as a Microcosm," in which lakes are considered as self-contained and circulating systems, the term "microcosm" has often been used in microbiology to refer to microbial cultivation systems containing essential components for their sustainable growth. Following experimental attempts to simulate lake ecosystems containing macro organisms such as zoobenthos and fish, the microcosms have been too small to ensure their sustainability. In order to fulfill energy and space requirements for the macro organisms, we have to provide them with a larger cultivation system. Such a self-contained experimental system, which is larger than microbial cultivation systems but smaller than natural ecosystems (i.e., on the meso-scale), is termed a "mesocosm." Mesocosm experiments enable us to manipulate a given factor by controlling all other physical, chemical and biological environments and, thereby, to assess the ecosystem effects of the focal factor (Fig. 2.3).

An interesting mesocosm experiment considering trophic polymorphism in alewives was undertaken by Palkovacs and Post (2009) who constructed solid walled polyethylene enclosures with 2 m diameter and 6 m depth in Rogers Lake, Connecticut, USA. Plankton communities were exposed to different predation regimes by introducing 15 YOY fish of either anadromous or landlocked alewives into each enclosure in order to examine effects of predator feeding functions on prey communities. Some enclosures were left unstocked (i.e., no fish) as a control. Mesocosm experiments were conducted during the summer season when the YOY fish cause top-down trophic cascades in natural zooplankton communities. Weekly sampling of zooplankton communities from the enclosures was undertaken.

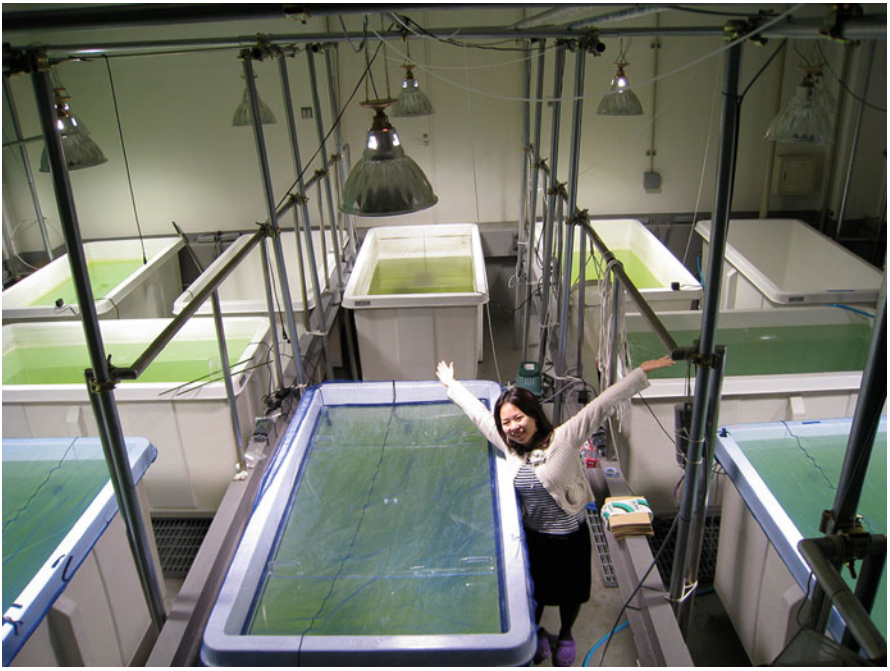


Fig. 2.3 Twelve 2,000 L mesocosms tanks set up in Center for Ecological Research, Kyoto University. It is possible to automatically control water temperature, light intensity and L:D length. They are useful for experiments to examine effects of fish predator manipulation on ecosystem properties (see Sect. 2.6.2)

Experimental results were consistent with those reported for natural lakes, with summer zooplankton body size and biomass significantly reduced only in systems containing anadromous alewives. In addition, the presence of anadromous alewives led to a marked reduction in species richness and the diversity index of zooplankton communities. Palkovacs and Post (2009) were successful in demonstrating that intraspecific variation in predator feeding functions alone could alter zooplankton size distribution and species composition using these mesocosm experiments. This may also support the previous conclusion that variation between lakes in primary productivity is due to differential trophic cascading effects caused by alewife morphs.

Similar results have been reported for another system exhibiting trophic polymorphism in fish predators. Harmon et al. (2009) conducted mesocosm experiments with a species pair of threespine sticklebacks that underwent adaptive divergence to benthic (i.e., benthivorous) and limnetic (i.e., planktivorous) morphs from a generalist ancestor. To examine the effects of evolutionary diversification of the threespine sticklebacks on ecosystem properties, they manipulated a combination of two specialist morphs or one generalist ancestor in large tanks to artificially simulate pond ecosystems including the plankton and benthos communities. They found strong effects of predator functional diversification on prey community composition and ecosystem processes such as primary productivity and water chemistry. One of the more remarkable outcomes was that they could detect synergistic effects of the predators' adaptive diversification on the pond ecosystems as well as differential effects of each morph, by comparing ecosystem consequences between simple and diverse feeding functions. The results have ecological implications for the evolutionary diversification of the sticklebacks because these morphs often coexist in natural ponds and lakes.

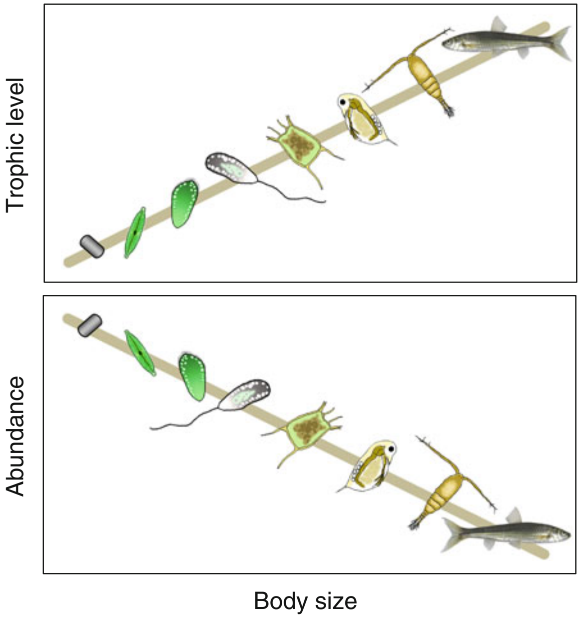
Intraspecific phenotypic diversity effects of fish predators can also appear through nutrient transportation. In guppies inhabiting streams in Trinidad, local populations are often isolated by natural barriers such as waterfalls and are exposed to different predation regimes from piscivorous fish. The high predation risk favors the evolution of life history traits in guppies, including a younger age at maturity, a smaller body size at maturity and higher reproductive rates. These life history traits are also linked with metabolic rate, which determines physiological performance such as respiration and excretion rate. The common garden experiments to manipulate fish from different populations showed that phenotypic diversification in guppies results in the divergence of community structure (benthic algal and invertebrate biomass) and ecosystem processes (gross primary productivity, leaf decomposition rates and nutrient flux), which are altered through nutrient transportation driven by intraspecific variation in the excretion rate of fish from different populations (Palkovacs et al. 2009; Bassar et al. 2010).

2.6.2 Food Web Properties as a Universal Measure

In previous sections, we cited some examples in which intraspecific phenotypic diversity in fish predators alters ecosystem properties. However, some ecosystem properties are system-specific (e.g., species composition) and others are just a functional trait of a specific guild (e.g., primary productivity by algae and decomposition rate by bacteria and fungi) rather than ecosystem functions performed by an entire community. How then can we generalize from a variety of results from different systems and what is a universal measure for ecosystem properties, which are ubiquitous and intrinsic to all aquatic systems, thus allowing comparisons to be made between systems? Here we focus on structural properties of food web as a universal measure for the entire community.

A food web is a diagram to depict the overall energy flows through trophic interactions within an entire community (Lindeman 1942). Since the Eltonian pyramid (Elton 1927), a variety of ideas have been proposed to describe structural properties of intricate food webs in nature. One of promising measures to characterize food web properties is food chain length (FCL), defined as the number of trophic transfers of energy from primary producers to a top predator, which has been easily measured and comparable across ecosystems, with the recent development of isotopic technique (Post 2002). In lake ecosystems, the FCL can be the best explained by the lake size in volume (Post et al. 2000). However, it also varies temporally even

Fig. 2.4 Allometric relationships between body size and trophic level or numerical abundance in aquatic communities



within a lake, as in the case of Lake Biwa (Okuda et al. 2012). The possible mechanism to cause temporal variation in the FCL may be compositional and functional changes in plankton and benthos prey communities, which can affect the number of trophic links.

In aquatic food webs, there also exists a general rule in which larger organisms eat smaller ones and becomes fewer in number, so that organisms increase their trophic levels and decrease abundance with their body mass (Fig. 2.4; also see Cohen et al. 2003). Based on the allometric relationship between body size and biomass (body mass multiplied by the numerical abundance in each size class), size distribution of entire community can be formulated as the size-biomass spectrum, defined as the slope of body mass–biomass regression (de Eyto and Irvine 2007; Jennings and Mackinson 2003). When the community size distribution skews toward smaller-sized organisms, the size-biomass spectrum slope become steeper. Jennings et al. (2002) also proposed a new method to predict predator–prey body-mass ratios (PPMR) in food webs, using their nitrogen stable isotope ratio as a proxy of trophic level. The PPMR can be calculated as the inverse of body size-trophic level regression slope in Fig. 2.4. The PPMR is an important factor determining interaction strength between preys and predators and in turn the stability of food webs (Emmerson and Raffaelli 2004).

To examine how evolutionary diversification of fish feeding traits alters food web properties of prey communities, we conducted mesocosm experiments that simulated conditions at Lake Biwa where ecological diversification occurred independently in some phylogenetically distant fish groups during the last 400,000 years

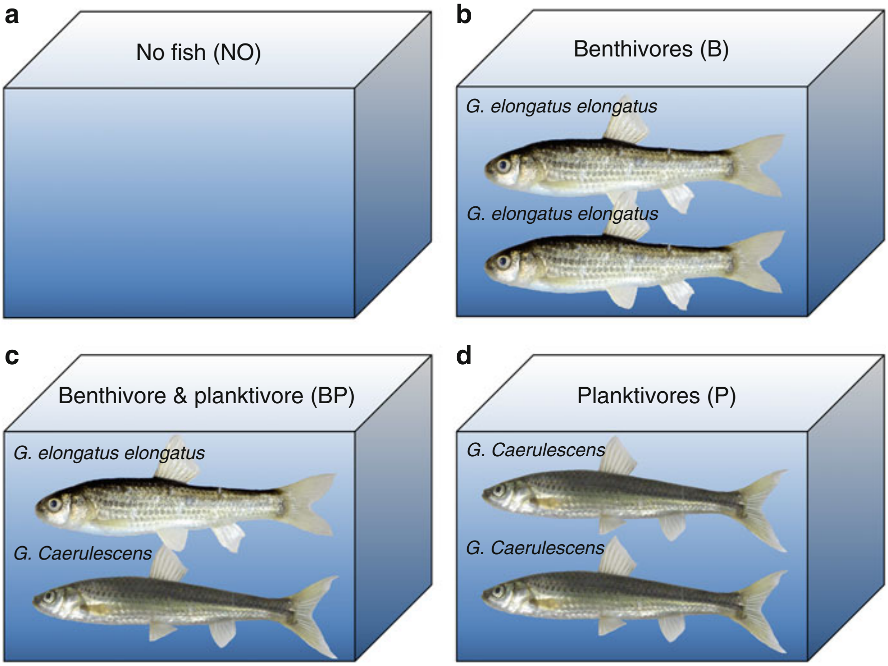


Fig. 2.5 An experimental design of predator manipulation. Each treatment corresponds to historical change in diversity of fish feeding functions in a lake. The lake has no fish in original condition (**a**), an ancestral benthivorous fish colonizes the lake (**b**), and then the colonized population experiences ecological speciation into benthivorous and planktivorous species (**c**). However, fish diversity decreases if either of these two becomes extinct. The ancestral benthivorous species may go extinct for some reason, e.g., destruction of coastal habitats under human disturbances (**d**)

after the development of deep pelagic habitats (see Sect. 2.4.3). We set up 12 mesocosm tanks in which abiotic environments (i.e., light intensity, L:D length, water temperature and nutrient levels) were controlled and then a plankton community and supplementary zoobenthos prey were provided (Fig. 2.3). We manipulated the phenotypic diversity of feeding functions in fish predators, using a species pair of *Gnathopogon* that had diverged into planktivorous *G. caerulescens* and benthivorous *G. elongatus elongatus* but remained reproductively compatible to each other (see Sect. 2.4.3). We conducted experiments with a full-factorial design for four treatments: no fish (NO), benthivorous *G. elongatus elongatus* (B), and both planktivorous *G. caerulescens* and benthivorous *G. elongatus elongatus* (PB), and planktivorous *G. caerulescens* (P), assuming historical change in diversity of fish feeding functions in a lake (Fig. 2.5).

We measured the size-biomass spectrum, FCL and PPMR of plankton prey communities in the mesocosm tanks. It was predicted that planktivorous fish would skew the plankton communities toward a smaller size distribution through a top-down trophic cascading effect, under which a large zooplankton biomass would be depressed and a smaller plankton biomass would be indirectly enlarged, resulting in a steeper slope of size-biomass spectrum in the order of $\mathrm{NO} < \mathrm{B} < \mathrm{PB} < \mathrm{P}$. Contrary to this prediction, the plankton size-biomass spectrum did not significantly differ among these four treatments though the presence of fish predator increased the biomass of phytoplankton (Fukumori et al. unpublished data). The benthivorous *G. elongatus elongatus* feeds mainly on benthos but also less efficiently on plankton, as is often the case in other benthivorous fishes. The mesocosm tanks with a volume of 2,000 L might not be large enough to control predation of benthivorous *G. elongatus elongates* on zooplankton.

However, we found significant differences in the FCL and PPMR among the treatments. Under the presence of benthivorous fish, the plankton FCL, defined as the highest trophic level observed for all samples of size-fractionated plankton communities, increased and the PPMR of plankton communities decreased (Sakai 2013). Although underlying mechanisms for these results remain unclear, selective predation of the two fishes on different species of large-sized zooplankton (e.g., cladocerans versus copepods) is likely to alter trophic relations within plankton communities. More interestingly, we detected synergetic effects of predator feeding functional diversity on both indices. Under the coexistence of fish with different feeding functions, fish production, particularly for benthivorous fish, increased, possibly due to reduced food resource competition between planktivorous and benthivorous fish: the benthivore can exploit benthic food exclusively in the absence of benthic competitors (Fukumori et al., unpublished data). Assuming that the nutrient excretion rate scales with fish body mass (Torres and Vanni 2007; McIntyre et al. 2008), the benthivorous fish coexisting with the planktivorous fish might enhance nutrient transportation from the benthic to the pelagic habitats, resulting in synergetic effects of top-down and bottom-up trophic cascades on the plankton food webs. Our experiments demonstrate that predator phenotypic diversity can alter food web properties of prey communities and thus the overall energy flows within an ecosystem.

2.7 Eco-Evolutionary Feedbacks

There is no doubt that intraspecific phenotypic diversity of fish predators is an important driver for altering prey community composition and thus ecosystem properties. However, we must also consider an overlooked point, which is that ecosystem alteration, as a consequence of fish phenotypic diversification, creates new aquatic environments, i.e., niche construction, which can shape the adaptive landscape for the evolution of predators themselves as well as prey species. Ecological interactions between a keystone species and other community members drive evolutionary changes in their adaptive traits through environmental alterations and, in turn, the adaptive evolutionary changes shape the form of ecological interactions. This process, in which ecology and evolution reciprocally interplay over contemporary time-scales, is termed “eco-evolutionary feedback” (Post and Palkovacs 2009;

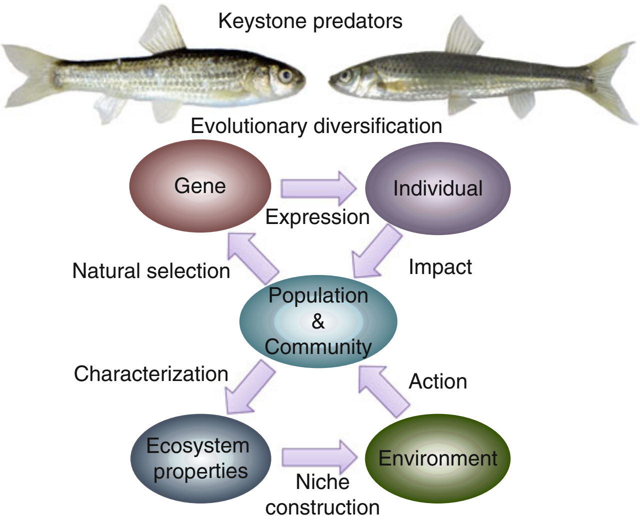


Fig. 2.6 A conceptual model for eco-evolutionary feedbacks. In aquatic ecosystems, fish predators often have evolved phenotypic polymorphism as a consequence of intraspecific resource partitioning in colonized populations or under newly created environments. When they alter ecosystem properties through compositional changes of prey communities, a new niche is constructed, which in turn molds fitness landscapes for themselves and other species, feeding back to metagenomic changes in the whole community

Fig. 2.6). Although eco-evolutionary feedbacks are poorly understood, some studies have provided evidence that such feedbacks do operate in natural conditions.

2.7.1 Feedback Loops

A good example of a widely studied system is that of alewife-zooplankton interactions in lakes. In landlocked lakes, intense and constant predation by alewives eliminates large-bodied zooplankton and skews the prey size toward a smaller distribution throughout the year. This results in individuals with smaller gape width and gill raker spacing being favored when foraging on smaller prey. Such a situation will place the landlocked alewives under strong directional selection for feeding on small-bodied zooplankton, driving the adaptive evolution of the landlocked morph from an anadromous ancestor (Palkovacs and Post 2008). In addition, sporadic occurrences of physical barriers to fish migration between freshwater and marine habitats promotes the parallel evolution of landlocked morphs independently in different locations, resulting in spatio-temporal heterogeneity in the geographic distribution of feeding traits within the species (Palkovacs et al. 2008).

It has been also suggested for *Gnathopogon* fishes that planktivorous morphs evolved from the fluvial ancestors with benthivorous morph independently in some lakes where there exist few fish competitors for zooplankton prey (Kakioka et al. 2013b). Among these populations with the great geographic variation in geometric morphology, a population endemic to Lake Biwa seems to have been most adapted for plankton feeding in pelagic environments, with its longest evolutionary history (Kakioka 2013).

Geographic variation in keystone predator phenotypes also has the potential to drive evolutionary divergence in their prey as well as to alter food web properties of prey communities. Walsh and Post (2011) recently evaluated the link between phenotypic variation in predators and their prey species by rearing water fleas, *Daphnia*, from lakes containing predatory alewives with different phenotypes under different water temperature and resource conditions, and then comparing their life history traits among these lakes. They found that *Daphnia* grew faster, matured earlier, and produced more offspring in lakes with anadromous alewives than in lakes with landlocked or no alewives. Although life history theory predicts that increased predation on large sized-zooplankton selects for maturity at smaller size, laboratory experiments showed that *Daphnia* matured at a slightly larger size in anadromous lakes, in which alewives have both a larger gape width and gill raker spacing to preferentially forage larger prey (see Sect. 2.4.4). This result seems to be inconsistent with the theory. The evolutionary response of *Daphnia* to divergent predation regimes can be best explained as an adaptation to a colder environment and shorter growing season known as countergradient variation (*sensu* Conover et al. 2009). For *Daphnia* from the anadromous lakes, the colder environment and shorter growing season results from the seasonal migration and predation by anadromous alewives, which substantially extirpated reproductive populations of *Daphnia* early in the summer. In this prey–predator system, prey life history evolution is facilitated by seasonal occurrence of increased predation, associated with predator life history traits rather than predation intensity and size-specific predation associated with predator feeding traits.

Walsh and Post (2012) also focused on how predator evolutionary divergence can mold the evolution of phenotypic plasticity in prey life history traits. It is well known that *Daphnia* alternate between sexual and asexual phases, producing parthenogenetic eggs (i.e., fully developed eggs without fertilization) throughout most of the year and sexual resting eggs during periods when environmental conditions deteriorate. Increased occurrence of predators selects for prey individuals that pass through the period of high predation as resting eggs. In lakes with landlocked alewives, *Daphnia* are under intense year-round predation, whereas they experience temporal but predictable predation in the anadromous lakes into which alewives seasonally migrate from marine habitats. According the theory, the temporal variation of alewife occurrence should affect a response of *Daphnia* engaged in sexual reproduction. To test this prediction, *Daphnia* from lakes with different alewife phenotypes were exposed to alewife kairomones as an environmental cue for the presence of predators. They found that, when exposed to the fish kairomones, *Daphnia* from the anadromous lakes invested more in sexual reproduction than those from the landlocked or alewife free lakes, suggesting a flexible life history trade-off in response to the predation risk. In conclusion, the divergent evolution of predator phenotypes has evolutionary consequences for phenotypic plasticity of prey life history traits.

2.7.2 Community Genomic Dynamics

In lake ecosystems, eco-evolutionary feedback loops can also cascade from *Daphnia* to microbes, such as bacteria, microalgae and protozoa, because *Daphnia* has strong impacts on microbial communities through resource competition and nutrient regeneration, due to its high grazing ability and excretion rate (Carpenter et al. 1985; Carpenter et al. 1992). However, such cascading effects have been hitherto evaluated only as the overall response of each trophic guild (e.g., primary producer, primary consumer or decomposer) or functional group (i.e., pico-, nano- or micro-plankton) rather than of each microbial taxon. Microbial diversity, particularly of bacteria, is primarily important in determining ecosystem functioning and, thus, ecosystem services for humankind, including the decomposition of organic matter, nutrient cycling and water purification (Bell et al. 2005; Cardinale 2011). Prompt responses of bacterial communities to changing environments are achieved by rapid evolution rates as well as by species turnover (Fukami et al. 2007; Gravel et al. 2011). Decades ago, the largest obstacle to disentangling the intricate relationships between bacterial diversity and ecosystem functioning was the difficulty in characterizing bacterial species composition *in situ* because most of them are uncultivable and thus cannot be isolated for species identification. However, recent advances in molecular techniques and bioinformatics have developed metagenomics or ecogenomics to characterize a profile of community-level genetic diversity *in situ* or comprehensively search for functional genes involved in phenotypic expression (see Chap. 3). The advent of next generation sequencer technologies has also accelerated ecological research as well as advancing our understanding of the molecular phylogenetics of aquatic microbial communities (Kalyuzhnaya et al. 2008).

As discussed previously, plankton communities can be affected by phenotypic polymorphism in fish predators. Recent molecular studies on fish phenotypic polymorphism suggest that alleles at a small number of loci have large effects on adaptively divergent traits (Colosimo et al. 2005), contrary to traditional views of quantitative genetics that consider polygenic variation in a large number of loci to have additive small effects on phenotypes. If it is general in fishes, such a gene with large effects may act as a “keystone gene” to influence metagenomic dynamics of whole plankton communities and, consequently, ecosystem properties. This is known to occur in terrestrial ecosystems where genetic variation within a population of foundation plant species is inherited through its phenotypic expression (e.g., concentration of chemical defense substances) to community and ecosystem phenotypes (e.g., species composition and interactions, nutrient cycling, and decomposition rate) (Whitham et al. 2006). It will not be long before we can examine the nature of the eco-evolutionary feedbacks as community genomic dynamics under water, through a molecular-scope.

2.8 Why is Predator Diversity Important?

Traditionally, evolutionary biologists have searched for an answer to the questions of how and when current biological communities diversified using fossil and molecular records, which help to infer the past changes in morphology and DNA sequence. However, ecologists have been more interested in what are the ecological implications for evolutionary diversification of current biological communities, often assuming that species' traits are static rather than variable. As demonstrated by an increasing number of studies, we now perceive that organismal traits are evolving at a faster rate than was previously assumed (Hairston et al. 2005), which leads to a new idea that the evolution of the organismal traits dynamically interplays with the ecology of populations, communities and ecosystems, and vice-versa (Post and Palkovacs 2009). Biological diversity observed in nature can therefore be viewed not only as a consequence of past evolutionary events but also as a product of ongoing evolution in existing communities. Diversity currently found within/among keystone predator populations can have the potential to influence the future direction of diversity at three levels of biological organization, from genes to ecosystems, through eco-evolutionary feedbacks.

At present, species extinction has progressed rapidly, with an accelerating rate, due to anthropogenic disturbances ranging from local human activities to global climate change. Biodiversity loss is particularly severe in freshwater ecosystems (Secretariat of the Convention on Biological Diversity 2010). Although much attention has been paid to the conservation of species, specifically those that are endangered, we also have to conserve the functional diversity of keystone species within/among populations, which may not necessarily be endangered. The effects of predator functional diversity can sometimes extend to ecosystem functioning, such as energy flows and nutrient cycling, from which we can enjoy a variety of ecosystem services profitable for human well-being.

In this chapter, the ecological and evolutionary importance of functional diversity of fish predators in the context of ecosystem management, as well as of traditional conservation biology, has been discussed. In order to deepen our understanding of the processes and mechanisms for generating and maintaining biological diversity, we have to further accumulate empirical data and establish a framework to integrate the theory of eco-evolutionary feedbacks. This idea is expected to develop a new paradigm for biological synthesis, linking from molecular biology to macroecology.

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