IMPACTS OF HABITAT DEGRADATION ON *FUNDULUS HETEROCLITUS* (LINNAEUS) IN URBAN TIDAL SALT MARSHES IN NEW YORK

by

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Abstract

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Despite considerable improvements in water quality over the last few decades, the ecological integrity of benthic habitats in the Arthur Kill (AK), New York, USA, largely remains altered. This dissertation explores how altered ecological status of benthic habitats directly and indirectly (via food webs) affected a resident forage fish, mummichogs (*Fundulus heteroclitus*), in highly urbanized tidal salt marshes in AK. A substantial portion of total abundance and biomass of benthic macroinvertebrates (a primary prey resource for mummichogs) in AK were comprised of only a few opportunistic oligochaete and polychaete species. And these alterations in benthic macroinfaunal communities in AK were strongly associated with the sediment-associated mercury level. Alterations in the AK benthic macroinfaunal assemblages were generally reflected in diet habits and strategies of mummichogs; a generalized feeding strategy with a broad diet niche breadth of mummichogs shifted to more specialized strategies for many of the AK populations. Although decapods (especially *Palaemonetes spp.*) were the predominant prey for all populations of mummichogs, the length-specific maximum sizes of *Palaemonetes spp.* ingested by some of the AK populations of mummichogs were about 2-fold smaller than those ingested by the reference population. These shifts in feeding habits were compensated for with an increased consumption of polychaetes by most of the AK populations and polychaetes contributed up to more than 40% of their gut

contents. Partial trophic decoupling between mummichogs and dominant benthic macroinvertebrates had further implications for biogeochemical cycling of trace metals and energy transfer in AK. Alterations in benthic macroinfaunal prey communities reduced trophic transfer efficiency (i.e., exposure levels) of metals to mummichogs. Furthermore, despite their compensatory food consumption, most of the AK populations of mummichogs had considerably elevated total metabolism, resulting in substantially reduced growth conversion efficiency. This reduction in energy conversion efficiency at the individual level can cascade through trophic chains, potentially leading to energetic bottlenecks at the community level. Altered salt marsh trophic structures in AK and their resultant impacts on mummichog (a crucial trophic link in urban estuaries) bioenergetics may thus disrupt energy translocation in this severely degraded coastal ecosystem.

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CHAPTER 1

General Introduction: *Background and Overview*

General Background

Due to high turnover rates of productivities, tidal salt marshes are among the most productive ecosystems (Evans, 1983; Kneib, 1997; Mitsch and Gosselink, 2000), providing essential habitats for resident fishes and shellfishes in coastal environments (Sardá *et al.*, 1998). Salt marshes are also important spawning and nursery grounds for migrant fish and shellfish species (Levin *et al.*, 2001). Trophic interactions between resident and migrant species within salt marshes facilitate energy transfer from primary producers to top predators in coastal marine habitats (Kneib and Wagner, 1994; Kneib, 1997; 2000). Tidal salt marshes thus play an critical role as a conduit for energy and material transport from/to surrounding coastal ecosystems (Kneib, 2000).

Salt marsh ecosystems are frequently associated with relatively low biodiversity (Waide *et al.*, 1999). As the physicochemical properties (e.g., salinity) of salt marshes are highly variable, salt marshes can be a stressful environment for aquatic organisms (Levin *et al.*, 2001). Many resident and migrant species thriving in salt marshes thus tend to be relatively tolerant to natural fluctuations in physicochemical properties of the environment (Moser and Gerry, 1989), or natural stressors. The dietary habits of salt marsh nekton are often flexible, depending on spatial and temporal variability in food resources (Baker-Dittus, 1978; Livingston, 2003). As a result, despite low biodiversity, trophic structures and community assemblages in salt marsh ecosystems can be complex (Kneib, 1986; Livingston, 2003) with highly variable interspecific interactions (e.g., predator-prey interactions) (Breitburg *et al.*, 1997). Furthermore, species-specific responses to tidal or seasonal fluctuations in environmental conditions can also complicate these interspecific interactions (Breitburg *et al.*, 1999; Livingston, 2003),

potentially influencing ecosystem functioning (e.g., energy transformation and transport within the system) (Livingston, 2003).

In urban tidal salt marshes, habitat quality is often degraded due to various anthropogenic stressors (e.g., chemical pollutants and eutrophication), adversely affecting fishes and shellfishes (Levin *et al.*, 2001; Livingston, 2003). Some sources of anthropogenic stressors include industrial and municipal runoff, atmospheric deposition, landfill leachate, accidental spills, and dumping of dredged materials (Crawford *et al.*, 1994; Wakeman and Themelis, 2001; Steinberg *et al.*, 2002). Salt marshes near highly industrialized and densely populated metropolitan areas are particularly at risk. For example, aquatic organisms living in urban coastal habitats are chronically exposed to toxic chemical pollutants (e.g., mercury and polychlorinated biphenyl) primarily generated by human activities (Gunster *et al.*, 1993; Bonnevie *et al.*, 1994; Crawford *et al.*, 1994; Guns *et al.*, 1999). Many of these chemicals can be assimilated by sediment-dwelling invertebrates (the base of benthic food webs) along with essential elements (e.g., nitrogen and carbon), and bioaccumulate in their tissues over time, potentially causing adverse effects (i.e., direct toxic effects) (Brown *et al.*, 2003). Some of the adverse effects include reduced individual growth rate, altered age/size structure of the populations (Brown *et al.*, 2003), and ultimately biodiversity loss (Marqués *et al.*, 2003).

Anthropogenic stressors can also cascade through trophic interactions to predators (i.e., indirect ecological effects), which may, in turn, disrupt a variety of ecosystem functions (Frost *et al.*, 1995). As many sediment-associated invertebrates serve as prey to benthivorous resident and migrant fishes and shellfishes, anthropogenic stressors can be transmitted through food chains (Palmer *et al.*, 2000), indirectly inducing functional

responses in these organisms (Sherwood et al., 2000). For example, altered prey availability can alter food consumption of fish and result in reduced growth as well as reproduction (Hammerschmidt *et al.*, 2002; Brown *et al.*, 2003). These individual-level responses can ultimately lead to population-level responses such as reduced population growth rate, productivity, and recruitment of predators (Sherwood *et al.*, 2000). Furthermore, species-specific responses to stressors may also lead to major shifts in community assemblage and trophic structure, potentially disrupting energy flow in ecosystems (Sherwood *et al.*, 2002). Anthropogenic impacts on sediment-dwelling invertebrates are thus likely to influence not only biogeochemical cycling of sediment-associated nutrients (Palmer *et al.*, 2000), but also transformation and transport of primary and secondary productions in coastal ecosystems (Levin *et al.*, 2001). In assessing the impacts of habitat degradation in urban salt marsh ecosystems, it is thus imperative to examine both direct and indirect effects of anthropogenic stressors.

Overview of the Dissertation

In this dissertation, direct and indirect impacts of habitat degradation on a resident forage fish, mummichogs (*Fundulus heteroclitus*) (Pisces: Cyprinodontidae), are investigated at highly urbanized tidal salt marshes in the Arthur Kill. This dissertation project integrates field-based studies on fish responses to habitat degradation at multiple levels of biological organization in urban tidal salt marshes. The responses at lower levels of biological organization (e.g., the subcellular level) may be highly sensitive to stressors, but they may not always be ecologically relevant (Luoma, 1995; Engel and Vaughan, 1996; Luoma, 1996). On the other hand, the responses at higher levels (e.g., the

community level) may be ecologically relevant, but they may not always be sensitive to stressors (Luoma, 1995; Engel and Vaughan, 1996; Luoma, 1996). By integrating anthropogenic effects at multiple levels of biological organization, structural and functional responses to habitat degradation in urban salt marsh ecosystems can be more appropriately assessed. Furthermore, an assessment of pollution-induced alterations can be an alternative approach in elucidating highly intricate structural and functional relationships in marine and freshwater ecosystems (Raffaelli, 2005; Woodward *et al.*, 2005).

Study site description

The Arthur Kill, part of the New York/New Jersey (NY/NJ) Harbor Estuary Complex, is a tidal waterway located between northern New Jersey and Staten Island, New York, connecting Newark Bay and Kill van Kull to the north, and Raritan Bay, New York Harbor, and the Atlantic Ocean to the south (Fig. 1-1). Due to the proximity to industrial facilities, petroleum refining facilities, heavy shipping traffic, and sewage treatment plants, the majority of physical, chemical, and biological characteristics of the NY/NJ Harbor Estuary have been substantially altered for more than a century (Franz, 1982; Berg and Levinton, 1985; Crawford *et al.*, 1994; Wakeman and Themelis, 2001; Steinberg *et al.*, 2004; Levinton and Waldman, 2006). A variety of anthropogenic disturbances have resulted in a considerable loss of biodiversity in this region over the years (Franz, 1982; Berg and Levinton, 1985; Crawford *et al.*, 1994; Steinberg *et al.*, 2004).

Among the anthropogenic stressors, chemical pollutants released with industrial and municipal discharges have been major contributors to the deterioration of trophic structures and ecosystem functions in this region (Adams *et al.*, 1998; Adams and Benyi, 2003; Bopp *et al.*, 2006). Furthermore, there have also been large-scale accidental chemical discharges such as the 1990 oil spill at the northern Arthur Kill, which had one of the most devastating ecological impacts on salt marsh ecosystems in this region in recent years (Packer, 2001). Since tides enter from both ends of the Arthur Kill, this region is often very poorly flushed, resulting in enhanced entrapment and accumulation of pollutants in sediments (Adams *et al.*, 1998; Adams and Benyi, 2003; Bopp *et al.*, 2006). Elevated levels of pollutants are among the most widespread anthropogenic stressors in the NY/NJ Harbor Estuary, and the highest levels of some pollutants occur in tributaries of the Arthur Kill (Bonnevie *et al.*, 1994; Packer, 2001; Weis *et al.*, 2001). Due to potential toxicity and transference up food chains, these pollutants are a major concern in this coastal ecosystem (Packer, 2001; Steinberg *et al.*, 2004; Bain *et al.*, 2007).

Despite its severely degraded conditions, the NY/NJ Harbor Estuary provides essential habitats for many aquatic and terrestrial organisms (Able *et al.*, 1998; Steinberg *et al.*, 2004). The NY/NJ Harbor Estuary is one of the richest fish habitats in the northwest Atlantic coast (Berg and Levinton, 1985; Able *et al.*, 1998; Duffy-Anderson *et al.*, 2003). Some of the most abundant species in this region include forage fishes such as mummichogs (*Fundulus heteroclitus*) and Atlantic silverside (*Menidia menidia*), as well as juvenile and adult piscivorous fishes such as bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), and summer flounder (*Paralichthys dentatus*) (Rountree and Able, 1992; Able *et al.*, 1998; Duffy-Anderson *et al.*, 2003). The tributaries of the Arthur

Kill are also foraging and nesting sites for wading birds such as black-crowned night-heron (*Nycticorax nycticorax*), glossy ibis (*Plegadis falcinellus*), great egret (*Ardea alba*), and snowy egret (*Egretta thula*) (Brzorad *et al.*, 2004; Steinberg *et al.*, 2004; Maccarone and Brzorad, 2005; Bernick, 2007).

Due to the recent reductions in industrial and municipal chemical discharges, restoration of tidal salt marshes, and abatement of sewage dumping, the water quality of the NY/NJ Estuary Complex including the Arthur Kill has substantially improved over the last few decades (Steinberg *et al.*, 2004; Bopp *et al.*, 2006). Dissolved oxygen levels have considerably increased, and levels of many pollutants have decreased (O'Shea and Brosnan, 2000). However, residual impacts of historic pollution can still be observed at many areas in the NY/NJ Harbor, including elevated levels of some pollutants in sediments and sediment-associated organisms and altered biological assemblages (Packer, 2001; Adams and Benyi, 2003; Bain *et al.*, 2007). Aquatic and terrestrial predators ingesting benthic organisms are thus still at risk of exposure to these pollutants (Steinberg *et al.*, 2004). As various areas in the NY/NJ Harbor Estuary are the subject of current and future restoration (Bain *et al.*, 2007), understanding the factors affecting trophic structures and ecosystem functions would provide baseline data upon which to evaluate the success of remediation.

Specific sampling sites chosen for this study were four tributaries of the Arthur Kill; Richmond Creek, Main Creek, Neck Creek, and Mill Creek, and two regional reference sites near Raritan Bay and New York Harbor; Lemon Creek and Great Kills Harbor (Fig. 1-1). Neck Creek, which is located on the northwestern Staten Island, NY, is polluted with various chemicals due to its proximity to many oil refineries as well as

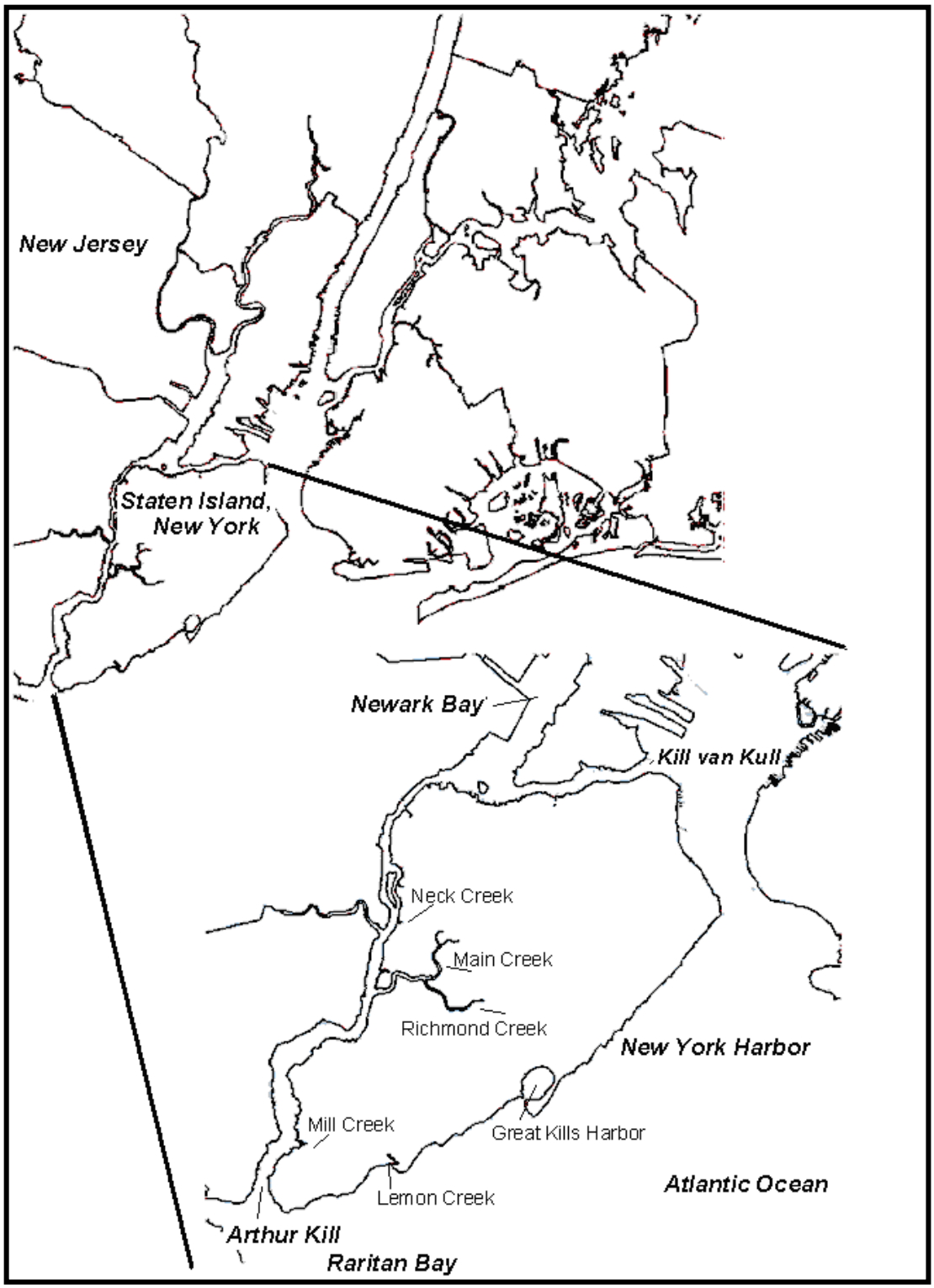
abandoned industrial facilities (Ward, 2002). This site was one of the areas heavily damaged in the Arthur Kill by the 1990 oil spill (Packer, 2001). Richmond Creek and Main Creek are tributaries of Fresh Kills Complex. Fresh Kills Complex is one of the largest salt marshes in New York State, located on the western shore of Staten Island. Both Richmond Creek and Main Creek are surrounded by Fresh Kills Landfill, the largest landfill in the United States (Siegel *et al.*, 2000). Mill Creek, on the southwestern shore of Staten Island, is located near the confluence of the Arthur Kill and Raritan Bay, and has been polluted from historic smelting activities, resulting in one of the highest sediment-associated copper, lead, and zinc levels in the NY/NJ Harbor Estuary Complex (Carmody *et al.*, 1973; Paulson *et al.*, 2001; Ward, 2002). Lemon Creek, which is located in the southeastern shore of Staten Island, is one of a few relatively undisturbed tidal salt marshes and receives tidal flows from the Raritan Bay. Great Kills Harbor is located on the eastern shore of Staten Island. Despite its proximity to sewage treatment plants, levels of most pollutants remain relatively low (Ward, 2002).

Project objectives

The overall objective of this dissertation project is to establish a possible link between anthropogenic disturbances, and benthic trophic structures and functions in urban tidal salt marshes in the Arthur Kill. The specific objective of Chapter 2 is to characterize alterations in benthic macroinvertebrate communities in the Arthur Kill. This chapter addresses structural and functional responses of potential prey resources of mummichogs, benthic macroinvertebrates, under severe chemical stresses. The relationships between benthic macroinvertebrate communities, and natural as well as

anthropogenic stressors were examined using multivariate statistical techniques. The objective of Chapter 3 is to evaluate how altered benthic macroinvertebrate communities affect the feeding habits of mummichogs in the Arthur Kill tributaries. This chapter addresses indirect pollution impacts on the feeding habits and strategies of mummichogs in the Arthur Kill using gut content analysis. The objective of Chapter 4 is to evaluate trophic availabilities of trace metals from prey and their relationships with trace metal bioaccumulation and handling in mummichogs in the Arthur Kill. This chapter addresses potential trophic availabilities of trace metals from the decapod *Palaemonetes spp.* and the polychaete *Nereis spp.* (two prey items commonly found in the diet of mummichogs), which were compared with trace metal handling (i.e., metal storage) in mummichogs by examining intracellular partitioning of trace metals. The objective of Chapter 5 is to evaluate how altered feeding habits as well as degraded environmental conditions affect bioenergetics of mummichogs in the Arthur Kill. This chapter addresses direct and indirect (via food webs) impacts of habitat degradation on bioenergetics (growth rate, food consumption rate, energy conversion efficiency, and total metabolic cost) of mummichogs in the Arthur Kill using field-based *in situ* estimates of food consumption rates with the mercury mass balance method. Finally, Chapter 6 synthesizes the findings obtained from the Chapter 2 to Chapter 5 as well as the literature and provides general conclusions for the entire project.

Figure 1-1. Map of study sites in the Arthur Kill (Mill Creek, Richmond Creek, Main Creek, and Neck Creek), Raritan Bay (Lemon Creek), and New York Harbor (Great Kills Harbor), New York.



CHAPTER 2

Alterations in composition, abundance, and biomass of soft-sediment benthic macroinvertebrates in urban tidal salt marshes in New York

CHAPTER SUMMARY

Habitat quality of the Arthur Kill (New York, USA) and its surrounding bodies of water have been severely degraded for more than a century. Despite recent improvements in water quality, biological communities in these areas still remain species-poor. In this study, chronic pollution impacts on benthic macroinfaunal assemblages were examined in highly urbanized tidal salt marshes in the Arthur Kill using univariate and multivariate methods. Compared to the local reference sites, benthic macroinfaunal communities at the Arthur Kill sites exhibited a relatively large temporal variability in both abundance and biomass. These changes in total abundance and biomass reflected major temporal compositional shifts in macroinfaunal assemblage at the Arthur Kill sites. Although a few relatively sensitive crustacean and molluskan species appeared at some of the Arthur Kill sites, a substantial portion of total abundances of benthic macroinvertebrates was comprised of a few opportunistic oligochaetes and polychaetes (especially, *Hobsonia florida* and *Nereis acuminata*). Both abundance- and biomass- derived non-metric multidimensional scaling (nMDS) plots and analysis of similarity (ANOSIM) revealed more consistent and clear patterns of compositional relationships among sites than univariate measures. Analysis of similarity percentages (SIMPER) revealed that the major contributing species to the dissimilarities in both abundance and biomass among sites were *Streblospio bendicti*, *H. florida*, and *N. acuminata*. Furthermore, canonical correspondence analysis (CCA) revealed that more than 70% of the total variances (71.3% for abundance and 74.5% for biomass) observed in macroinfaunal community composition were explained by the environmental variables measured, particularly, salinity and total mercury (Hg). Partial CCA with sediment grain size or total organic

carbon as a covariance also revealed that total Hg remained as the main factor responsible for the variances in both abundance and biomass of benthic macroinfaunal communities among sites. These findings suggest that chronic chemical pollution is partially responsible for the current status of soft-sediment macroinfaunal communities in tidal salt marshes in the Arthur Kill, and may have important implications for nutrient cycling and energy flow in this heavily urbanized coastal ecosystem.

INTRODUCTION

Soft-sediment benthic macroinfaunal communities are the most ubiquitous components of coastal marine ecosystems (Wilson, 1991; Snelgrove, 1999) and play an essential role in various ecosystem functions, including the maintenance of physicochemical properties of sediments and microbial activities (i.e., bioturbator) (Rhoads *et al.*, 1977; Levinton, 1995; Somerfield *et al.*, 2006). These macroinvertebrates facilitate essential biogeochemical processes in sediments such as sediment oxygenation and mobilization of sediment-associated materials including essential trace elements in benthic habitats (Levin *et al.*, 2001; Somerfield *et al.*, 2006). Furthermore, the importance of benthic macroinvertebrates as prey for fishes and shellfishes has also been widely documented (Kneib, 1984; Sardá *et al.*, 1995; Levin *et al.*, 2001). Benthic macroinvertebrates comprise a substantial part of many predatory fish and shellfish prey resources in coastal habitats (Chapter 3; Kneib and Stiven, 1978; Weisberg and Lotrich, 1982; Kneib, 1986). Understanding how biological and physical factors affect species occurrence/co-occurrence in benthic macroinfaunal communities in natural habitats is thus critical to the assessment of coastal ecosystems (Warwick and Clarke, 1984; Clements and Newman, 2002; Garvey *et al.*, 2003).

Urban coastal habitats are frequently suffered from widespread marine pollution (e.g., eutrophication and chemical discharges) (e.g., Agard *et al.*, 1993; Warwick, 1993; Somerfield *et al.*, 1994; Tuck *et al.*, 1998; Savage *et al.*, 2001). Benthic macroinvertebrates are particularly at risk of exposure to a variety of anthropogenic stressors (Pearson and Rosenberg, 1978; Boesch and Rosenberg, 1981; Wilson and Jeffrey, 1994). Anthropogenic disturbances can be physical (e.g., trawling), chemical

(e.g., chemical discharges), and biological (e.g., invasive species) (Levin *et al.*, 2001; Savage *et al.*, 2001; Zajac and Whitlatch, 2001; Able and Duffy-Anderson, 2006). Among these stressors, elevated levels of chemical pollutants can have especially persistent effects on sediment-dwelling invertebrates (Luoma, 1996; Lindegarth and Underwood, 2002). Many anthropogenically introduced chemicals in the environment tend to be bound to suspended particles, which eventually accumulate in sediments (Boesch, 1982). Due to their close association with sediments, marine benthic macroinvertebrates are vulnerable to these pollution-induced alterations in sediment physicochemical properties of coastal habitats (Pearson and Rosenberg, 1978; Sardá *et al.*, 1995).

In addition to physicochemical properties of the environment, biological factors including life history characteristics (Kneib, 1984; Weston, 1990; Zajac *et al.*, 1998) and intra-/inter- specific interactions (Kneib, 1984; Whitlatch and Zajac, 1985; Zajac *et al.*, 1998) can also influence benthic macroinfaunal assemblages. Many benthic macroinvertebrate species in coastal habitats are inherently resilient to a certain level of natural (e.g., wide fluctuations in salinity) and anthropogenic (e.g., toxic substances) environmental stresses (Boesch and Rosenberg, 1981). As these species possess differential levels of tolerance to these variables, however, they exhibit species-specific life history responses, which can result in highly variable community compositions along environmental gradients (Pearson and Rosenberg, 1978; Warwick and Clarke, 1993; Zajac *et al.*, 1998; Norkko *et al.*, 2006). For example, organic enrichment often co-occurs with other anthropogenic stressors including chemical pollutants in urban coastal habitats (Breitburg *et al.*, 1999). Organically enriched sediments can have positive effects on

some opportunistic species (e.g., *Streblospio benedicti* and *Capitella spp*.), such as enhanced population growth and biomass. These eutrophication effects may, as a result, mask or offset adverse effects of chemical pollution on these species and, in turn, community assemblage (Pearson and Rosenberg, 1978; Weston, 1990; Breitburg *et al.*, 1999).

Many experimental studies on effects of anthropogenic stressors are often based on species responses to an individual factor (Posthuma *et al.*, 2002), excluding or ignoring other (environmental or biological) factors that may be concurrently affecting species in the natural habitats (Lenihan *et al.*, 2003). However, as multiple factors simultaneously and often interactively affect biological assemblages (Levin and Talley, 2000; Lenihan *et al.*, 2003; Hewitt *et al.*, 2005), species-specific responses of benthic macroinvertebrates to each stressor can lead to unpredictable community compositions in urban coastal habitats (Warwick and Clarke, 1993; Hewitt *et al.*, 2005; Raffaelli, 2006).

In chronically degraded habitats, the development of tolerance to anthropogenic stressors by opportunistic species can also complicate the assessment of ecological impacts on species distribution patterns and successional processes along environmental gradients (Warwick, 1986; Warwick and Clarke, 1993; Wilson and Jeffrey, 1994; Lindegarth and Hoskin, 2001; Lindegarth and Underwood, 2002). Furthermore, species-specific development of tolerance to stressors may obscure the ecological relevance of experimental studies using naïve populations of macroinvertebrate species in understanding species distribution patterns in chronically degraded habitats. Some tolerance to relatively ‘novel’ stressors in urban habitats such as anthropogenically introduced chemicals can be developed by macroinvertebrate species within a relatively

short time, which can result in the evolution of a resistant strain (Klerks and Levinton, 1989; Klerks and Levinton, 1993). For example, a deposit-feeding oligochaete species (*Limnodrilus hoffmeisteiri*) rapidly (< 4 generations) developed heritable resistance to an elevated level of cadmium in the environment (Klerks and Levinton, 1989). They also developed adaptive strategies to reduce the effects of chemical stressors (Klerks and Bartholomew, 1991; Wallace *et al.*, 1998).

One of challenging tasks in assessing chronic anthropogenic impacts on biological assemblages is to differentiate pollution-induced effects from responses to natural fluctuations in environmental conditions (Warwick, 1993; Warwick and Clarke, 1993; Lenihan *et al.*, 2003; Morrisey *et al.*, 2003). Several theoretical and conceptual models have been introduced to describe and predict species responses to natural and anthropogenic stressor gradients (e.g., Connell and Slatyer, 1977; Pearson and Rosenberg, 1978; Menge and Sutherland, 1987). However, spatial and temporal variability associated with magnitude, scale, and intensity of natural stressors can often complicate responses and successional processes of benthic macroinfaunal communities (Warwick and Clarke, 1993; Zajac *et al.*, 1998; Lindegarth and Underwood, 2002; Morrisey *et al.*, 2003; Hewitt *et al.*, 2005; Norkko *et al.*, 2006). For example, species diversity of benthic macroinfaunal communities is highly sensitive to natural environmental variability, which introduces additional uncertainties in an overall assessment of anthropogenic impacts (Warwick and Clarke, 1993). Furthermore, the uncertainties associated with natural variability in environmental conditions may also lead to a misidentification of 'pollution-indicator species' or pollution level in chronically degraded habitats (Warwick, 1993; Rakocinski *et al.*, 1997).

Regional pollution history may also contribute to the variability in biological assemblages in chronically degraded aquatic ecosystems (Clements, 1997), especially in an area with multiple sources of anthropogenic stressors (Hewitt *et al.*, 2005). Historic pollution impacts by multiple anthropogenic stressors can have persistent, cumulative effects on structuring community assemblages and successional patterns of benthic macroinvertebrates (Clements, 1997; Zajac *et al.*, 1998; Kelaher *et al.*, 2003). Some major pollution events such as oil spills, though much less frequent than other disturbances, can have large-scale and long-lasting impacts on coastal biological communities (Ellis *et al.*, 2000). Recolonization and succession following such major disturbances can also be affected by species-specific differential responses to altered environmental conditions and interspecific interactions (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978; Whitlatch and Zajac, 1985; Chapman, 2007).

Although there are certain limitations to field observational studies in elucidating factors structuring biological assemblages, monitoring and characterizing the community assemblages in chronically degraded habitats is imperative to understand and accurately assess region-specific key factors influencing coastal ecosystems (Underwood and Peterson, 1988; Warwick, 1993; Weisberg *et al.*, 1997; Hewitt *et al.*, 2005; Norkko *et al.*, 2006). Alterations in benthic macroinfaunal community assemblages can potentially disrupt ecosystem functioning (e.g., biogeochemical cycling of essential materials) in coastal environments (Gray, 1974; Boesch, 1982; Levin *et al.*, 2001), and have secondary implications for functional responses (e.g., feeding habits and energetics) of benthivorous predators in coastal habitats (Chapters 3 and 5; Rakocinski *et al.*, 1997; Breitburg *et al.*, 1999; Ellis *et al.*, 2000; Levin *et al.*, 2001). Habitat degradation in coastal environments

may, therefore, have substantial repercussions not only in structural and functional integrity in benthic macroinfaunal communities, but also in overall trophic structures, nutrient cycling, and energy flow in ecosystems (Pearson and Rosenberg, 1978; Rakocinski *et al.*, 1997; Levin *et al.*, 2001; Warwick, 2001). In the present study, chronic chemical pollution impacts on the community structures of soft-sediment benthic macroinvertebrates were examined in highly urbanized tidal salt marshes in the Arthur Kill (New York, USA).

MATERIALS AND METHODS

Field Sampling

Samplings of benthic macroinvertebrates were conducted during daytime low tide in the summers (June to September) of 2000, 2001, and 2004. Specific sampling sites were four tributaries of the Arthur Kill; Richmond Creek, Main Creek, Neck Creek, and Mill Creek, and two regional reference sites near Raritan Bay and New York Harbor; Lemon Creek and Great Kills Harbor (see Chapter 1 for site description). Benthic macroinvertebrates were collected by taking bulk surficial (top ~5 cm) sediments (one replicate per a randomly chosen 100 m^2 area) from the intertidal marsh at each study site, using a 15 x 15 cm-quadrat sampler (n = 5). Each sample was sieved through a 500 μm-mesh in the field and fixed with 10% formalin stained with Rose Bengal in a glass jar, which was then transported to laboratory.

Laboratory Sample Processing

In the laboratory, the samples were left in formalin for at least 7 days, and then preserved in 70% ethanol until species identification. Macroinvertebrates were identified to the lowest possible taxonomic category (mostly species) under a stereo microscope, using available species keys (Fauchald, 1977; Weiss, 1995; Merritt and Cummins, 1996; Pollock, 1998). As QA/QC, 10% of randomly chosen samples from each sampling year were re-identified. Each species was counted to estimate its abundance, and subsequently dried in an oven at 60 °C for ~2 hours to estimate its biomass.

Physicochemical Properties of the Environment (2004)

To examine the relationships between benthic macroinfaunal assemblages and environmental characteristics of the study sites, variables associated with surface water [temperature, pH, salinity, and dissolved oxygen (DO)] and sediments [grain size, total organic carbon (TOC) content, and trace metal concentrations (silver, cadmium, copper, mercury, nickel, lead, and zinc)] were measured at each site in 2004. Surface water temperature, pH, DO (with a digital portable pH/temperature/DO meter), and salinity (with a hand-held refractometer) were measured within the proximity of each replicate sample of benthic macroinvertebrates.

Surficial (top ~5 cm) sediment samples were collected for grain size, TOC, and trace metal analyses. Sediment samples were sieved through a 500 μm-mesh to eliminate large objects (e.g., detritus) and macroinvertebrates. Subsamples of sieved sediment samples (< 500 μm) were sieved further through a 73 μm-mesh, and oven-dried (at 80 °C for ~48-72 hours) to estimate % fine sediment particles (< 73 μm). The remaining sieved sediment subsamples (< 500 μm) were homogenized, oven-dried (at 60 °C for ~48-72

hours), and then divided for TOC and trace metal analyses. TOC was determined by combustion of dried, ground sediments with a benchtop muffle furnace (Type 1400, Barnstread International) at 550 °C for 6 hours.

Analyses of Trace Metals in Sediments

Oven-dried (60 °C) samples of surficial sediments were divided further into two subsamples [one for silver (Ag), cadmium (Cd), copper (Cu), nickel (Ni), lead (Pb), and zinc (Zn); one for total mercury (Hg)]. For Ag, Cd, Cu, Ni, Pb, and Zn, subsamples (~0.3 g dry weight) were digested under reflux with concentrated Trace Metal Grade nitric acid (5 ml) overnight at room temperature (~20 ºC) and subsequently on a hotplate (~80 ºC) for ~48 to 72 hours (Csuros and Csuros, 2002). Once digested, samples were evaporated to dryness, re-suspended in 2% nitric acid (8 ml), and filtered (0.45 µm). Metal concentrations in samples were analyzed with graphite furnace atomic absorption spectrometer (for Ag, Cd, Cu, Ni, and Pb) or flame atomic absorption spectrophotometer (for Zn) (Perkin Elmer 3100AAS).

For Hg, dried subsamples (~0.1 g dry weight) were weighed and transferred to an acid-washed 60 ml-BOD bottle. Samples were digested with a mixture (1:4) of concentrated Trace Metal Grade nitric and sulfuric acid (10 ml) in a water bath (~60 ºC) for ~3 hours and cooled in a refrigerator (USEPA, 1992). Samples were then oxidized with 5% potassium permanganate (10 ml) and 5% potassium persulfate (5 ml) at room temperature overnight (USEPA, 1992). The digested samples were transferred into a 100 ml-volumetric flask, and 12% sodium chloride-hydroxylamine chloride was added to reduce excess potassium permanganate (USEPA, 1992). Samples were then brought to

final volume with NANOpure® (reagent-grade) water, filtered (0.45 μm), and refrigerated (< 2 to 3 days) or analyzed immediately with cold vapor atomic absorption spectrometer (Perkin Elmer Flow Injection Mercury System, FIMS 100) using stannous chloride as a reducing reagent. Finally, measured concentrations of sediment-associated Ag, Cd, Cu, Ni, Pb, Zn, and Hg were compared with the Effects Range Median (ERM) levels proposed by Long and Morgan (1990), which indicate the threshold levels of metals for adverse effects in marine and estuarine organisms.

As quality assurance, standard reference material, SRM 2976 (mussel tissue, National Institute of Standards and Technology, USA), for Ag, Cd, Cu, Pb, and Zn, and certified reference material, DORM-2 (dogfish muscle tissue, National Research Council Canada), for total Hg were processed and analyzed for metals in the same manner as described above. The average recovery rates of Ag, Cd, Cu, Pb, Zn, and total Hg were 95.3, 100.3, 105.7, 63.5, 96.3%, and 95.4%, respectively. Procedural and reagent blanks were also analyzed for potential secondary metal contamination. The calibration standard solutions of each metal were analyzed every 10 samples. When the deviation from the initial value was more than ± 10%, the instrument was recalibrated. The correlation coefficients of calibration curves were maintained > 0.999 for the analysis. All standard solutions and samples were prepared with NANOpure® water. All glassware was soaked in 10% hydrochloric acid (for Ag, Cd, Cu, Ni, Pb, and Zn) or 20% nitric acid (for Hg) overnight, rinsed once with deionized water, and rinsed twice with NANOpure® water.

Numerical Analyses: Univariate Analyses

Site-specific univariate measures of benthic macroinfaunal assemblages were characterized using the following indices; total abundance, total biomass, total number of species (S), species richness [Margalef's index, $d = (S - 1)/\log_e N$; N = the total number of individuals] (Clifford and Stephenson, 1975), species diversity [Shannon-Wiener index, $H' = -\Sigma\, p_i \cdot \log_e(p_i)$; p_i = the proportion of the i th species in the total abundance] (Shannon and Weaver, 1949), species evenness [Heip's evenness = $(e^{H'} - 1)/(S - 1)$] (Heip, 1974), and abundance-biomass comparison (ABC) curve statistic [$W = \Sigma\,(B_i - A_i)/50(S - 1)$; B_i = the biomass of the i th species, A_i = the abundance of the i th species] (Clarke, 1990). The raw data were transformed using a logarithmic transformation [$\log_e(x + 1)$ for the abundance data and $\log_e(x + 0.001)$ for the biomass data] (McCune and Grace, 2002), where necessary.

The normality of data was tested using Shapiro-Wilk's W test. The homogeneity of variance was tested using Levene's test. The statistical significance of differences in the univariate measures among the study sites and sampling years was tested using 2-way (site x year) analysis of variance (ANOVA), which, if significant, was followed by Tukey's honestly significant difference (HSD) test. The ABC curve statistic W was calculated using PRIMER v6.1.9 (PRIMER-E Ltd, Plymouth, UK). All univariate statistical analyses were performed using Statistica 7.1 (Statsoft, Inc®, USA).

Numerical Analyses: Multivariate Analyses

Relative similarities in abundance and biomass of benthic macroinfaunal assemblages among the study sites and sampling years were graphically analyzed using a non-metric multidimensional scaling (nMDS) ordination technique with Bray-Curtis

similarity index (Clarke and Gorley, 2006). Bray-Curtis similarity index was calculated with $\log_e(x+1)$-transformed data for abundance and square-root transformed data for biomass. The reliability of nMDS representations of the assemblage similarities was assessed with their stress values; stress < 0.2 was considered to be acceptable (Clarke and Warwick, 2001). To ensure the accuracy of nMDS representations (i.e., convergence to a global minimum), each nMDS was run multiple times (the number of restarting = 50).

The statistical significance of differences in abundance and biomass of the community assemblages among the sites and years was tested using non-parametric 2-way crossed analysis of similarity (ANOSIM) with randomization permutation (n = 9999), which was followed by 2-way crossed analysis of similarity percentages (SIMPER) to identify dominant species contributions to overall dissimilarities (Clarke and Warwick, 2001). The index of multivariate dispersion (IMD) was also used to assess the disturbance level in benthic macroinfaunal communities, in which an increased variability among replicates indicates an increased disturbance level in communities (Warwick and Clarke, 1993). All analyses of nMDS, ANOSIM, SIMPER, and IMD were performed using PRIMER 6.19 (PRIMER-E Ltd, Plymouth, UK).

To examine the relationships between benthic macroinfaunal assemblages and physicochemical properties of the environment, direct (constrained) gradient analysis was performed on the year 2004 data. In this gradient analysis, species data were iteratively constrained to linear combinations of environmental gradient axes (ter Braak and Šmilauer, 2002). Because the results from detrended canonical analysis indicated that the species responses along environmental variables were moderately unimodal (standard deviation = ~3.1), non-linear canonical correspondence analysis (CCA) with Hill's

scaling on inter-species distances was performed (ter Braak, 1986; ter Braak and Šmilauer, 2002). Additionally, as sediment grain size and total organic carbon content are known to affect the adsorption of trace metals to sediments, and subsequently their potential bioavailability and toxicity to benthic macroinvertebrates (Rakocinski *et al.*, 1997; Peeters *et al.*, 2000), partial CCA (pCCA) was also performed by removing the variance associated with % fine sediment particle or % total organic carbon as a covariable.

Prior to CCA or pCCA, all assemblage data were transformed using logarithmic transformations [$\log_e(x + 1)$ for the abundance data and $\log_e(x + 0.001)$ for the biomass data] (McCune and Grace, 2002) and rare species were downweighted, while all the environmental variables were normalized (i.e., mean = 0, standard deviation =1) (ter Braak and Šmilauer, 2002). The statistical significance of all canonical axes together as well as each of the first 4 canonical axes individually was tested using a Monte Carlo permutation test (999 unrestricted permutations under reduced model at $p < 0.05$) (Lepš and Šmilauer, 2003). To test the significance of the second and higher canonical axes individually, pCCA was performed using the sample scores for the lower canonical axis (e.g., the 1st axis sample scores for testing the 2nd axis) derived from the environmental data as a covariable (Lepš and Šmilauer, 2003). Redundant environmental variables with Variance Inflation Factor (VIF) > 20 (an indication of multicollinearity) were removed from further analyses (Peeters *et al.*, 2000; ter Braak and Šmilauer, 2002).

The importance of environmental variables was based on intraset correlation with the CCA axes (ter Braak, 1986). The relative importance of environmental variables after removal of redundant variables was ranked using forward selection with Monte Carlo

permutation tests (999 unrestricted permutations under full model at $p < 0.05$) (ter Braak and Šmilauer, 2002; Lepš and Šmilauer, 2003). All CCAs and pCCAs were performed using CANOCO 4.5 (Microcomputer Power, Ithaca, New York, USA).

RESULTS

Univariate Characteristics of Benthic Macroinfaunal Assemblages

Two-way ANOVAs on both total abundance and biomass of benthic macroinvertebrates showed significant differences among the sites as well as sampling years (Table 2-1). Due to site-specific differences in temporal changes, there were significant interactions between sites and years for both the abundance and biomass data (Table 2-1), which were especially apparent for the Arthur Kill sites (Fig. 2-1a through 2-1f). Among-site comparisons with 1-way ANOVA followed by Tukey's HSD test showed some inconsistent trends for the abundance and biomass data (Fig. 2-1a through 2-1f). Compared to Lemon Creek (one of the reference sites), where the benthic macroinvertebrates maintained a relatively stable abundance (1,000 to 4,000 individuals$\cdot m^{2-1}$) and biomass (1 to 7 dry g$\cdot m^{2-1}$), those at the Arthur Kill sites exhibited a large temporal variability in both abundance (e.g., Main Creek: 10,000 individuals$\cdot m^{2-1}$ in year 2000 to 1,000 individuals$\cdot m^{2-1}$ in year 2001) and biomass (e.g., Main Creek: 1 dry g$\cdot m^{2-1}$ in year 2001 to 27 dry g$\cdot m^{2-1}$ in year 2004) (Fig. 2-1a through 2-1f).

Substantial temporal changes in total abundance and biomass appeared to reflect shifts in % contribution by the comprising taxonomic groups (Appendix 2-A). Specifically, in year 2000, a significant portion (62.2% to 89.4%) of the total abundance of benthic macroinvertebrates at the Arthur Kill sites consisted of small-bodied

oligochaetes (mostly Naididae), which substantially decreased in year 2001 and 2004 (e.g., Main Creek: 54.5% in year 2001 and 25.0% in year 2004), while at Lemon Creek and Great Kills Harbor, oligochaetes comprised only 46.4% and 7.8% of the total abundance in year 2000, respectively (Appendix 2-A). The situation was reversed for the other dominant taxonomic class, polychaetes, which contributed much lower proportions to the total abundance at the Arthur Kill sites (10% to 37.0%) in year 2000, and then increased in year 2001 and 2004 (e.g., Main Creek: 44.6% in year 2001 and 71.7% in year 2004) (Appendix 2-A). At Lemon Creek and Great Kills Harbor, polychaetes were a numerically dominant class (47.9% to 89.8%) in all years (Appendix 2-A).

Due to their small body size, however, the numerical dominance of oligochaetes was not proportionally reflected in biomass; only at Main Creek in year 2000, was the biomass of oligochaetes larger than that of polychaetes (58.5% vs. 41.5, respectively, Appendix 2-A). At other sites (including Lemon Creek and Great Kills Harbor), polychaetes were dominant in biomass, except in year 2004, when gastropods became the most dominant group at Great Kills Harbor and Mill Creek (52.2% and 68.6%, respectively, Appendix 2-A).

Despite relatively large temporal shifts in total abundance and biomass as well as dominant taxonomic groups, the average number of species and species richness per sample showed relatively similar patterns throughout the years (Fig. 2-2a through 2-2f). Due to some temporal changes at a few sites, however, 2-way ANOVA showed a significant interaction among sites and sampling years for the number of species (Table 2-1). The most distinct pattern in the among-site comparisons was that the number of species and species of richness at Main Creek were consistently lower than those at the

reference sites (Lemon Creek and Great Kills Harbor) (1-way ANOVA with Tukey's HSD test, Fig. 2-2a through 2-2f).

Similar trends were also observed for species diversity and evenness (Fig. 2-3a through 2-3f). Among-site comparisons with 1-way ANOVA followed by Tukey's HSD test showed that in general, Shannon-Weiner diversity and Heip's evenness indices were consistently high at one of the reference sites, Lemon Creek, while these indices were more variable at the other sites (Fig. 2-3a through 2-3f). Another distinct trend in species diversity and evenness was that, unlike the number of species and species richness, these indices were consistently low at another reference site, Great Kills Harbor (Fig. 2-3a through 2-3f).

The abundance-biomass comparison *W* statistic showed relatively inconsistent patterns (Fig. 2-4a through 2-4c). Some of the characteristics include negative values (i.e., a 'heavily disturbed condition') at all sites in year 2000 (Fig. 2-4a). In year 2001, negative values were observed at Lemon Creek, Great Kills Harbor, and Mill Creek (Fig. 2-4b). In year 2004, negative values were observed at Great Kills Harbor and Mill Creek (Fig. 2-4c). However, positive values (i.e., an 'undisturbed condition') at many of the Arthur Kill sites were observed in year 2001 and 2004 (Fig. 2-4b and 2-4c).

Multivariate Characteristics of Benthic Macroinfaunal Assemblages

A 2-dimentional configuration of nMDS plots for the abundance and biomass of benthic macroinfaunal communities showed fairly consistent patterns of compositional relationships among sites (Fig. 2-5a through 2-5f). The stress values of nMDS plots (with the exception of the year 2001 biomass-derived plot) were less than 0.1 (Fig. 2-5a

through 2-5f), indicating an excellent representation of structural similarity in community composition among the sites. In general, both abundance- and biomass- derived nMDS plots showed more distinct separation on the horizontal axis than on the vertical axis (Fig. 2-5a through 2-5f). Overall compositional dissimilarities among the sites and years revealed by both abundance- and biomass- derived nMDS plots were also in agreement with the results of 2-way crossed global ANOSIM (sites: abundance-R = 0.939, p = 0.001% and biomass-R = 0.904, p = 0.001%; years: abundance-R = 0.929, p = 0.001% and biomass-R = 0.948, p = 0.001%).

The analysis of 2-way SIMPER showed that largest average dissimilarity was observed between Great Kills Harbor and Main Creek (73.25 in abundance and 90.02 in biomass, Appendix 2-B). These SIMPER results were in agreement with a distinct horizontal separation on the nMDS plots between Great Kills Harbor and Main Creek (Fig. 2-5a through 2-5f). The major contributing species (> 10%) to this dissimilarity were *Streblospio benedicti* (14.76%), *Hobsonia florida* (14.21%), and *Nereis acuminata* (13.1%) in abundance, and *N. acuminata* (19.84%), *H. florida* (14.9%), *S. benedicti* (12.57%) in biomass (Appendix 2-B). The major species responsible for the dissimilarity between year 2000 and 2001 were oligochaeta (11.54%) and *H. florida* (11.53%) in abundance, and *N. acuminata* (17.63%), oligochaeta (17.14%), and *H. florida* (16.94%) in biomass (Appendix 2-C). The major species responsible for the dissimilarity between 2001 and 2004 were *S. benedicti* (11.46%) in abundance, and *N. acuminata* (26.18%), *Ilyannasa trivittata* (13.43%), and *H. florida* (10.52%) in biomass (Appendix 2-C). With the exception of a slight shift to the center of the plots in year 2001, Lemon Creek was located near Great Kills Harbor (Fig. 2-5a through 2-5f). The Index of Multivariate

Dispersion for Lemon Creek was consistently lower than those of the other sites, including Great Kills Harbor, indicating the stability of the macroinfaunal community at Lemon Creek (Table 2-2). A notable temporal change (year 2000 to 2004) was observed at Mill Creek, which gradually shifted its location closer to Great Kills Harbor (Fig. 2-5a through 2-5f). A complete overlap between Richmond Creek and Main Creek was observed in both abundance- and biomass- derived nMDS plots in 2004 (Fig. 2-5c and 2-5f).

Physicochemical Properties of the Environment (2004)

The physicochemical properties of the environment measured in the summer of 2004 were considerably varied among sites (Table 2-3). Salinity of surface water ranged from 5.0‰ at Richmond Creek to 25.0‰ at Great Kills Harbor (Table 2-3). Total organic carbon (TOC) content of the sediment ranged from 2.4% at Richmond Creek to 12.5% at Neck Creek (Table 2-3). The percentage of fine grain sediment ranged from 17.5% at Main Creek to 74.7% at Mill Creek (Table 2-3). The lowest surface dissolved oxygen content (near hypoxia) was found in tributaries of the Fresh Kills Complex (3.1 $mg \cdot l^{-1}$ at Richmond Creek and 2.8 $mg \cdot l^{-1}$ Main Creek), whereas supersaturation (16.1 $mg \cdot l^{-1}$) of dissolved oxygen was observed at Neck Creek (Table 2-3). Temperature and pH of surface water varied little among sites (25.2 to 31.6 °C and 7.26 to 8.7, respectively, Table 2-3).

Silver, cadmium, and nickel contents in sediments varied among sites from ~0.48 to 1.6, ~1.1 to 2.9, and ~28 to 70 $\mu g \cdot g^{-1}$ dry, respectively (Table 2-3). Copper, lead, and zinc contents were substantially higher in sediments from Mill Creek (911, 655, and 1193

$\mu g \cdot g^{-1}$ dry, respectively) than those from the other sites (~92 to 216, ~84 to 215, and ~188 to 411 $\mu g \cdot g^{-1}$ dry, respectively) as well as the Effects Range Median (ERM) levels (Table 2-3). Only total mercury content of the sediment at the Arthur Kill sites (varying from 0.80 $\mu g \cdot g^{-1}$ dry at Richmond Creek to 2.46 $\mu g \cdot g^{-1}$ dry at Neck Creek) was consistently above the ERM level (Table 2-3). None of trace metals measured at Great Kills Harbor and Lemon Creek exceeded the ERM levels (Table 2-3).

Relationships between Environmental Characteristics and Benthic Macroinfaunal Assemblages (2004)

A global Monte Carlo permutation test on canonical correspondence analysis (CCA) showed significant relationships between environmental factors and benthic macroinfaunal community compositions in both abundance (F =10.84, p = 0.0001) and biomass (F =14.058, p = 0.0001). More than 70% of the total variances (100*0.586/0.822 = 71.3% for abundance and 100*0.919/1.233 = 74.5% for biomass) in macroinfaunal community compositions was explained by the environmental variables measured (Table 2-4). The majority of the variance was explained by the first two statistically significant canonical axes (Monte Carlo permutation test, p = 0.0001) for both abundance (46.2% by the 1st axis + 10.6% by the 2nd axis = 56.8% of the total variance, Table 2-4) and biomass data (50.8% by the 1st axis + 13.2% by the 2nd axis = 64.0% of the total variance, Table 2-4).

Stepwise forward selection identified and ranked the environmental variables that significantly contributed to the total explained variance in macroinfaunal compositions. For the abundance data, salinity (eigenvalue, λ = 0.22; % variance explained = 26.8%),

total Hg (λ = 0.14; 17.0%), surface dissolved oxygen (λ = 0.09; 10.9%), Ag (λ = 0.09; 10.9%), and Cd (λ = 0.05; 6.0%) significantly contributed to the total variance (Fig. 2-6a and Table 2-4). For the biomass data, salinity (λ = 0.36; 29.2%), total Hg (λ = 0.23; 18.7%), Cd (λ = 0.15; 12.2%), total organic carbon (λ = 0.12; 9.7%), and Ag (λ = 0.06; 4.9%) significantly contributed to the total variance (Fig. 2-6b and Table 2-4).

When the variance accounted for by fine-grain sediment was removed as a covariable, partial CCA (pCCA) followed by forward selection ranked total Hg as the most important factor responsible for the variance in both the abundance (eigenvalue, λ = 0.16; % variance explained = 19.5%) and biomass data (λ = 0.28; 22.7%), which was followed by TOC (λ = 0.15; 18.2%), pH (λ = 0.12; 14.6%), and Cd (λ = 0.04; 4.87%) for abundance, and salinity (λ = 0.19; 15.4%), Ni (λ = 0.16; 13.0%), and Cd (λ = 0.13; 10.5%) for biomass (Fig. 2-7a and 2-7b, and Table 2-5).

When the variance accounted for by total organic carbon content in sediments was removed as a covariable, pCCA followed by forward selection ranked pH as the most important factor responsible for the variance in both the abundance (eigenvalue, λ = 0.31; % variance explained = 37.7%) and biomass data (λ = 0.51; 41.4%), which was followed by Hg (λ = 0.09; 10.9%), Ag (λ = 0.05; 6.08%), and Cd (λ = 0.03; 3.64%) for abundance, and Hg (λ = 0.17; 13.8%), salinity (λ = 0.12; 9.73%), and Ag (λ = 0.04; 3.24%) for biomass (Fig. 2-8a and 2-8b, and Table 2-6).

DISCUSSION

Many areas of the New York/New Jersey Harbor Estuary Complex, particularly the Arthur Kill, have been chronically exposed to a variety of anthropogenic stressors (Franz

and Harris, 1988; Adams *et al.*, 1998; Adams and Benyi, 2003). As a result, benthic macroinfaunal communities in these areas tend to be species-poor (Franz, 1982; Berg and Levinton, 1985). In urban coastal habitats, benthic macroinfaunal communities frequently exhibit characteristics such as reduced taxonomic diversity (Weston, 1990), numerical dominance of opportunistic small-bodied annelids (e.g., oligochaetes) (Pearson and Rosenberg, 1978; Weston, 1990; Warwick, 2001; Norkko *et al.*, 2006), and disappearance of sensitive large-bodied taxonomic groups (e.g., crustaceans and gastropods) (Weston, 1990; Warwick and Clarke, 1994; Warwick, 2001). In the current study, in spite of substantial taxonomic differences among sites, the traditional univariate indices (i.e., the number of species, species richness, Shannon-Wiener species diversity index, and Heip's evenness index) for benthic macroinfaunal communities were not sensitive enough to differentiate some of the Arthur Kill sites (e.g., Mill Creek and Neck Creek in 2004) from the reference sites.

Large fluctuations in abundances of a few polychaetes (e.g., *Nereis acuminata*) observed in the current study may also have contributed to inconsistent trends in abundance-biomass comparison (ABC) statistic *W* (Clarke, 1990; Meire and Dereu, 1990). Shifts in average body size spectrum can be an ecologically relevant indicator for cumulative pollution impacts on ecosystem processes (e.g., energy flux) (Schwinghamer, 1981; Warwick and Clarke, 1984; Warwick, 1993; Basset *et al.*, 2004; Stead *et al.*, 2005). This particular phenomenon of shifts in body size structure described with the ABC curves is based on the premise that in severely degraded communities, due to increased abundance of relatively small-bodied opportunistic species (e.g., oligochaetes), the abundance-derived k-dominance curve tends to be above the biomass-derived k-

dominance curve (Warwick, 1986; Warwick *et al.*, 1987; Warwick, 1993). The dominance of a few opportunistic annelid species is frequently observed at grossly polluted coastal marine communities (Warwick and Clarke, 1993). As environmental conditions improve and recovery progresses, relatively large-bodied benthic macroinvertebrate taxonomic groups, such as bivalves and gastropods, usually begin to appear (Rhoads *et al.*, 1977; Pearson and Rosenberg, 1978; Somerfield *et al.*, 2006). This type of taxonomic shifts can considerably affect the total biomass of communities (Clarke and Warwick, 2001). In the current study, a large reduction in the abundance of small-bodied oligochaetes (e.g., Naididae) during the study period was followed by only an increased number of slightly larger polychaetes, and did not lead to any clear trend in k-dominance curves at most of the Arthur Kill sites.

The total abundance and biomass of benthic macroinvertebrates in both the Arthur Kill and reference sites also failed to show a consistent trend in the present study. A similar trend was also observed in previous studies on the assessment of benthic macroinfaunal communities in severely metal-polluted habitats (e.g., Foundry Cove, New York, USA) (Klerks and Levinton, 1993; Kelaher *et al.*, 2003). Despite a substantial difference in species diversity, these studies have shown no consistent differences in total densities between polluted and reference sites (Klerks and Levinton, 1993; Kelaher *et al.*, 2003). The present study also showed, compared to Lemon Creek (one of regional reference sites), substantial temporal variability in the total abundance and biomass of macroinvertebrates at the Arthur Kill sites as well as Great Kills Harbor. This high variability appears to be associated with shifts in major taxonomic groups in these communities. For example, a decrease in total abundance at most of the Arthur Kill sites

during the study period was a result of a disproportionate decrease in the abundance of oligochaetes, which were replaced by opportunistic polychaetes species (e.g., *Hobsonia florida*, *Streblospio benedicti*, and *N. acuminata*).

An early colonizing species assemblage following anthropogenic disturbances may dictate how the subsequent communities respond to changing environmental conditions (Zajac and Whitlatch, 1982; Sardá *et al.*, 1995; Norkko *et al.*, 2006; Chapman, 2007). These early colonizers often have opportunistic life history characteristics (e.g., short life span and high reproductive output), and are likely to benefit by reduced, or lack of interspecific competition, which would allow them to numerically dominate disturbed communities. Surface tube-building deposit-feeders such as *H. florida* and *S. benedicti* are frequently encountered in chronically disturbed salt marshes (Gaston and Young, 1992; Weis *et al.*, 2004). A substantial increase in the abundances of these tube-builders may, however, prevent larvae of other deposit-feeders as well as suspension-feeders from settling in sediments (Woodin, 1974; Whitlatch and Zajac, 1985).

Theoretical and experimental evidence indicate that interspecific interactions influence species-specific abundance and biomass of benthic macroinfaunal communities (Woodin, 1974; Gallagher *et al.*, 1983; Whitlatch and Zajac, 1985). In general, as the recovery processes of biological communities progress following anthropogenic disturbances, interspecific interactions can play a progressively important role in structuring the community assemblage (Rhoads *et al.*, 1977; Whitlatch *et al.*, 1998; Zajac *et al.*, 1998). Due to logistical difficulties in assessing the importance of interspecific interactions in field studies (Clements, 1997; Norkko *et al.*, 2006), however, there is a limited understanding of how these interactions and species-specific abundance or

biomass can shape chronically degraded communities at successional stages (Clements, 1997; Clements and Newman, 2002).

At a series of successional stages in urban coastal habitats, opportunistic pollution-tolerant species are often quickly replaced by other opportunistic species (Grassle and Grassle, 1974; McCall, 1977; Whitlatch and Zajac, 1985). As a result, univariate indices for biodiversity may be able to detect only severely disturbed communities (Clarke, 1999; Hewitt *et al.*, 2005). Moreover, species diversity and evenness indices of community composition can also be influenced by disproportionately abundant species (Clarke, 1993; Tuck *et al.*, 1998). Benthic macroinfaunal communities containing a few disproportionately abundant taxa, which are frequently observed in highly eutrophied coastal habitats, may even be erroneously categorized as, or not be distinguished from those at chemically polluted habitats (Rakocinski *et al.*, 1997). Although univariate measures of community compositions (e.g., Shannon-Wiener index) are frequently used in the assessment of environmental impacts on biological assemblages, these indices may be insensitive to subtle structural differences, or even misleading, particularly for highly dynamic communities such as marine benthic macroinfaunal assemblages (Somerfield *et al.*, 1994; Clarke, 1999; Olsgard, 1999; Warwick *et al.*, 2002; Hewitt *et al.*, 2005).

At one of the Arthur Kill sites, Main Creek (also one of tributaries of the Fresh Kills Complex), benthic macroinfaunal communities consistently showed characteristics of high-level degradation, which were even detected by the univariate indices. More than 90% of the macroinfaunal community at Main Creek was comprised of only oligochaetes and two polychaete species (*H. florida* and *N. acuminata*) in all the sampling years. The dramatic changes over time in total biomass and abundance at Main Creek appear to be

due to shifts in the relative proportions of these taxa (e.g., a decrease of oligochaetes and an increase of polychaetes). A decrease in relative abundances of oligochaetes is frequently noted as an indication of improved habitat quality in coastal wetlands (Kelaher *et al.*, 2003). Furthermore, the abundance of the isopod *Cyathura polita*, which is not known as a pollution-tolerant species (Steimle and Caracciolo-Ward, 1989; Weis *et al.*, 2004), substantially increased at Main Creek over time. It is thus possible that the environmental conditions at Main Creek gradually improved. Still, the benthic macroinfaunal community at Main Creek, as well as that at Richmond Creek (another tributary of the Fresh Kills Complex), remained species-poor, suggesting that the cumulative effects of historic pollution at the Fresh Kills Complex may have strong impacts on its biological assemblages.

In general, multivariate approaches tend to be more sensitive and informative than univariate approaches in detecting pollution impacts on benthic communities (e.g., Warwick and Clarke, 1991; Somerfield *et al.*, 1994; Drake and Arias, 1997; Olsgard, 1999; Hewitt *et al.*, 2005). In the present study, 2-dimensional representations of non-metric multidimensional scaling (nMDS) plots and analysis of similarity (ANOSIM) revealed distinct patterns in among-site differences as well as overall temporal changes in benthic macroinfaunal communities. Despite its considerable temporal variability in univariate measures, both the abundance and biomass of benthic macroinfaunal community at Great Kills Harbor (a moderately organically-enriched site) were consistently similar to those at Lemon Creek. This trend suggests that the effects of chemical pollution on benthic macroinfaunal communities in the Arthur Kill may be stronger than those of eutrophication observed at many of the study sites including Great

Kills Harbor. Moreover, the nMDS plots also clearly showed a gradual shift of the macroinfaunal community at one of the Arthur Kill sites, Mill Creek, toward those of Lemon Creek and Great Kills Harbor. The results of similarity percentages (SIMPER) analyses also revealed a compositional shift in proportional contributions (in abundance) by species at Mill Creek from the numerical dominance by a few opportunistic species (e.g., oligochaetes and pollution-tolerant polychaetes such as *S. benedicti*) to more diverse species including the appearance of molluskan species. These shifts in the macroinfaunal community at Mill Creek can frequently be observed during recovery processes in historically polluted regions (Norkko *et al.*, 2006; Somerfield *et al.*, 2006).

Although sediment-associated copper (Cu), lead (Pb), and zinc (Zn) levels at Mill Creek were considerably elevated, multivariate analyses indicated that the benthic macroinfaunal community at this site was more similar to those at Lemon Creek and Great Kill Harbor than the other Arthur Kill sites (Richmond Creek, Main Creek, and Neck Creek). Contrary to some studies (e.g., Hall and Frid, 1995; Olsgard, 1999; Lenihan *et al.*, 2003), the results from the present study suggest that the impacts of elevated levels of these metals at Mill Creek may not be as strong as those of other anthropogenic stressors (e.g., mercury) in influencing macroinfaunal communities. A similar result was also observed by Steimle and Caracciolo-Ward (1989); benthic macroinfaunal communities in the southern Arthur Kill region were comparable to those at much less polluted areas in the northwest Atlantic coast. A lack of significant effects of Cu, Pb, and Zn on marine benthic macroinfaunal communities was also observed in a field-experimental study conducted in Port Hacking, Australia (which incidentally had similar

levels of these sediment-associated metals to Mill Creek in the current study) (Lindegarth and Underwood, 2002).

Bioavailabilities of trace metals are known to influence their potential ecological effects on marine macroinvertebrates (Luoma, 1996). The bioaccumulation study (Chapter 4) suggest, however, that Cu, Pb, and Zn in some macroinvertebrates at Mill Creek were also elevated, and thus, it is unlikely that metal bioavailability alone is the major factor explaining the result observed in the present study. Vitaliano and Bejda (2001) have also shown that despite the elevated levels of Cu, Pb, and Zn in tissues, ribbed mussels (*Geukensia demissa*) from Mill Creek had a considerably higher growth rate and body size than those from the northern Arthur Kill sites.

Anthropogenic impacts on soft-sediment benthic macroinfaunal communities in urban coastal habitats have been extensively investigated (Clarke, 1999). However, it is often difficult to establish a generalized relationship between the extent of habitat degradation and alterations in benthic macroinfaunal communities. Urban coastal ecosystems are usually simultaneously exposed to multiple anthropogenic stressors, many of which covary with one another (Rakocinski *et al.*, 1997; Lenihan *et al.*, 2003). Some environmental factors with a strong gradient can also mask the effects of other forces (Somerfield *et al.*, 1994; Rakocinski *et al.*, 1997). In the current study, canonical correspondence analysis (CCA) indicated that a relatively large proportion (> 70%) of among-site variances in both abundance and biomass of benthic macroinfaunal communities was strongly associated with a few environmental variables measured, particularly, sediment-associated total mercury (Hg) and salinity. The importance of salinity on benthic macroinfaunal assemblages in tidal salt marshes is well documented,

as many estuarine macroinfaunal species occur within a certain species-specific optimal range of salinity (Strayer, 2006; Dauvin, 2008). When the variance associated with fine sediment grain was removed through partial CCA, total Hg remained the major factor influencing benthic macroinfaunal community at the Arthur Kill sites. Similar patterns were also observed when the variance associated with total organic carbon content in sediments was removed; total Hg was still among the major environmental factors affecting benthic macroinfaunal assemblages, regardless of the differences in other sediment characteristics. These results suggest a strong impact of sediment-associated total Hg on benthic macroinfaunal assemblages in the Arthur Kill. The unexplained portion of among-site variances in benthic macroinfaunal communities in the current study was relatively small (< 30%), which might have been accounted for by biological factors (e.g., predation) as well as other anthropogenic stressors (e.g., polycyclic aromatic hydrocarbons) in the Arthur Kill (Adams and Benyi, 2003; Adams et al., 1998).

Conclusions

The Arthur Kill and its surrounding bodies of water have been severely polluted for more than a century (Crawford *et al.*, 1994). Despite considerable improvements in the habitat quality in the last few decades (Bopp *et al.*, 2006), benthic macroinfaunal communities in these areas still exhibited the characteristics of degraded communities (Crawford *et al.*, 1994; Adams *et al.*, 1998; Adams and Benyi, 2003; Cerrato, 2006). In the present study, although a few crustacean and molluskan species appeared at some of the Arthur Kill sites, typical characteristics of chronically disturbed benthic macroinfaunal communities (e.g., numerical dominance by opportunistic species) were

still observed. Moreover, despite a substantial reduction in total abundances of opportunistic species such as oligochaetes, they were still abundant at many of the Arthur Kill sites.

The current study also showed that marine benthic macroinvertebrates exhibit species-specific differential responses to specific anthropogenic stressors (e.g., eutrophication vs. chemical pollution), as previously suggested (Pearson and Rosenberg, 1978; Somerfield *et al.*, 1994; Rakocinski *et al.*, 1997). For instance, the lack of, or low abundance of capitellid species, which are often abundant in eutrophied urban coastal habitats (Grassle and Grassle, 1974; Zajac and Whitlatch, 2001), at the Arthur Kill sites suggests that these polychaetes may be less tolerant to chemical pollution (e.g., trace metals) than eutrophication (Warwick, 2001). Among the anthropogenic stressors measured, multivariate analyses revealed that sediment-associated total Hg were particularly strongly associated with the overall patterns in abundance and biomass of benthic macroinvertebrates in the Arthur Kill. The findings from the present as well as previous studies suggest that anthropogenic impact assessments of benthic macroinvertebrates may require a more biologically based approach incorporating species-specific responses (e.g., life history responses), rather than generalization of univariate trends (e.g., species diversity) in chronically degraded ecosystems.

Tidal salt marshes in the Arthur Kill provide an essential habitat for resident and migrant nekton in the NY/NJ Estuary ecosystems (Berg and Levinton, 1985; Able *et al.*, 1998; Duffy-Anderson *et al.*, 2003). As many of the nekton primarily feed on benthic macroinvertebrates (Chapter 5; Steimle, 2001; Weis, 2005; Dittel *et al.*, 2006), pollution-induced alterations in benthic macroinfaunal communities are likely to have cascading

(positive or negative) effects on trophic structure and ecosystem function (e.g., energy flow and nutrient cycling) in the Arthur Kill (Chapters 5 and 6; Boesch, 1982; Carlisle, 2000; Clements and Newman, 2002).

Table 2-1. Results of 2-way analysis of variance (ANOVA) for the effects of sampling year and site on the univariate measures of benthic macroinfaunal communities. *DF* = degrees of freedom, *SS* = sum of squares, and *MS* = mean square. Statistically significant differences are indicated in **bold** ($p < 0.05$)

Abundance

Effect	*DF*	*SS*	*MS*	*F*-value	*p*-value
Intercept	1	1283.8	1283.8	71186	**0.000**
Year	2	0.476	0.238	13.19	**0.000**
Site	4	1.364	0.341	18.90	**0.000**
Year*Site	8	3.398	0.425	23.55	**0.000**
Residual	50	0.902	0.018		

Species Diversity, *H′*

Effect	*DF*	*SS*	*MS*	*F*-value	*p*-value
Intercept	1	0.038	0.038	10.08	**0.003**
Year	2	0.501	0.250	66.99	**0.000**
Site	4	0.779	0.195	52.12	**0.000**
Year*Site	8	0.275	0.034	9.182	**0.000**
Residual	48	0.179	0.004		

Biomass

Effect	*DF*	*SS*	*MS*	*F*-value	*p*-value
Intercept	1	27.29	27.29	859.4	**0.000**
Year	2	7.038	3.519	110.8	**0.000**
Site	4	1.467	0.367	11.55	**0.000**
Year*Site	8	3.712	0.464	14.61	**0.000**
Residual	50	1.588	0.032		

Evenness

Effect	*DF*	*SS*	*MS*	*F*-value	*p*-value
Intercept	1	8.004	8.004	550.1	**0.000**
Year	2	10.587	5.294	363.8	**0.000**
Site	4	0.903	0.226	15.51	**0.000**
Year*Site	8	0.920	0.115	7.908	**0.000**
Residual	48	0.698	0.015		

 # Species, *S*

Effect	*DF*	*SS*	*MS*	*F*-value	*p*-value
Intercept	1	27.29	27.29	859.4	**0.000**
Year	2	7.038	3.519	110.8	**0.000**
Site	4	1.467	0.367	11.55	**0.000**
Year*Site	8	3.712	0.464	14.61	**0.000**
Residual	50	1.588	0.032		

ABC *W*

Effect	*DF*	*SS*	*MS*	*F*-value	*p*-value
Intercept	1	0.032	0.032	3.244	0.078
Year	2	0.332	0.166	16.73	**0.000**
Site	4	0.228	0.057	5.743	**0.001**
Year*Site	8	0.287	0.036	3.623	**0.002**
Residual	48	0.476	0.010		

Species Richness, *d*

Effect	*DF*	*SS*	*MS*	*F*-value	*p*-value
Intercept	1	0.431	0.431	54.10	**0.000**
Year	2	0.276	0.138	17.34	**0.000**
Site	4	0.836	0.209	26.25	**0.000**
Year*Site	8	0.106	0.013	1.666	0.131
Residual	48	0.382	0.008		

Figure 2-1. Mean values (± 1 SE) of benthic macroinvertebrate abundance in (a) 2000, (b) 2001, and (c) 2004, and biomass in (d) 2000, (e) 2001, and (f) 2004. Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test). Note that samples from Richmond Creek were not available in 2000.

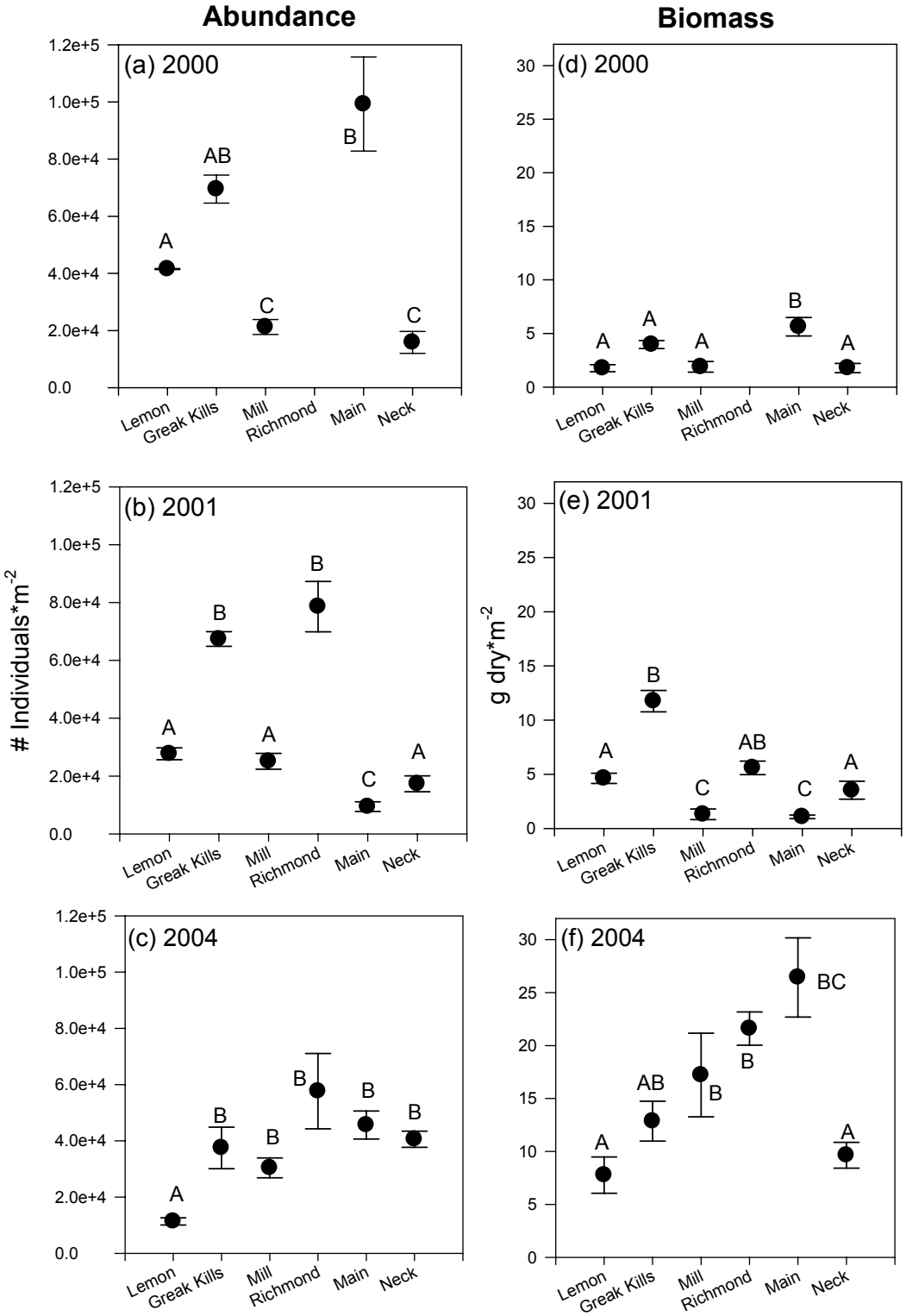


Figure 2-2. Mean values (± 1 SE) of number of benthic macroinvertebrate species in (a) 2000, (b) 2001, and (c) 2004, and Margalef's species richness in (d) 2000, (e) 2001, and (f) 2004. Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test). Note that samples from Richmond Creek were not available in 2000.

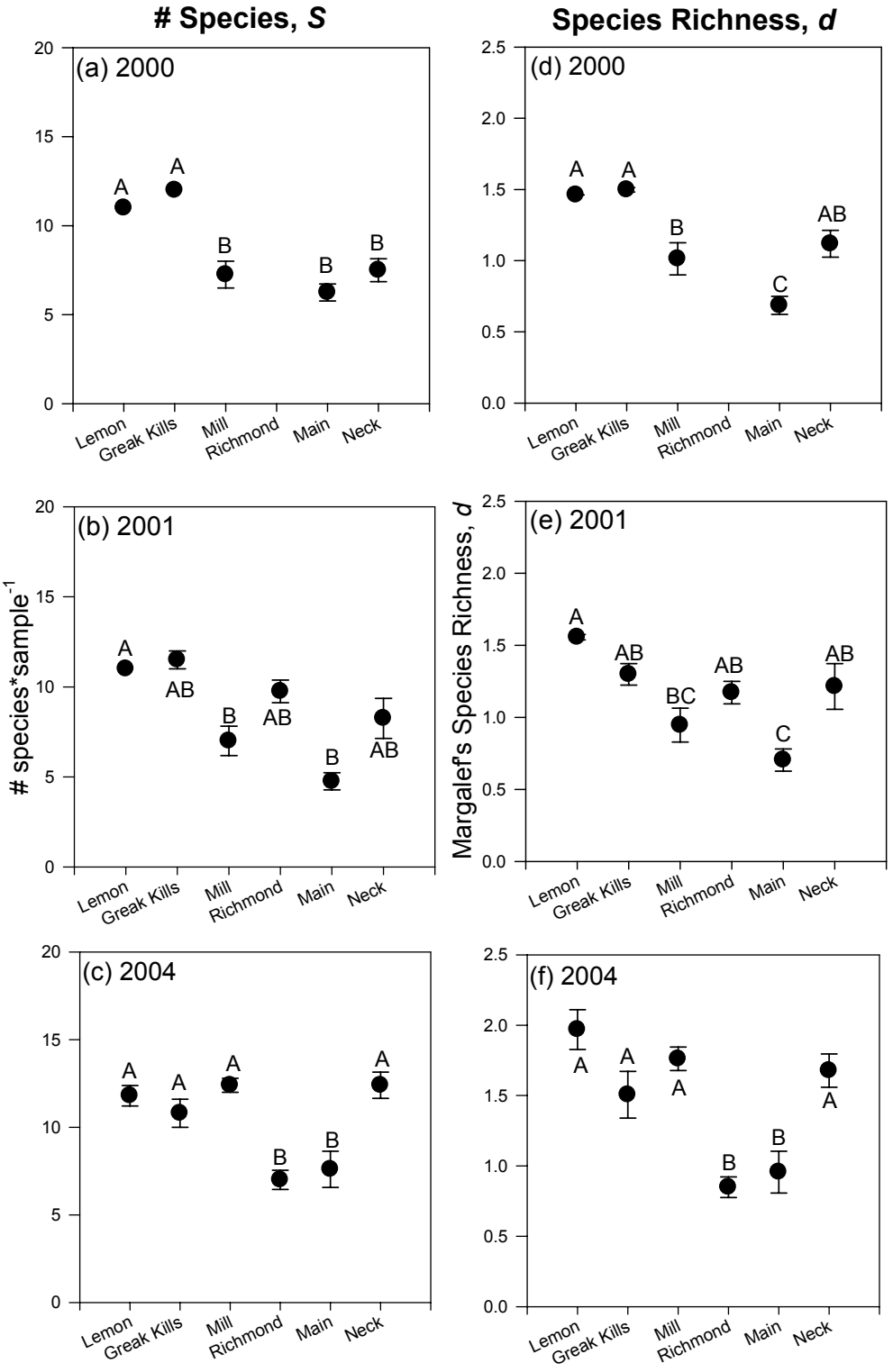


Figure 2-3. Mean values (± 1 SE) of Shannon-Weiner's species diversity of benthic macroinvertebrates in (a) 2000, (b) 2001, and (c) 2004, and Heip's evenness in (d) 2000, (e) 2001, and (f) 2004. Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test). Note that samples from Richmond Creek were not available in 2000.

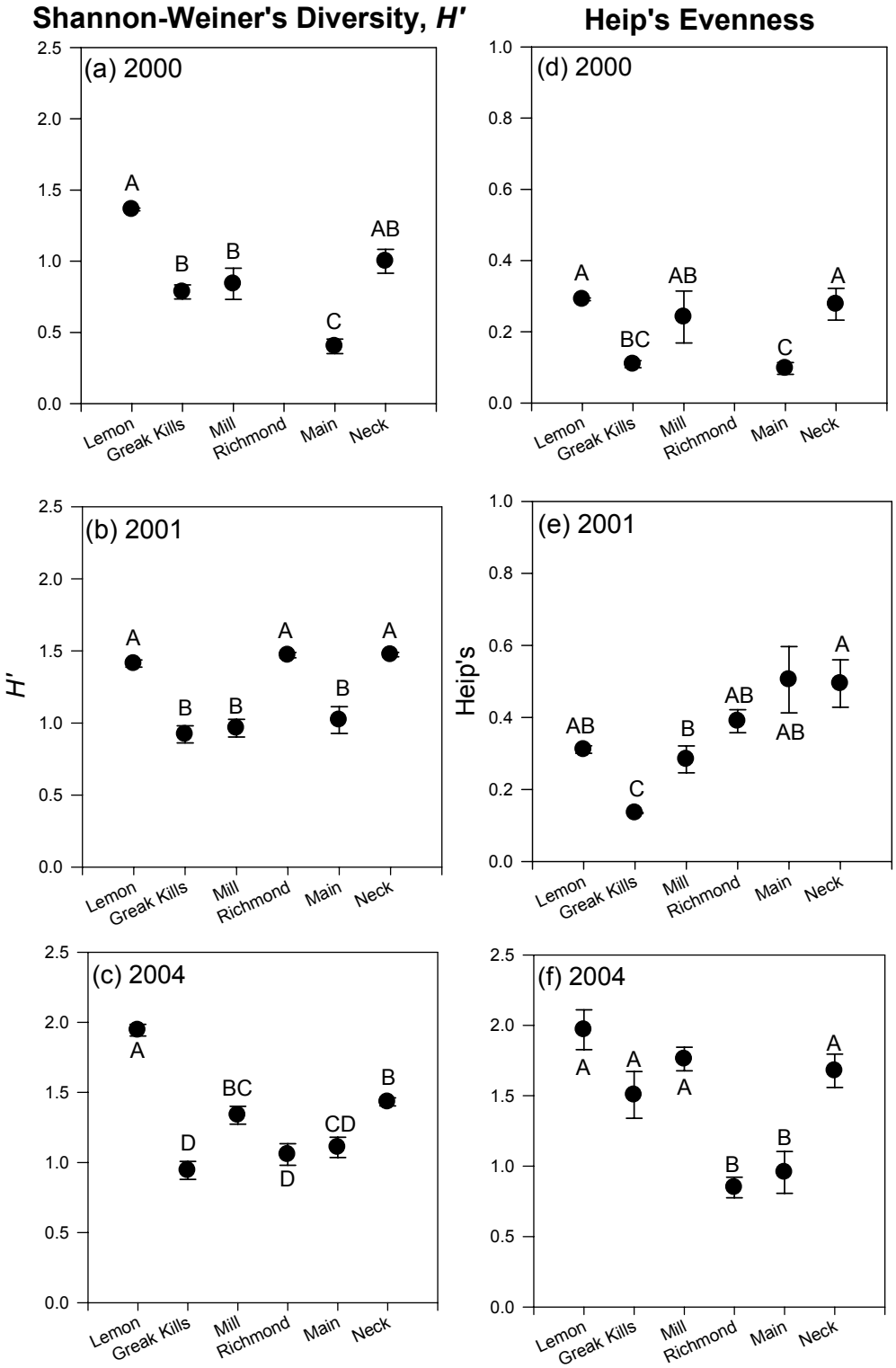


Figure 2-4. Mean values (± 1 SE) of abundance-biomass comparison (ABC) statistic *W* of benthic macroinvertebrates in (a) 2000, (b) 2001, and (c) 2004. Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test). Note that samples from Richmond Creek were not available in 2000.

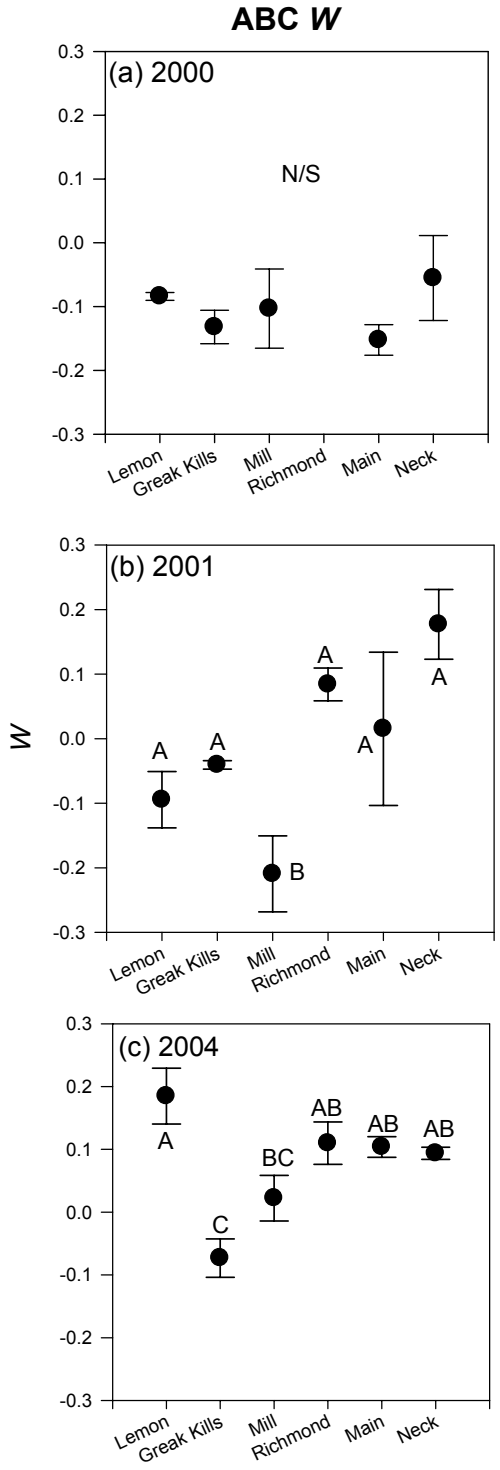


Figure 2-5. 2-dimensional plots of non-metric multidimensional scaling (nMDS) ordination (based on Bray-Curtis similarities of $\log_e(x+1)$-transformed data for abundance and square-root transformed data for biomass) on benthic macroinvertebrate abundance in (a) 2000, (b) 2001, and (c) 2004, and biomass in (d) 2000, (e) 2001, and (f) 2004 from Great Kills Harbor (●), Lemon Creek (●), Mill Creek (▼), Richmond Creek (▲), Main Creek (■), and Neck Creek (■). Note that samples from Richmond Creek were not available in 2000.

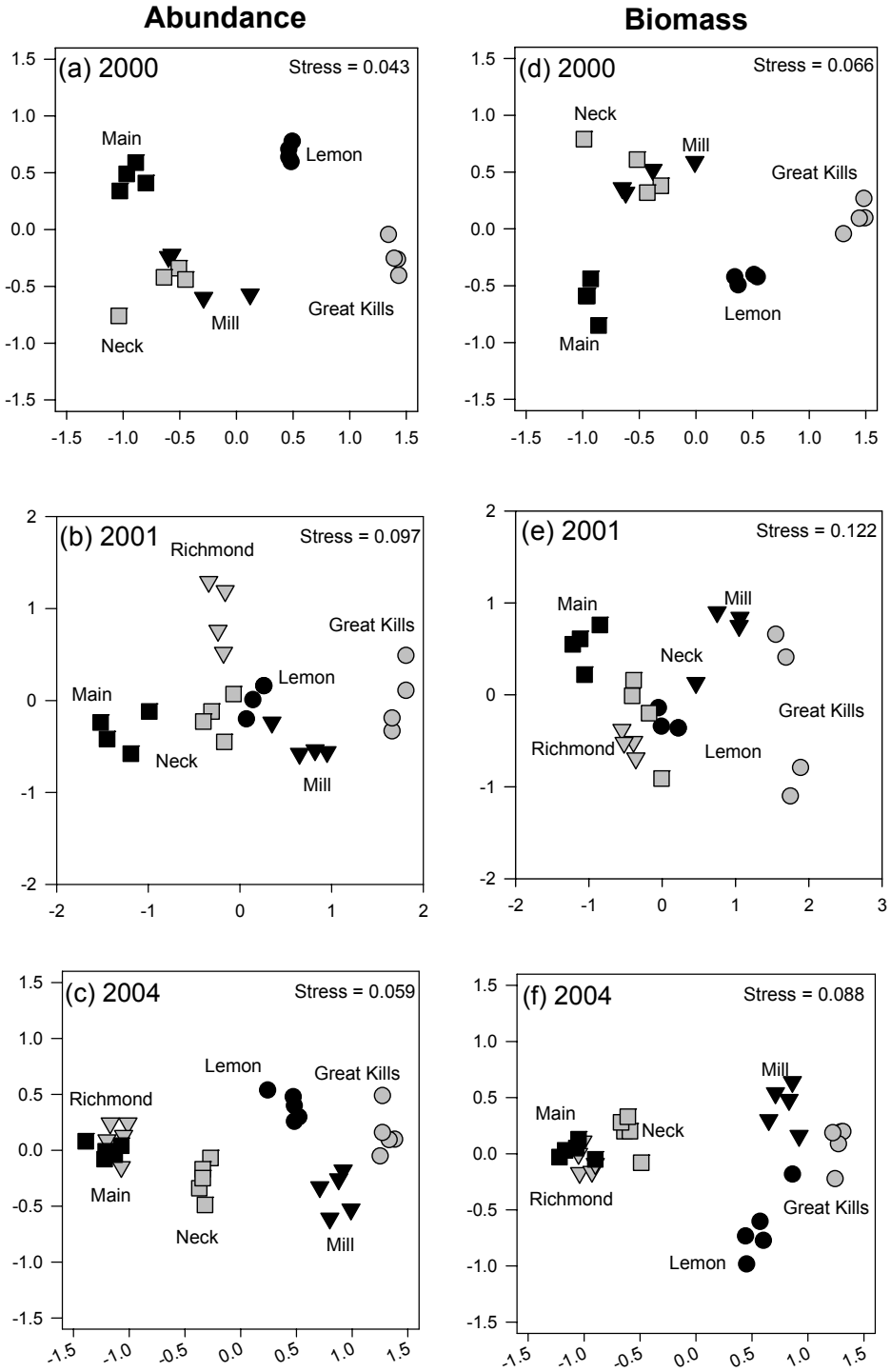


Table 2-2. Global analysis and pairwise comparison of index of multivariate dispersion (IMD) of benthic macroinvertebrates in Lemon Creek, Great Kills Harbor, Mill Creek, Richmond Creek, Main Creek, and Neck Creek in 2000, 2001, and 2004. Note that samples from Richmond Creek were not available in 2000.

Global Analysis				**Pairwise Comparisons**			
Study Sites	2000	2001	2004	Study Sites	2000	2001	2004
Lemon Creek	0.376	0.573	0.633	Great Kills vs. Lemon	0.722	1.000	0.360
Mill Creek	1.328	0.802	0.728	Great Kills vs. Richmond	-	1.000	0.200
Richmond Creek	-	0.906	0.915	Great Kills vs. Main	0.333	1.000	0.300
Neck Creek	1.344	1.26	1.059	Great Kills vs. Neck	-0.278	1.000	0.120
Main Creek	0.871	1.302	1.108	Great Kills vs. Mill	-0.361	1.000	-0.320
Great Kills Harbor	1.081	1.938	1.557	Lemon vs. Rchmond	-	-0.389	-0.300
				Lemon vs. Main	-0.778	-0.722	-0.160
				Lemon vs. Neck	-1.000	-0.722	-0.540
				Lemon vs. Mill	-0.722	-0.278	-0.880
				Richmond vs. Main	-	-0.444	0.200
				Richmond vs. Neck	-	-0.389	-0.180
				Richmond vs. Mill	-	0.111	-0.640
				Main vs. Neck	-0.556	0.111	-0.460
				Main vs. Mill	-0.556	0.500	-0.860
				Neck vs. Mill	-0.056	0.556	-0.700

Table 2-3. Physicochemical characteristics of Lemon Creek, Great Kills Harbor, Mill Creek, Richmond Creek, Main Creek, and Neck Creek during the summer of 2004. Metal concentrations above the ERM levels are indicated in **bold**.

		Study Sites					
Environmental Variables	ERM*	Lemon Creek	Great Kills Harbor	Mill Creek	Richmond Creek	Main Creek	Neck Creek
Temperature (°C)		25.2	28.0	28.3	29.6	26.0	31.6
Dissolved Oxygen ($mg \cdot L^{-1}$)		6.13	6.30	6.53	3.07	2.80	16.1
Salinity (‰)		6.3	25.0	14.7	5.0	6.0	14.0
pH		7.68	7.83	7.26	7.88	7.93	8.70
Fine Sediment Particles (%)		33.5	55.7	74.7	63.8	17.5	59.5
TOC (%)		5.95	8.70	4.92	2.38	5.43	12.5
Trace Metals ($\mu g \cdot g^{-1}$)							
Ag	3.7	0.83	0.48	1.38	0.78	1.59	1.37
Cd	9.6	1.20	1.14	2.88	1.58	2.90	1.08
Cu	270	125	92.2	**912**	99.7	216	153
Hg	0.71	0.28	0.27	**0.98**	**0.80**	**1.86**	**2.46**
Ni	51.6	27.9	50.9	36.5	34.0	**70.3**	49.0
Pb	218	83.9	98.7	**656**	91.9	171	215
Zn	410	220	188	**1190**	289	**411**	339

*ERM = Effects Range Median (Long and Morgan, 1990).

Table 2-4. Results of canonical correspondence analysis (CCA) on (a) abundance and (b) biomass of benthic macroinvertebrates in relation to environmental variables at study sites in 2004. Environmental variables that significantly contributed to total eigenvalue (λ) are ranked in importance on basis of marginal and conditional effects. Significance of each environmental variable is based on a Monte Carlo permutation test with 999 random permutations at $p < 0.05$.

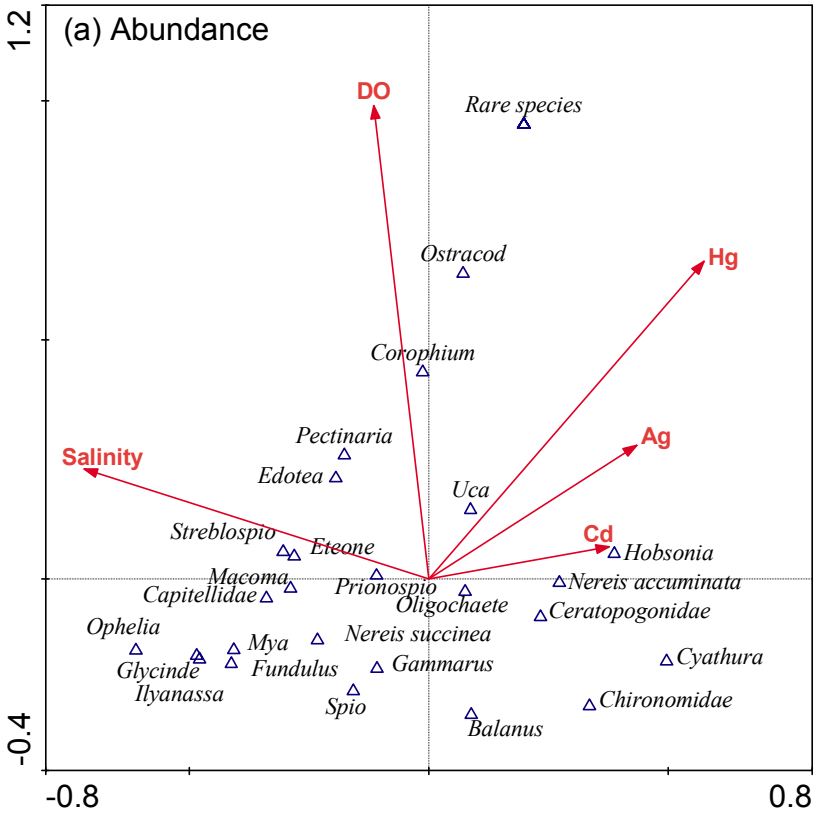
(a) Abundance	Axes				
	1	2	3	4	Total Inertia
Eigenvalues (λ):	0.380	0.087	0.061	0.028	**0.822**
Species-environment correlations :	0.994	0.967	0.925	0.846	
Cumulative % variance of species data :	46.2	56.8	64.2	67.6	
Cumulative % variance of species-environment relation:	66.7	81.9	92.6	97.5	

	Intraset correlations		Marginal Effects	Conditional Effects		
Selected variable	Axis 1	Axis 2	λ_M	λ_C	*F*-value	*p*-value
Salinity	-0.720	0.235	0.220	0.220	10.9	0.001
Hg	0.575	0.666	0.170	0.140	8.57	0.001
Ag	0.435	0.281	0.100	0.090	8.47	0.001
DO	-0.113	0.991	0.080	0.090	6.49	0.001
Cd	0.169	-0.490	0.060	0.050	3.92	0.001
Total canonical eigenvalue				**0.586**		

(b) Biomass	Axes				
	1	2	3	4	Total Inertia
Eigenvalues (λ):	0.626	0.162	0.075	0.046	**1.23**
Species-environment correlations :	0.994	0.905	0.948	0.864	
Cumulative % variance of species data :	50.8	64.0	70.0	73.8	
Cumulative % variance of species-environment relation:	68.2	85.8	93.9	99.0	

	Intraset correlations		Marginal Effects	Conditional Effects		
Selected variable	Axis 1	Axis 2	λ_M	λ_C	*F*-value	*P*-value
Salinity	0.709	-0.394	0.360	0.360	11.8	<0.001
Hg	-0.568	0.165	0.250	0.230	10.2	<0.001
Ag	-0.455	-0.311	0.170	0.060	4.68	<0.001
Cd	-0.160	-0.514	0.090	0.150	7.87	<0.001
TOC	0.158	0.039	0.080	0.120	8.79	<0.001
Total canonical eigenvalue				**0.919**		

Figure 2-6. Biplot representation (Axes 1 and 2) of canonical correspondence analysis (CCA) on (a) abundance and (b) biomass of benthic macroinvertebrates in relation to environmental variables at study sites in 2004. Environmental variables are represented by arrows; species are represented by open triangles. The length of arrows indicates the relative importance of environmental variables. Arrows pointing in the same direction indicate positive correlation, while arrows pointing in the opposite direction indicate negative correlation. DO = dissolved oxygen. TOC = total organic carbon. *Eteone = Eteone lactea*, *Hobsonia = Hobsonia florida*, *Streblospio = Streblospio benedicti*, *Edotea = Edotea triloba*, *Macoma = Macoma balthica*, *Mya = Mya arenaria*, *Cyathura = Cyathura polita*, *Gammarus = Gammarus mucronatus*, *Ilyanassa = Ilyanassa trivittata*, *Glycinde = Glycinde salitaria*, *Balanus = Balanus improvises*, *Prionospio = Prionospio sp.*, *Pectinaria = Pectinaria gouldii*, *Corophium = Corophium volutator*, *Uca = Uca pugnax*, *Ophelia = Ophelia denticulate*, *Spio = Spio setosa*, *Fundulus = Fundulus heteroclitus*, Rare species = *Leitoscoloplos fragilis*, *Tetrastemma candidum*, *Phascolopsis gouldii*, *Nematostella vectensis*, *Lacuna vincta*, and *Amphitrite ornate*.


(a) Abundance
1.2
-0.4
-0.8
0.8
DO
Rare species
Ostracod
Hg
Corophium
Pectinaria
Ag
Salinity
Edotea
Uca
Streblospio
Eteone
Cd
Hobsonia
Macoma
Prionospio
Nereis accuminata
Capitellidae
Oligochaete
Ceratopogonidae
Ophelia
Mya
Nereis succinea
Glycinde
Fundulus
Gammarus
Cyathura
Ilyanassa
Spio
Chironomidae
Balanus

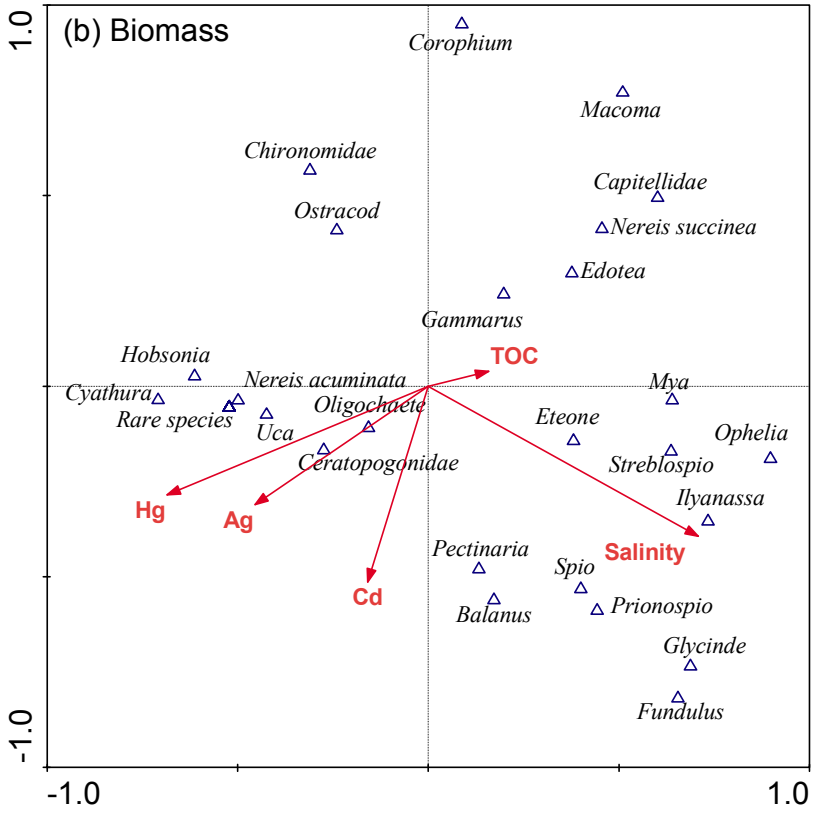

(b) Biomass
1.0
-1.0
-1.0
1.0
Corophium
Macoma
Chironomidae
Capitellidae
Ostracod
Nereis succinea
Edotea
Gammarus
Hobsonia
TOC
Nereis acuminata
Mya
Cyathura
Oligochaete
Rare species
Eteone
Uca
Ophelia
Ceratopogonidae
Streblospio
Hg
Ilyanassa
Ag
Pectinaria
Salinity
Spio
Cd
Balanus
Prionospio
Glycinde
Fundulus

Table 2-5. Results of partial canonical correspondence analysis (pCCA) on (a) abundance and (b) biomass of benthic macroinvertebrates in relation to environmental variables at study sites in 2004 with % fine sediment particle as a covariable. Environmental variables that significantly contributed to total eigenvalue (λ) are ranked in importance on basis of marginal and conditional effects. Significance of each environmental variable is based on a Monte Carlo permutation test with 999 random permutations at $p < 0.05$.

(a) Abundance	Axes					
	1	2	3	4	∑Eigenvalues	Total inertia
Eigenvalues (λ):	0.313	0.083	0.042	0.028	0.719	**0.822**
Species-environment correlations :	0.993	0.963	0.896	0.853		
Cumulative % variance of species data :	43.6	55.2	61.1	64.9		
Cumulative % variance of species-environment relation:	67.2	85.1	94.1	100		

	Intraset correlations		Marginal Effects	Conditional Effects		
Selected variable	Axis 1	Axis 2	λ_M	λ_C	*F*-value	*p*-value
Hg	0.623	0.554	0.160	0.160	7.74	<0.001
pH	0.469	0.794	0.130	0.120	9.97	<0.001
TOC	-0.139	0.906	0.080	0.150	9.58	<0.001
Cd	0.125	-0.605	0.060	0.040	3.77	<0.001
Total canonical eigenvalue				**0.467**		

(b) Biomass	Axes					
	1	2	3	4	∑Eigenvalues	Total inertia
Eigenvalues (λ):	0.520	0.130	0.068	0.043	1.07	**1.23**
Species-environment correlations :	0.994	0.886	0.938	0.85		
Cumulative % variance of species data :	48.4	60.5	66.8	70.8		
Cumulative % variance of species-environment relation:	68.4	85.5	94.4	100		

	Intraset correlations		Marginal Effects	Conditional Effects		
Selected variable	Axis 1	Axis 2	λ_M	λ_C	*F*-value	*p*-value
Hg	0.686	-0.173	0.280	0.280	9.43	<0.001
Salinity	-0.609	-0.399	0.240	0.190	8.5	<0.001
Ni	0.226	-0.768	0.130	0.160	8.97	<0.001
Cd	0.103	-0.728	0.100	0.130	9.77	<0.001
Total canonical eigenvalue				**0.760**		

Figure 2-7. Biplot representation (Axes 1 and 2) of partial canonical correspondence analysis (pCCA) on (a) abundance and (b) biomass of benthic macroinvertebrates in relation to environmental variables at study sites in 2004 with % fine sediment particle as a covariable. Environmental variables are represented by arrows; species are represented by open triangles. The length of arrows indicates the relative importance of environmental variables. Arrows pointing in the same direction indicate positive correlation, while arrows pointing in the opposite direction indicate negative correlation. TOC = total organic carbon. *Eteone = Eteone lacteal*, *Hobsonia = Hobsonia florida*, *Streblospio = Streblospio benedicti*, *Edotea = Edotea triloba*, *Macoma = Macoma balthica*, *Mya = Mya arenaria*, *Cyathura = Cyathura polita*, *Gammarus = Gammarus mucronatus*, *Ilyanassa = Ilyanassa trivittata*, *Glycinde = Glycinde salitaria*, *Balanus = Balanus improvises*, *Prionospio = Prionospio sp.*, *Pectinaria = Pectinaria gouldii*, *Corophium = Corophium volutator*, *Uca = Uca pugnax*, *Ophelia = Ophelia denticulate*, *Spio = Spio setosa*, *Fundulus = Fundulus heteroclitus*, Rare species = *Leitoscoloplos fragilis*, *Tetrastemma candidum*, *Phascolopsis gouldii*, *Nematostella vectensis*, *Lacuna vincta*, and *Amphitrite ornate*.

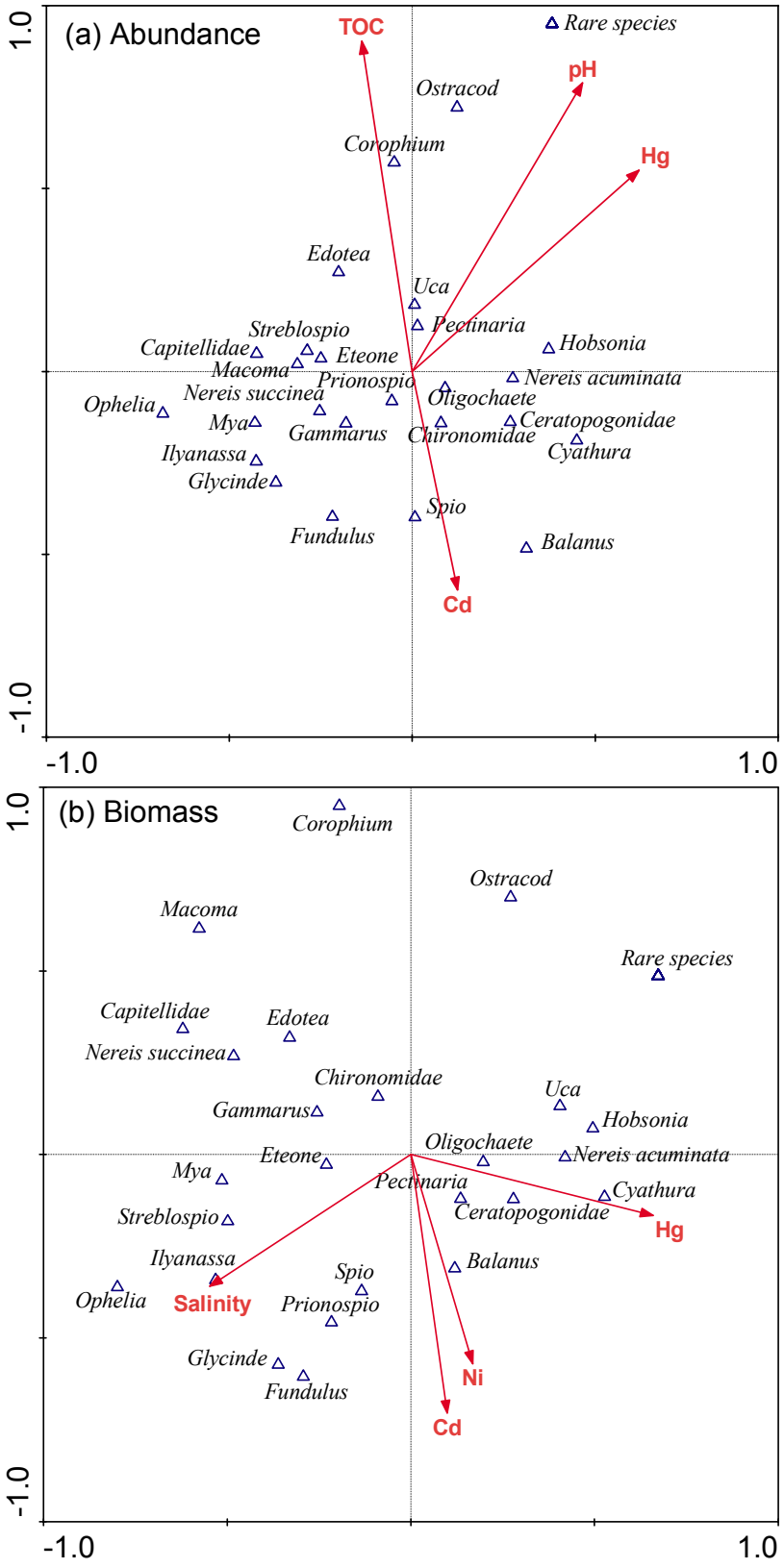

(a) Abundance
TOC
Rare species
pH
Ostracod
Corophium
Hg
Edotea
Uca
Pectinaria
Streblospio
Capitellidae
Eteone
Hobsonia
Macoma
Prionospio
Nereis acuminata
Nereis succinea
Oligochaete
Ophelia
Mya
Gammarus
Ceratopogonidae
Chironomidae
Cyathura
Ilyanassa
Glycinde
Spio
Fundulus
Balanus
Cd
1.0
-1.0
-1.0
1.0
(b) Biomass
Corophium
Ostracod
Macoma
Rare species
Capitellidae
Edotea
Nereis succinea
Chironomidae
Uca
Gammarus
Hobsonia
Oligochaete
Eteone
Nereis acuminata
Mya
Pectinaria
Cyathura
Ceratopogonidae
Hg
Streblospio
Ilyanassa
Balanus
Spio
Ophelia
Salinity
Prionospio
Glycinde
Ni
Fundulus
Cd
1.0
-1.0
-1.0
1.0

Table 2-6. Results of partial canonical correspondence analysis (pCCA) on (a) abundance and (b) biomass of benthic macroinvertebrates in relation to environmental variables at study sites in 2004 with total organic carbon as a covariable. Environmental variables that significantly contributed to total eigenvalue (λ) are ranked in importance on basis of marginal and conditional effects. Significance of each environmental variable is based on a Monte Carlo permutation test with 999 random permutations at $p < 0.05$.

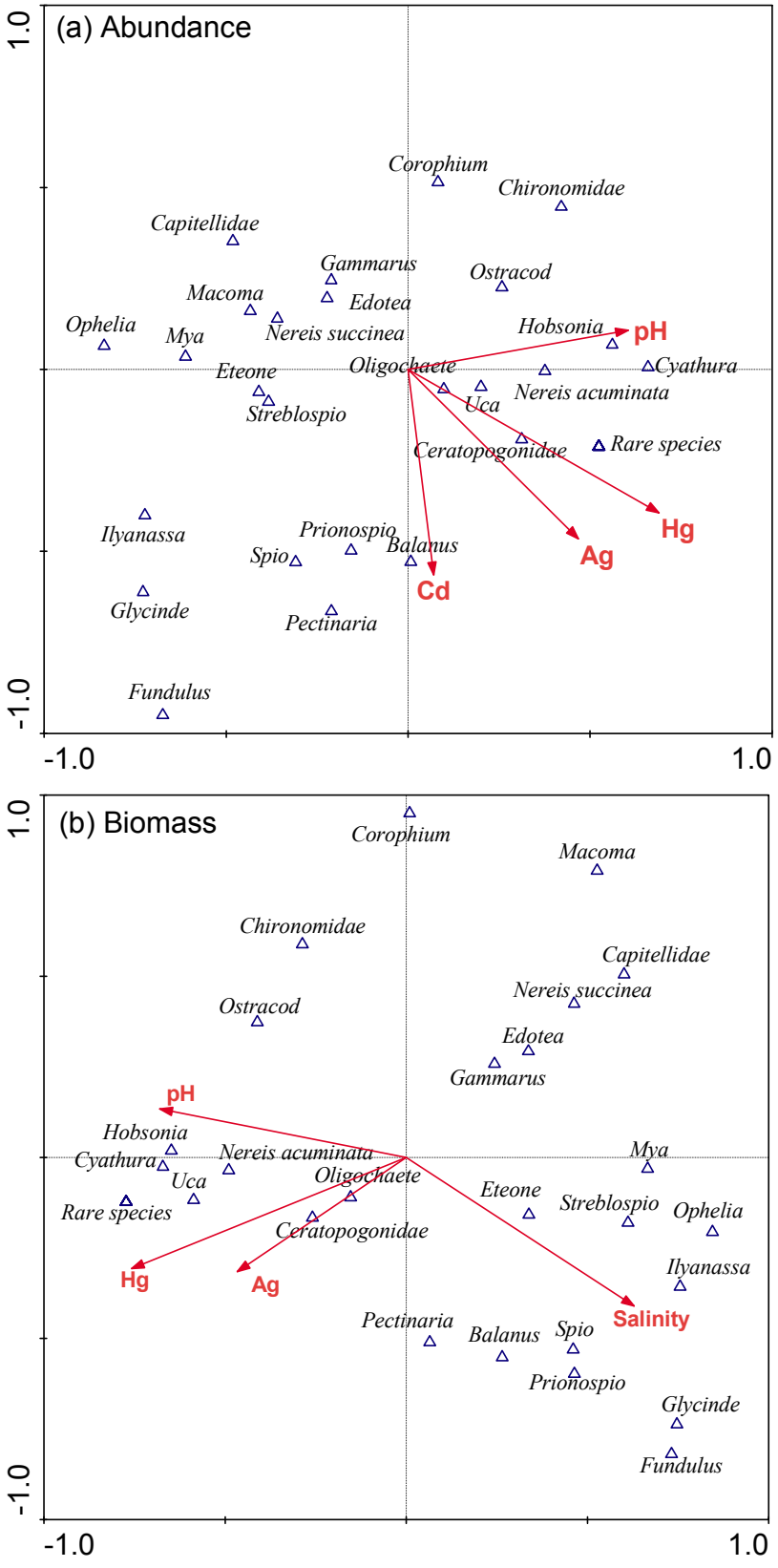
(a) Abundance	Axes					
	1	2	3	4	∑Eigenvalues	Total inertia
Eigenvalues (λ):	0.369	0.061	0.034	0.019	0.736	**0.822**
Species-environment correlations :	0.993	0.925	0.900	0.745		
Cumulative % variance of species data :	50.2	58.5	63.1	65.7		
Cumulative % variance of species-environment relation:	76.4	89.1	96.1	100		

			Marginal Effects	Conditional Effects		
Selected variable	Axis 1	Axis 2	λ_M	λ_C	*F*-value	*p*-value
pH	0.913	0.162	0.310	0.310	19.9	<0.001
Hg	0.815	-0.465	0.260	0.090	6.81	<0.001
Ag	0.472	-0.469	0.110	0.050	4.34	<0.001
Cd	0.082	-0.660	0.040	0.030	3.18	<0.001
Total canonical eigenvalue				**0.483**		

(b) Biomass	Axes					
	1	2	3	4	∑Eigenvalues	Total inertia
Eigenvalues (λ):	0.613	0.162	0.048	0.014	1.15	**1.23**
Species-environment correlations :	0.994	0.905	0.885	0.723		
Cumulative % variance of species data :	53.3	67.3	71.5	72.7		
Cumulative % variance of species-environment relation:	73.2	92.6	98.3	100		

			Marginal Effects	Conditional Effects		
Selected variable	Axis 1	Axis 2	λ_M	λ_C	*F*-value	*p*-value
pH	-0.909	0.178	0.510	0.510	21.9	<0.001
Hg	-0.832	-0.337	0.450	0.170	8.87	<0.001
Salinity	0.762	-0.498	0.400	0.120	8.75	<0.001
Ag	-0.468	-0.316	0.170	0.040	2.85	0.001
Total canonical eigenvalue				**0.837**		

Figure 2-8. Biplot representation (Axes 1 and 2) of partial canonical correspondence analysis (pCCA) on (a) abundance and (b) biomass of benthic macroinvertebrates in relation to environmental variables at study sites in 2004 with total organic carbon as a covariable. Environmental variables are represented by arrows; species are represented by open triangles. The length of arrows indicates the relative importance of environmental variables. Arrows pointing in the same direction indicate positive correlation, while arrows pointing in the opposite direction indicate negative correlation. *Eteone = Eteone lacteal*, *Hobsonia = Hobsonia florida*, *Streblospio = Streblospio benedicti*, *Edotea = Edotea triloba*, *Macoma = Macoma balthica*, *Mya = Mya arenaria*, *Cyathura = Cyathura polita*, *Gammarus = Gammarus mucronatus*, *Ilyanassa = Ilyanassa trivittata*, *Glycinde = Glycinde salitaria*, *Balanus = Balanus improvises*, *Prionospio = Prionospio sp.*, *Pectinaria = Pectinaria gouldii*, *Corophium = Corophium volutator*, *Uca = Uca pugnax*, *Ophelia = Ophelia denticulate*, *Spio = Spio setosa*, *Fundulus = Fundulus heteroclitus*, Rare species = *Leitoscoloplos fragilis*, *Tetrastemma candidum*, *Phascolopsis gouldii*, *Nematostella vectensis*, *Lacuna vincta*, and *Amphitrite ornate*.


(a) Abundance
1.0
-1.0
-1.0
1.0
Corophium
Chironomidae
Capitellidae
Gammarus
Ostracod
Macoma
Edotea
Ophelia
Mya
Nereis succinea
Hobsonia
pH
Eteone
Oligochaete
Cyathura
Uca
Nereis acuminata
Streblospio
Ceratopogonidae
Rare species
Hg
Ilyanassa
Prionospio
Balanus
Spio
Ag
Cd
Glycinde
Pectinaria
Fundulus
(b) Biomass
1.0
-1.0
-1.0
1.0
Corophium
Macoma
Chironomidae
Capitellidae
Nereis succinea
Ostracod
Edotea
Gammarus
pH
Hobsonia
Cyathura
Nereis acuminata
Mya
Uca
Oligochaete
Eteone
Streblospio
Ophelia
Rare species
Ceratopogonidae
Ilyanassa
Hg
Ag
Salinity
Pectinaria
Balanus
Spio
Prionospio
Glycinde
Fundulus

Appendix 2-A. Average abundance and biomass contributions (%) by major benthic macroinvertebrate classes in Lemon Creek, Great Kills Harbor, Mill Creek, Richmond Creek, Main Creek, and Neck Creek in 2000, 2001, and 2004.

2000	Average Abundance%						Average Biomass%					
	Lemon	Great Kills	Mill	Richmond†	Main	Neck	Lemon	Great Kills	Mill	Richmond†	Main	Neck
Polychaeta	47.9	89.8	26.9	-	10.4	37.0	81.0	81.4	72.3	-	41.5	81.7
Insecta	0.1	0.0	0.0	-	0.0	0.0	0.2	0.0	0.0	-	0.0	0.0
Crustacea	5.6	1.3	0.6	-	0.1	0.4	4.3	14.9	0.2	-	0.0	8.4
Bivalvia	0.0	0.1	0.0	-	0.0	0.1	0.0	0.0	0.0	-	0.0	0.8
Oligochaeta	46.4	7.8	72.4	-	89.4	62.2	14.5	3.0	27.4	-	58.5	9.0
Gastropoda	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0
Nemertinea	0.0	0.0	0.0	-	0.0	0.3	0.0	0.0	0.0	-	0.0	0.2
Sipunculodea	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0
Anthozoa	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0
Osteichthyrs	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0
Nematoda	0.0	1.0	0.0	-	0.0	0.0	0.0	0.7	0.0	-	0.0	0.0
Arachnida	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0
2001	Lemon	Great Kills	Mill	Richmond	Main	Neck	Lemon	Great Kills	Mill	Richmond	Main	Neck
Polychaeta	89.2	59.1	37.3	62.1	44.6	86.4	93.9	39.7	71.7	88.2	87.1	98.3
Insecta	0.2	0.0	0.0	0.1	0.2	0.0	0.3	0.0	0.0	0.1	1.6	0.0
Crustacea	1.1	0.2	0.2	0.3	0.7	0.3	0.6	0.3	0.3	1.2	1.3	0.2
Bivalvia	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oligochaeta	9.4	40.6	62.4	37.1	54.5	12.9	5.2	27.4	27.4	10.0	10.0	1.4
Gastropoda	0.0	0.1	0.0	0.0	0.0	0.0	0.0	32.6	0.0	0.0	0.0	0.0
Nemertinea	0.0	0.0	0.1	0.0	0.0	0.4	0.1	0.0	0.6	0.0	0.0	0.1
Sipunculodea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anthozoa	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Osteichthyrs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arachnida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2004	Lemon	Great Kills	Mill	Richmond	Main	Neck	Lemon	Great Kills	Mill	Richmond	Main	Neck
Polychaeta	66.4	88.5	57.7	60.1	71.7	67.4	62.3	45.2	25.9	91.3	92.0	94.4
Insecta	0.5	0.0	0.1	0.1	0.2	0.1	0.2	0.0	0.0	0.0	0.1	0.0
Crustacea	4.4	0.4	0.6	2.0	3.1	1.1	1.5	0.3	0.4	4.8	6.1	1.9
Bivalvia	3.5	0.9	1.6	0.0	0.0	0.1	22.2	1.4	2.2	0.0	0.0	0.3
Oligochaeta	25.1	9.9	39.6	37.8	25.0	30.3	0.9	0.9	2.9	3.8	1.8	3.0
Gastropoda	0.1	0.3	0.5	0.0	0.0	0.0	12.8	52.2	68.6	0.0	0.0	0.0
Nemertinea	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.3
Sipunculodea	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1
Anthozoa	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1
Osteichthyrs	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arachnida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

†Note that samples from Richmond Creek were not available in 2000.

Appendix 2-B. Results of analysis of similarity percentages (SIMPER) on contributions by the major benthic macroinvertebrate species to total dissimilarity in pairwise comparisons of benthic macroinvertebrate abundance and biomass between the study sites. AvDiss = average dissimilarity between sites for each contributing dietary category, Diss/SD = ratio of average dissimilarity divided by standard deviation, Contrib% = contribution (%) to total average dissimilarity by each dietary category, and Cum% = cumulative contribution (%) to total average dissimilarity.

	Abundance					**Biomass**				
Study sites	Species	Ave Diss	Diss /SD	Contrib%	Cumulat%	Species	Ave Diss	Diss /SD	Contrib%	Cumulat%
Great Kills - Lemon	Average dissimilarity = **37.02**					Average dissimilarity = **51.48**				
	Hobsonia florida	6.02	2.81	16.26	16.26	*Ilyanassa trivittata*	9.53	1.01	18.52	18.52
	Nereis acuminata	4.53	1.4	12.24	28.5	*Streblospio benedicti*	8.27	2.74	16.06	34.58
	Streblospio benedicti	3.69	2.28	9.96	38.46	*Hobsonia florida*	5.99	1.45	11.63	46.21
Great Kills - Main	Average dissimilarity = **73.25**					Average dissimilarity = **90.02**				
	Streblospio benedicti	10.81	3.75	14.76	14.76	*Nereis acuminata*	17.86	1.87	19.84	19.84
	Hobsonia florida	10.4	8.46	14.21	28.97	*Hobsonia florida*	13.42	4.72	14.9	34.74
	Nereis acuminata	9.59	2.76	13.1	42.07	*Streblospio benedicti*	11.31	3.33	12.57	47.31
Lemon - Main	Average dissimilarity = **47.52**					Average dissimilarity = **65.24**				
	Streblospio benedicti	7.48	2.2	15.73	15.73	*Nereis acuminata*	13.53	1.48	20.73	20.73
	Eteone lactea	5.66	2.28	11.92	27.65	*Hobsonia florida*	9.36	2.43	14.35	35.08
	Capitellidae	5.06	2.1	10.66	38.31	*Streblospio benedicti*	7.37	1.23	11.3	46.38
Great Kills - Neck	Average dissimilarity =**55.18**					Average dissimilarity = **79.51**				
	Nereis acuminata	8.33	5.62	15.1	15.1	*Nereis acuminata*	13.44	3.43	16.91	16.91
	Hobsonia florida	7.57	2.45	13.73	28.82	*Hobsonia florida*	11.12	1.84	13.99	30.9
	Eteone lactea	4.73	1.87	8.58	37.4	*Ilyanassa trivittata*	11.05	1.13	13.89	44.79
Lemon - Neck	Average dissimilarity = **36.56**					Average dissimilarity = **55.8**				
	Hobsonia florida	4.26	1.72	11.64	11.64	*Nereis acuminata*	10.95	2.15	19.62	19.62
	Capitellidae	3.51	1.65	9.61	21.26	*Hobsonia florida*	8.44	2.12	15.13	34.74
	Eteone lactea	3.41	1.37	9.32	30.58	*Nereis succinea*	7.86	1.99	14.08	48.82
Main - Neck	Average dissimilarity = **33.78**					Average dissimilarity = **45.65**				
	Streblospio benedicti	6.88	1.89	20.36	20.36	*Hobsonia florida*	9.82	1.45	21.5	21.5
	Hobsonia florida	3.4	0.92	10.08	30.44	*Nereis acuminata*	8.79	1.35	19.26	40.76
	Oligochaeta	3.16	1.31	9.35	39.79	Oligochaeta	7.26	0.77	15.91	56.67
Great Kills - Mill	Average dissimilarity = **36.51**					Average dissimilarity = **52.34**				
	Nereis acuminata	5.53	5.68	15.15	15.15	*Nereis acuminata*	8.41	2.14	16.06	16.06
	Capitellidae	3.53	2.17	9.67	24.82	*Streblospio benedicti*	7.76	1.46	14.83	30.89
	Prionospio sp.	3.4	2.12	9.3	34.13	*Nereis succinea*	6.07	2.9	11.6	42.49
Lemon - Mill	Average dissimilarity = **35.68**					Average dissimilarity = **54.8**				
	Hobsonia florida	5.8	2.2	16.27	16.27	*Nereis acuminata*	8.49	1.36	15.5	15.5
	Nereis acuminata	3.24	1.39	9.09	25.35	*Ilyanassa trivittata*	8.23	0.73	15.01	30.51
	Streblospio benedicti	2.77	2.09	7.75	33.1	*Hobsonia florida*	7.17	1.41	13.09	43.6

Appendix 2-B.
(Continued)

Main - Mill	Average dissimilarity = **51.98**					Average dissimilarity = **68.45**				
	Hobsonia florida	9.54	3.29	18.34	18.34	*Hobsonia florida*	13.71	3.3	20.03	20.03
	Streblospio benedicti	8.46	1.98	16.28	34.62	*Nereis acuminata*	12.65	1.91	18.47	38.5
	Eteone lactea	6.06	1.78	11.66	46.28	*Ilyanassa trivittata*	8.31	0.82	12.15	50.65
Neck - Mill	Average dissimilarity = **34.48**					Average dissimilarity = **53.32**				
	Hobsonia florida	6.85	1.94	19.87	19.87	*Hobsonia florida*	12.42	1.66	23.28	23.28
	Nereis acuminata	3.13	1.84	9.08	28.95	*Ilyanassa trivittata*	9.53	0.82	17.86	41.15
	Eteone lactea	2.93	1.23	8.49	37.44	*Nereis acuminata*	6.03	1.94	11.31	52.45
Great Kills - Richmond	Average dissimilarity = **69.73**					Average dissimilarity = **84.73**				
	Nereis acuminata	11.44	6.41	16.4	16.4	*Nereis acuminata*	22.72	3.88	26.81	26.81
	Hobsonia florida	10.3	12.82	14.78	31.18	*Ilyanassa trivittata*	14.69	2.28	17.34	44.15
	Streblospio benedicti	9.93	2.31	14.24	45.42	*Hobsonia florida*	12.08	2.65	14.26	58.41
Lemon - Richmond	Average dissimilarity = **45.9**					Average dissimilarity = **59.51**				
	Capitellidae	5.14	1.63	11.2	11.2	*Nereis acuminata*	14.59	1.53	24.52	24.52
	Eteone lactea	4.6	2.59	10.02	21.23	*Hobsonia florida*	7.67	2.67	12.88	37.4
	Streblospio benedicti	4.19	1.36	9.14	30.37	*Nereis succinea*	6.24	2.08	10.48	47.89
Main - Richmond	Average dissimilarity = **27.91**					Average dissimilarity = **31.39**				
	Streblospio benedicti	4.86	0.88	17.41	17.41	*Hobsonia florida*	8.24	1.37	26.24	26.24
	Prionospio sp.	3.39	1.23	12.16	29.57	*Nereis acuminata*	6.15	1.57	19.6	45.84
	Oligochaeta	3.37	1.51	12.06	41.64	Oligochaeta	4.14	1.45	13.18	59.02
Neck - Richmond	Average dissimilarity = **34.48**					Average dissimilarity = **37.28**				
	Streblospio benedicti	4.67	2.03	13.53	13.53	*Nereis acuminata*	11.17	3.05	29.97	29.97
	Eteone lactea	2.77	1.32	8.04	21.57	*Cyathura polita*	4.15	1.9	11.12	41.09
	Prionospio sp.	2.75	1.22	7.99	29.56	Oligochaeta	4.03	1.4	10.8	51.89
Mill - Richmond	Average dissimilarity = **55.19**					Average dissimilarity = **69.85**				
	Hobsonia florida	9.09	4.09	16.48	16.48	*Nereis acuminata*	15.77	5.53	22.58	22.58
	Streblospio benedicti	6.94	1.8	12.57	29.05	*Hobsonia florida*	13.42	2.27	19.21	41.79
	Eteone lactea	6.03	3.4	10.93	39.97	*Ilyanassa trivittata*	11.98	1.12	17.16	58.95

Appendix 2-C. Results of analysis of similarity percentages (SIMPER) on contributions by the major benthic macroinvertebrate species to total dissimilarity in pairwise comparisons of benthic macroinvertebrate abundance and biomass between the sampling years. AvDiss = average dissimilarity between sites for each contributing dietary category, Diss/SD = ratio of average dissimilarity divided by standard deviation, Contrib% = contribution (%) to total average dissimilarity by each dietary category, and Cum% = cumulative contribution (%) to total average dissimilarity.

	Abundance					**Biomass**				
Sampling year	Species	Av.Diss	Diss/SD	Contrib%	Cum.%	Species	Av.Diss	Diss/SD	Contrib%	Cum.%
2000 vs. 2001	Average dissimilarity = **30.35**					Average dissimilarity = **47.77**				
	Oligochaeta	3.5	1.14	11.54	11.54	*Nereis acuminata*	8.42	1.39	17.63	17.63
	Hobsonia florida	3.5	1.16	11.53	23.07	Oligochaeta	8.19	0.87	17.14	34.77
	Streblospio benedicti	2.98	0.94	9.82	32.89	*Hobsonia florida*	8.09	1.13	16.94	51.7
	Nereis acuminata	2.97	1.3	9.77	42.66	*Streblospio benedicti*	4.95	1.32	10.36	62.06
	Eteone lactea	2.72	1.01	8.96	51.62	Capitellidae	3.7	1.05	7.74	69.8
2001 vs. 2004	Average dissimilarity = **33.18**					Average dissimilarity = **55.44**				
	Streblospio benedicti	3.8	1.13	11.46	11.46	*Nereis acuminata*	14.51	1.24	26.18	26.18
	Capitellidae	2.85	1.44	8.58	20.04	*Ilyanassa trivittata*	7.44	0.58	13.43	39.6
	Hobsonia florida	2.57	1.15	7.74	27.78	*Hobsonia florida*	5.83	1	10.52	50.12
	Prionospio sp.	2.49	1.1	7.51	35.29	*Streblospio benedicti*	4.12	1.3	7.44	57.56
	Cyathura polita	2.39	0.92	7.22	42.51	*Nereis succinea*	4.1	1.02	7.4	64.96

CHAPTER 3

Altered feeding habits and strategies of mummichogs (*Fundulus heteroclitus*) in urban tidal salt marshes in New York

CHAPTER SUMMARY

Mummichogs (*Fundulus heteroclitus*) are an abundant forage fish and an important trophic link in urban tidal creeks and salt marshes in the northwest Atlantic coast. In this study, responses in feeding habits of mummichogs to altered potential prey resources (benthic macroinvertebrates) were examined in highly urbanized tidal salt marshes in the Arthur Kill (New York, USA). Most of the Arthur Kill populations of mummichogs had nearly 2 to 3 times less food in their gut than the reference population. Decapods (mainly *Palaemonetes spp.*) were generally the predominant prey, and the amount and body size of ingested *Palaemonetes spp*. by mummichogs increased with mummichog total length at all sites. The length-specific maximum sizes of *Palaemonetes spp.* ingested by some of the Arthur Kill populations were, however, nearly half the sizes of shrimp ingested by the reference population. Furthermore, these Arthur Kill populations ingested polychaetes (e.g., *Nereis spp.*) more frequently than the reference population, and these polychaetes contributed up to more than 40% (by weight) to the total gut contents. Gastropods, arachnids, and insects were found only in the reference population. Multivariate analyses indicated that the feeding habits of the Arthur Kill populations of mummichogs were significantly different from that of the reference population, mainly due to substantial differences (by weight) in gastropods, insects, and polychaetes. The Costello graphical method indicated that mummichogs generally use a feeding strategy of generalists with a broad population- and individual- level diet niche breadth. This pattern, however, appeared to break down in some of the Arthur Kills populations. The partial decoupling of trophic links between mummichogs and benthic macroinvertebrates, particularly

decapods (*Palaemonetes spp.*), observed at these Arthur Kill sites may contribute to disruptions in ecosystem functioning in these severely urbanized tidal salt marshes.

INTRODUCTION

Urban coastal habitats are often highly degraded due to a variety of human activities (e.g., accidental chemical discharges and dredging) (Boesch, 1982; Able *et al.*, 1998; Levin *et al.*, 2001). Coastal habitat degradation can alter food web structures and ecosystem functions including biogeochemical cycling of materials from terrestrial, freshwater, and marine environments (Boesch, 1982; Levin *et al.*, 2001). Among anthropogenic stressors, elevated levels of chemical pollutants can have particularly persistent effects on aquatic organisms (Boesch *et al.*, 2001). As the majority of these anthropogenically introduced chemicals are bound to bottom sediments, benthic organisms (e.g., sediment-dwelling invertebrates) are especially vulnerable (Clements and Newman, 2002). Furthermore, these benthic organisms can exhibit species-specific differential tolerance to a variety of chemical pollutants, ultimately altering the community structures and functions of benthic habitats (Weis *et al.*, 1999; Clements and Newman, 2002).

Anthropogenic stressors such as chemical pollutants can alter foraging behaviors (e.g., prey capture and predator avoidance) of fish (Smith and Weis, 1997; Zhou and Weis, 1998; Clements and Newman, 2002). Due to logistical difficulties, however, it is often difficult to elucidate how altered foraging behaviors affect the feeding habits of wild populations of fish (Jeffree and Williams, 1980; Weis *et al.*, 2001; Clements and Newman, 2002). As both predator and prey are exposed to anthropogenic stressors in urban habitats, species-specific differential sensitivities to these stressors can result in a variety of altered (often unpredictable) predator-prey relationships (Jeffree and Williams, 1980; Livingston, 1984; Steimle *et al.*, 1993; Weis *et al.*, 1999; McCann *et al.*, 2005).

Anthropogenic stressors in urban coastal environments can also indirectly affect community structures and functions in benthic habitats, and these indirect effects are often mediated through trophic relationships (Jeffree and Williams, 1980; Boesch, 1982; Clements and Livingston, 1983; Eby *et al.*, 2005). Deposit-feeding invertebrates, a common trophic group in marine benthic habitats, are an important prey resource for benthivorous fishes, shellfishes, and wading birds in coastal habitats, and anthropogenic impacts on these invertebrates can potentially have cascading effects at the community level (Pinnegar *et al.*, 2000). Due to their intimate association with cycling of materials and energy in ecosystems, altered trophic interactions among benthic organisms can have further implications to ecosystem functioning in coastal marine habitats (Clements and Newman, 2002; de Ruiter *et al.*, 2005; Woodward *et al.*, 2005). Direct impacts of habitat degradation on marine benthic macroinfaunal assemblages have been extensively investigated (Boesch, 1982). However, there have been relatively few attempts to examine indirect effects of pollution, including the feeding habits of benthivorous predators in marine and estuarine ecosystems (e.g., Steimle *et al.*, 1993; Carlson *et al.*, 1997; Hinz *et al.*, 2005; Powers *et al.*, 2005). As a result, there is little mechanistic understanding of pollution-induced alterations in trophic structure and ecosystem function (Clements and Livingston, 1983; Livingston, 1984; Rose, 2000).

In certain cases, alterations in interspecific interactions (e.g., reduced competition and predation) in degraded habitats may benefit pollution-tolerant species (Boesch, 1982; Steimle *et al.*, 1993; Weis *et al.*, 1999). For example, pollution-tolerant benthic invertebrates (e.g., opportunistic deposit-feeding annelids) often dramatically increase in abundance at the initial stage of recolonization following anthropogenic disturbances,

which may in turn provide an increased prey resource to their predators (Jeffree and Williams, 1980; Boesch, 1982; Carlson *et al.*, 1997; Powers *et al.*, 2005). The benefit of an enhanced prey resource, however, often depends on the "preferred" prey type of predators (Steimle *et al.*, 1993; Steimle, 1994). Some potential benthic prey species (e.g., subsurface deposit-feeding invertebrates) are not easily accessible to all predators (Steimle *et al.*, 1993; Steimle, 1994; Carlson *et al.*, 1997). An increased abundance of these prey species may thus not necessarily benefit all benthivorous predators (Steimle *et al.*, 1993; Carlson *et al.*, 1997).

Altered prey resources may also induce functional responses in predators such as food consumption and growth rates, potentially influencing trophically mediated ecosystem functions (e.g., energy flow and nutrient cycling) (Chapter 5; Livingston, 1984; Pihl, 1994; Peterson *et al.*, 2000; Rose, 2000; Eby *et al.*, 2005). Functional responses of predators with flexible foraging habits may, however, not necessarily be affected by alterations in prey availability (e.g., reduced abundances of sensitive species) (Jeffree and Williams, 1980; Steimle, 1994; Clements and Rees, 1997). Omnivory is commonly observed in aquatic predators (Gerking, 1994; Clements and Newman, 2002), and considered as an adaptive strategy (trophic adaptability) to gain sufficient energy in order to maintain growth in response to fluctuations in prey availability (Jeffree and Williams, 1980; Gerking, 1994; Elser and Hessen, 2005; Woodward *et al.*, 2005). Due to their trophic plasticity, omnivorous predators generally possess weak trophic links with their potential prey species, which may contribute to overall trophic stability (e.g., maintaining coexistence of competing prey species) (Kondoh, 2005). Moreover, flexible foraging by omnivores can also maintain coupling of spatially semi-compartmentalized

trophic components within heterogeneous habitats (McCann *et al.*, 2005) such as tidal salt marshes.

Tidal salt marshes are among the most productive environments (Kneib, 2000; Levin *et al.*, 2001), supporting adjacent coastal ecosystems (Nixon and Oviatt, 1973; Deegan *et al.*, 2000; Mitsch and Gosselink, 2000). The exportation of marsh production is likely to be mediated through trophic interactions in coastal habitats (Kneib and Wagner, 1994; Kneib, 1997; 2000). Kneib (1997) has hypothesized that the spatial movement of marsh production toward open coastal habitats is intimately associated with the trophic interactions between resident and migrant nekton ("trophic relay") in salt marshes (Kneib, 1997; 2000). Many adult resident and juvenile migrant nekton temporarily share a common habitat within tidal salt marshes (i.e., "intertidal-subtidal corridors") (Kneib and Wagner, 1994; Kneib, 2000; Levin *et al.*, 2001). As a result, marsh production incorporated by resident benthivorous nekton through the ingestion of benthic invertebrates is likely to be transported to open coastal habitats by migrant piscivorous nekton feeding on resident nekton, along with ontogenetic migration by migrant benthivorous nekton (Deegan, 1993; Kneib, 1997; Deegan *et al.*, 2000; Kneib, 2000). Altered trophic interactions within urban tidal salt marshes induced by habitat degradation could, therefore, disrupt secondary production transport in coastal habitats.

Mummichogs, *Fundulus heteroclitus* (Pisces: Cyprinodontidae), are among the most abundant and productive fishes in tidal creeks and salt marshes in the northwest Atlantic coast (Nixon and Oviatt, 1973; Valiela *et al.*, 1977; Meredith and Lotrich, 1979). Mummichogs play an essential role in salt marsh food webs as an intermediate predator linking benthic invertebrates, and piscivorous fishes and wading birds (Valiela *et al.*,

1977; Kneib, 1986; Kneib and Wagner, 1994). Within salt marshes, mummichogs exhibit a distinct ontogenetic shift in habitat use from vegetated intertidal pools and creeks during larval and juvenile stages to primarily subtidal creeks as an adult (Kneib and Wagner, 1994; Kneib, 1997; Teo and Able, 2003). Subtidal food resources may, however, not be sufficient or easily accessible to adult mummichogs (Weisberg *et al.*, 1981; Weisberg and Lotrich, 1982). In foraging for sufficient prey resources, adult mummichogs thus regularly migrate from subtidal marshes to intertidal marsh surface following tidal cycles (Kneib and Wagner, 1994; Kneib, 1997; Teo and Able, 2003).

Because of their ontogenetic tidal migration and strong site fidelity within salt marshes (Lotrich, 1975; Teo and Able, 2003; McMahon *et al.*, 2005; Skinner *et al.*, 2005; Able *et al.*, 2006), mummichogs are also considered as a key species in transporting secondary production of salt marsh ecosystems in the northwest Atlantic coast (Valiela *et al.*, 1977; Kneib *et al.*, 1980; Kneib and Wagner, 1994). A subtidal component of these salt marshes are frequently used as a feeding ground by juvenile and adult migrant fish and shellfish species such as blue crab (*Callinectus sapidus*), white perch (*Morone americana*), striped bass (*Morone saxatilis*), and bluefish (*Pomatomus saltatrix*), which are potential predators as well as competitors of mummichogs (Kneib, 1982a; Peters and Schaaf, 1991; Nemerson and Able, 2003; Weis, 2005; Dittel *et al.*, 2006). As a result, these migrant fishes and shellfishes are likely to transport marsh production incorporated by mummichogs to open coastal ecosystems (Valiela *et al.*, 1977; Kneib *et al.*, 1980; Kneib, 1997; 2000). Through these trophic interrelationships, tidal migration of mummichogs from intertidal marsh surface to subtidal creeks may also couple spatially semi-compartmentalized trophic components (i.e., benthic invertebrates in intertidal

marshes and migrant piscivores in subtidal creeks and open bays) (Valiela *et al.*, 1977; Weisberg *et al.*, 1981; Kneib, 1997). This cyprinodontid fish thus plays a critical role in integrating and transporting a substantial portion of marsh productions to adjacent coastal ecosystems (Valiela *et al.*, 1977; Kneib and Wagner, 1994; Kneib, 1997; Smith *et al.*, 2000).

Their relatively high tolerance to a variety of natural and anthropogenic stressors often allows mummichogs to thrive even at highly polluted coastal habitats (Weis *et al.*, 1999; Weis, 2002; Wirgin and Waldman, 2004; Schulte, 2007). Mummichogs are frequently used in the assessment of structural and functional recovery of restored salt marshes (e.g., Moy and Levin, 1991; Allen *et al.*, 1994; James-Pirri *et al.*, 2001; Steimle, 2001). As mummichogs are also an important trophic link in urban coastal habitats, alterations in their prey resources (e.g., local elimination of benthic invertebrate species) may disrupt the trophic coupling in urban tidal salt marshes (Kneib, 2003). This decoupling of salt marsh food chains may have important implications for ecosystem functioning (e.g., local biogeochemical cycling of materials) (Clements and Newman, 2002; McCann *et al.*, 2005; Woodward *et al.*, 2005; Able and Duffy-Anderson, 2006). Understanding the effects of habitat degradation on the trophic ecology of mummichogs is, therefore, highly relevant to the structural and functional assessment of salt marsh restoration (Moy and Levin, 1991; Steimle, 2001).

In the present study, the impacts of habitat degradation on benthic trophic structures were investigated by examining the feeding habits and strategies of mummichogs in urban tidal salt marshes in the Arthur Kill (New York, USA). Due to its proximity to highly industrialized region, the Arthur Kill is one of the most severely

polluted areas in the New York/New Jersey (NY/NJ) Harbor Estuary system (Wakeman and Themelis, 2001; Steinberg *et al.*, 2004). Chemical pollution is among the most widespread environmental problems in the NY/NJ Harbor Estuary (Bonnevie *et al.*, 1994; Packer, 2001; Weis *et al.*, 2001; Adams and Benyi, 2003). Despite its degraded conditions, the NY/NJ Harbor Estuary is an essential habitat for resident and migrant aquatic and terrestrial species (Able *et al.*, 1998; Steinberg *et al.*, 2004). Due to potential toxicity and transference up food chains, chemical pollution is a major concern in this coastal ecosystem (Packer, 2001; Steinberg *et al.*, 2004; Bain *et al.*, 2007).

MATERIALS AND METHODS

Field Sampling

Sampling sites chosen for this study were four tributaries of the Arthur Kill; Richmond Creek, Main Creek, Neck Creek, and Mill Creek, and one regional reference site (near Raritan Bay) external to the Arthur Kill; Lemon Creek (see Chapter 1 for site description). Sampling of mummichogs (*Fundulus heteroclitus*) was conducted in an intertidal area of each site during daytime in the summer (July to September) of 2004. Mummichogs were collected using a 3.05 x 1.22 m-seine net with 6 mm-polyester mesh or unbaited cylindrical minnow trap with 6 mm-mesh. To maximize sampling efficiency and minimize the digestion of gut contents, fish were collected within approximately 90 minutes after daytime high tides, which is the peak of mummichogs' daily foraging activity (Weisberg *et al.*, 1981; Allen *et al.*, 1994). When using minnow traps, fish were removed every 15 to 30 minutes to minimize the digestion of gut contents (Beauchamp *et*

al., 2007). Fish samples were immediately placed on ice upon capture, and then later fixed with 10% formalin in the field (Weisberg *et al.*, 1981; Bowen, 1996).

Laboratory Sample Processing

In the laboratory, fish samples were preserved in formalin for at least 1 week, and rinsed with tap water to eliminate excess formalin (Bowen, 1996). Each fish was sexed, measured (total length ± 0.01 mm), and weighed (wet weight ± 0.01 g). Then, the entire intestinal tract was excised and preserved individually in 70% ethanol (Bowen, 1996). Only the contents of the anterior 2/3 of intestines (equivalent to 'stomach') (Babkin and Bowie, 1928) were removed from the intestine, blotted dry, and placed on a pre-weighed Petri dish to weigh. All prey items were identified to the lowest practical taxonomic level under a dissecting microscope, using available species keys in literature (Fauchald, 1977; Weiss, 1995; Merritt and Cummins, 1996; Pollock, 1998). The diet composition was quantified by frequency of occurrence, count, and weight of each prey item (Bowen, 1996). To estimate the % contribution by weight for small prey (e.g., meiofauna) and particulate matter (e.g., detritus) items, a modified version of the method by Penczak (1985a) was used. Briefly, once identified, each diet item was separately squashed to a uniform depth (assuming 1 mm^3 = 1 mg wet weight) between glass slides (Penczak, 1985a). Then, to increase accuracy, the area of each diet item was captured with a digital camera through a dissecting microscope (Bowen, 1996) and measured (± 0.001 mm^2) using a digital imaging software (Motic Images Plus 2.0 ML). The total reconstructed weight estimates of diet items were then compared with the actual wet weight of gut contents to ensure the accuracy of the method (Bowen, 1996).

Dietary Data Analyses: Univariate Analyses

Overall site-specific characteristics of the diet composition of mummichogs were examined using the following univariate measures; gut fullness index (= 100 x wet weight of gut contents/wet weight of fish) (Weisberg *et al.*, 1981; Allen *et al.*, 1994; Fell *et al.*, 1998), prey species richness [Margalef's index, $d = (S - 1)/\log_e N$; S = the total number of prey species, N = the total number of individuals] (Clifford and Stephenson, 1975), niche breadth [Shannon-Wiener diversity index, $H' = -\Sigma\, p_i \cdot \log_e(p_i)$ (Shannon and Weaver, 1949) and normalized Levins index, $B_A = (1/\Sigma\, p_i^2 - 1)/(S - 1)$ (Levins, 1968); p_i = the proportion of the abundance of the i th prey species, as suggested by Marshall and Elliott (1997)], and prey species evenness [Heip's evenness = $(e^{H'} - 1)/(S - 1)$] (Heip, 1974). The representativeness of diet composition derived from the samples collected was evaluated using a species-accumulation curve, which was based on a cumulative number of species in the samples taken in a random order with 9999 permutations (Clarke and Gorley, 2006). The sample size was considered adequate if the species-accumulation curves reached an asymptote.

The site-specific relative importance of each prey item (i) was evaluated by 2 approaches; the index of relative importance (IRI_i) (Bowen, 1996) and the modified Costello's graphical method (Amundsen *et al.*, 1996). The IRI_i is based on percentage contributions by frequency of occurrence ($\%FO_i$), count ($\%N_i$), and weight ($\%W_i$) [$IRI_i = \%FO_i$ x ($\%N_i + \%W_i$)] (Bowen, 1996; Cortés, 1997; Beauchamp *et al.*, 2007; Chipps and Garvey, 2007), which was then adjusted to percentage for each prey item ($\%IRI_i = 100$ x $IRI_i / \sum IRI_i$), as suggested by Cortés (1997).

In the modified version of the Costello's graphical method proposed by Amundsen *et al.* (1996), a measure of prey importance is described as a function of prey-specific percentage contribution and frequency of occurrence (Amundsen *et al.*, 1996). The *i* th prey-specific percentage contribution (%P_i, in this study, by weight) is calculated as following;

(1) $$\%P_i = 100 \text{ x } (\sum G_i / \sum G_{Ti})$$

where G_i is defined as the gut content (g) comprised by the *i* th prey; and

G_{Ti} is defined as the total gut content (g) of only the individuals containing the *i* th prey item.

Then, %P_i was plotted against %FO_i. In the graphical form (Fig. 3-1), this plot of %P_i vs. %FO_i allows an interpretation of feeding strategy (the vertical axis) and inter- and intra-individual components of diet niche width (the diagonal axis from the upper left to the lower right), in addition to prey importance (the diagonal axis from the lower left to the upper right) (Amundsen *et al.*, 1996). In interpreting feeding strategy, prey items at the lower half indicate generalization and those at the upper half indicate specialization, which is divided further into 2 types of specialization; prey items at the upper right indicate specialization at the population level (i.e., a population with a narrow niche width), while those at the upper left indicate specialization at the individual level (i.e., a population with a broad niche width) (Amundsen *et al.*, 1996). Additionally, prey items at the upper left and those at the lower right both indicate a broad population-level niche

width, while at the individual level, each individual fish in these 2 categories of feeding strategy contribute differently to the overall population-level niche width (high variation in diet niche width among individuals at the upper left, but low at the lower right) (Amundsen *et al.*, 1996). In this study, the diet data were pooled into 15 diet categories, according to their taxonomic relationships (mostly > the class level) for the modified Costello plots.

The univariate measures were transformed using a logarithmic transformation, where necessary. The normality of data was tested using Shapiro-Wilk's *W* test. The homogeneity of variance was tested using Levene's test. The statistical significance of differences in the univariate measures among study sites was tested using 1-way analysis of variance (ANOVA), which, if significant, was followed by Tukey's honestly significant difference (HSD) test. All univariate statistical analyses were performed using Statistica 7.1 (Statsoft, Inc®, USA).

Dietary Data Analyses: Multivariate Analyses

Relative similarities in count, weight, frequency of occurrence, and relative importance (*IRI*) of dietary items of mummichogs among sites were graphically analyzed using non-metric multidimensional scaling (nMDS) with Bray-Curtis similarity index on square root-transformed data (Clarke, 1993; Clarke and Gorley, 2006). In the nMDS plots, to increase its visual interpretability, prey items were grouped into higher taxonomic categories (> class), and site-specific average values for each length class (10 mm total length intervals) were used (Platell *et al.*, 1998a; Platell *et al.*, 1998b; Schafer *et al.*, 2002). The reliability of nMDS representation of diet similarity among sites was

assessed with its stress value; stress < 0.2 was considered to be acceptable (Clarke and Warwick, 2001). To ensure the accuracy of nMDS plots (i.e., convergence to a global minimum), each nMDS was rerun multiple times (the restarting number = 50).

The statistical significance of differences in count and weight of dietary composition among sites and length classes was tested using 2-way crossed analysis of similarity (ANOSIM) with randomization permutation (n = 9999) at the significance level of 5%, which, if significant, was followed by pairwise comparisons (Clarke, 1993; Clarke and Gorley, 2006). Two-way crossed analysis of similarity percentages (SIMPER) was then used to identify dominant diet categories contributing to dissimilarity among sites and length classes (Clarke, 1993; Clarke and Warwick, 1994; Platell *et al.*, 1998a). In ANOSIM and SIMPER, the diet data for length classes, 60+ mm, 70+ mm, and 80+ mm were used, as only these length classes were reasonably represented at all sites. All analyses of nMDS, ANOSIM, and SIMPER were performed using PRIMER v6.1.9 (PRIMER-E Ltd, Plymouth, UK).

RESULTS

Univariate Comparisons of Diet Characteristics

Only a small fraction of the fish gut samples examined in this study had an empty gut at all sites; 0% at Lemon Creek (n = 44) and Mill Creek (n = 44), 1.6% at Richmond Creek (n = 62), 5.6% at Main Creek (n = 73), and 5.9% at Neck Creek (n = 68). Species accumulation curves showed that the number of prey species in the gut had reached an asymptote at all sites (Appendix 3-A1 through 3-A5), indicating the adequacy of sample size for the diet analysis.

There were significant differences in average gut fullness among sites ($F_{4, 282}$ = 37.04, $p < 0.001$), in which fish from Lemon Creek and Mill Creek had nearly 2 times more food (~90 mg·fish g^{-1}) than those from Richmond Creek (~50 mg·fish g^{-1}), and 3 times more than those from Main Creek and Neck Creek (~30 mg·fish g^{-1}) (Tukey HSD test, Fig. 3-2a). Although there were significant differences in prey species richness among sites ($F_{4, 249}$ = 2.59, $p < 0.05$), the magnitude of the differences were small (Fig. 3-2b). Only fish from Main Creek and Neck Creek had significantly lower prey species richness than those from Lemon Creek (Tukey HSD test, Fig. 3-2b). A similar trend was also observed for diet niche breadth based on Shannon-Wiener index ($F_{4, 251}$ = 4.19, $p <$ 0.01), in which fish from Main Creek had a significantly lower niche breadth than those from Lemon Creek (Tukey HSD test, Fig. 3-2c). Levins index was, however, lowest at Lemon Creek (0.17), which was followed by Mill Creek (0.20) < Neck Creek (0.27) < Main Creek (0.32) < Richmond Creek (0.35). No significant difference was observed in prey species evenness among sites ($F_{4, 251}$ = 1.54, p = 0.192, Fig. 3-2d).

In general, decapods (mainly *Palaemonetes spp.*) were the predominant (in %*FO*, %*W*, and %*IRI*) prey category observed at all sites, though there was some ontogenetic variation, especially at the Arthur kill sites (Fig. 3-3, 3-4, and 3-5, and Table 3-1). The importance of decapods (i.e., %*IRI*) increased with the increasing total length of fish at all sites (Fig. 3-5a through 3-5e). A moderate amount (%*W* = 10.7% to 34.9%) of detritus was also frequently (%*FO* = 30.0% to 100%) found in the gut of mummichogs at all sites (Fig. 3-4 and Table 3-1). At the Arthur Kill sites (except for Mill Creek), another dominant prey group was polychaetes (mostly *Nereis spp.*), which were frequently observed (%*FO* = 30.0% to 81.8%) and contributed up to more than 40% by weight to

the total gut contents (Table 3-1 and Fig. 3-4). Gastropods (mostly *Melampus bidentatus*), arachnids (mostly trombidiidae and ixodides), and insects (mostly diptera larvae) were frequently observed only in fish from Lemon Creek (especially larger fish, >70+ mm TL) (%*FO* = 18.2% to 66.7% for gastropods, 16.7% to 61.5% for arachnids, and 33.3% to 61.3% for insects) (Table 3-1). Nematodes, though their contribution to the total gut content weight was negligible (< 1.0%), were also frequently observed in the guts of fish from all sites (%*FO* = 5.6% to 50.0%, Table 3-1). Cirripedes (*Balanus spp.*) were frequently observed in the guts of fish from Mill Creek, Richmond Creek, and Main Creek (%*FO* =9.1% to 50.0%, Table 3-1). Oligochaetes, bivalves, and teleosts were rarely found in the gut of mummichogs at these 3 sites.

The graphical representation of diet composition with the modified Costello plots showed that the ranking of prey importance (i.e., from the lower left to the upper right) mostly corresponded to the results of %*IRI*. In these plots, decapods were the most important prey item at all site, followed by gastropods and teleosts at Lemon Creek, algae at Mill Creek, polychaetes at Richmond Creek and Neck Creek, and algae, gastropods, and polychaetes at Main Creek (Fig. 3-6a through 3-6e). Note that in these plots, the prey items that were low in frequency of occurrence but high in prey-specific % contribution (i.e., teleosts at Lemon Creek, and algae and gastropods at Main Creek) ranked high in prey importance (Fig. 3-6a through 3-6e). Rare prey items (i.e., both %*P* and %*FO* < ~10%) aggregated at the lower left corner of the plot.

In general, the modified Costello plots showed that mummichogs use a generalized feeding strategy (i.e., lower half of the plots), with an indication of population-level specialization (i.e., high in both %*P* and %*FO*) on decapods at all sites (Fig. 3-6a through

3-6e). Furthermore, there were also some indications of individual-level specialization (i.e., high in %*P* and low in %*FO*) on teleosts at Lemon Creek, and algae and gastropods at Main Creek (Fig. 3-6a and 3-6d). These specialized feeding patterns by a few individuals resulted in high inter-individual variations in their contributions to diet niche breadth (i.e., the upper left) at Lemon Creek and Main Creek (Fig. 3-6a and 3-6d). Overall, however, the plots showed that mummichogs have a generalized feeding strategy with a broad population- and individual- level diet niche breadth (Fig. 3-6a through 3-6e). This pattern seemed to break down slightly at Main Creek, where higher inter-individual variations in diet niche breadth contributions (in gastropods, algae, and decapods) were observed than at the other sites (Fig. 3-6a through 3-6e).

Mummichogs–Palaemonetes spp. Body Size Relationships

The weight of an individual *Palaemonetes spp.* ingested by mummichogs was significantly correlated with the total length of mummichogs from all sites (Lemon Creek: $R^2 = 0.467$, Mill Creek: $R^2 = 0.601$, Richmond Creek: $R^2 = 0.158$, Main Creek: $R^2 = 0.429$, and Neck Creek: $R^2 = 0.096$, $p < 0.05$, Fig. 3-7a through 3-7e). However, there was a substantial difference in the length-specific maximum size of *Palaemonetes spp.* ingested by mummichogs among sites. Specifically, the gut contents of mummichogs from Main Creek and Neck Creek contained mostly small *Palaemonetes spp*. (< ~0.2 g), and only a few individuals larger than 0.4 g (Fig. 3-7d and 3-7e).

Multivariate Comparisons of Diet Compositions

The 2-dimensional nMDS plots derived from the diet data by frequency of occurrence, average weight, average count, and *IRI* showed that data points representing the site-specific diet compositions of mummichogs generally highly interspersed (Fig. 3-8a through 3-8d). The stress levels of all the plots were less than 0.2, indicating reasonable representations of the relative similarity among sites. Compared to the diet compositions of fish from the Arthur Kill, which were highly dispersed in the plots, the data points based on those from Lemon Creek were relatively close to each other and reasonably distinguishable from the Arthur Kill sites (Fig. 3-8a through 3-8d). This interpretation of the nMDS plots was confirmed with 2-way ANOSIM on the diet data by weight and count (Table 3-2). Although the diet compositions were significantly different among sites (p = 0.1% by weight and p = 0.1% by count) as well as length classes (p = 2.9% by weight and p = 3.4% by count), the global R values for the among-site comparisons (R = 0.268 by weight and R = 0.294 by count) were considerably higher than those for the among-length class comparisons (R = 0.044 by weight and R = 0.043 by count) (Table 3-2), which were almost negligible.

The *post-hoc* pairwise comparisons by weight indicated that with the exception of the Mill Creek population (R = 0.244, p = 7.1%), the diet composition of Lemon Creek fish was significantly different from those of the Arthur Kill populations (R = 0.492 to 0.713, p = 0.8% to 1.6%), (Table 3-2). The analyses of 2-way SIMPER revealed that the differences in diet composition among these sites were mainly due to fish from Lemon Creek ingesting substantially more gastropods and less polychaetes (relative % contributions to dissimilarity = 22.3% to 25.3% by gastropods and 11.43% to 18.86% by polychaetes) than those from Richmond Creek, Main Creek, and Neck Creek, as well as

more decapods than those from Main Creek (relative % contributions to dissimilarity = 19.1%) (Appendix 3-B).

The pairwise comparisons by count also showed that the diet composition of fish from Lemon Creek was significantly different from all the Arthur Kill populations (R = 0.300 to 0.781, p = 0.8% to 4.0%) (Table 3-2). A significant difference was also found between Mill Creek and Richmond Creek (R = 0.375, p = 2.9%) (Table 3-2). These differences by count between Lemon Creek and the Arthur Kill sites were due to the ingestion of more insects and gastropods by fish from Lemon Creek than those from Mill Creek, Main Creek, and Neck Creek (relative % contributions to dissimilarity = 14.51% to 17.42% for insects and 11.74% to 16.81% for gastropods), whereas fish from Richmond Creek ingested fewer gastropods and more polychaetes than those from Lemon Creek (relative % contributions to dissimilarity = 16.34% for gastropods and 13.57% for polychaetes) (Appendix 3-B).

DISCUSSION

Chronic habitat degradation has substantially altered biological assemblages of benthic habitats in the Arthur Kill (Chapter 2; Crawford *et al.*, 1994; Wakeman and Themelis, 2001; Steinberg *et al.*, 2004). Benthic macroinfaunal assemblages in most of the Arthur Kill salt marshes still exhibit characteristics frequently observed in chronically degraded coastal habitats, including numerical dominance by a few small-bodied polychaete and oligochaete species (Chapter 2). Although mummichogs have frequently been used to assess structural and functional recovery of restored urban salt marshes (e.g., Moy and Levin, 1991; Allen *et al.*, 1994; James-Pirri *et al.*, 2001; Wozniak *et al.*, 2006),

there are few studies assessing the trophic ecology of mummichogs in chemically polluted habitats (e.g., Smith and Weis, 1997; Steimle, 2001; Weis *et al.*, 2001). The results of the current study indicated that the feeding habits of mummichogs in the Arthur Kill salt marshes were markedly different from that of fish in a salt marsh near Raritan Bay. The average relative gut fullness of mummichogs at the peak of their feeding activity (i.e., daytime ebbing tides) was substantially lower at most of the Arthur Kill sites (especially, Main Creek and Neck Creek) than at the reference site (Lemon Creek). This disparity in gut fullness among sites was partly due to the body size of grass shrimp (*Palaemonetes spp.*) found in the gut of mummichogs. Grass shrimp were one of the most frequently found prey items at both the Arthur Kill and reference sites. The amount of grass shrimp ingested by mummichogs was, however, considerably lower at two of the Arthur Kill sites, Main Creek and Neck Creek, than at the other sites. Furthermore, diet niche breadth based on Shannon-Wiener index and prey species richness of mummichogs were considerably lower at these northern Arthur Kill sites (Main Creek and Neck Creek), where the benthic macroinfaunal communities were also highly impaired (e.g., lower species diversity), than at the other sites (Chapter 2). Diet niche breadth based on Levins index, however, showed a contradictory result to that based on Shannon-Wiener index, most likely due to down-weighting rare prey items in Levins index (Marshall and Elliott, 1997).

Non-metric multidimensional scaling (nMDS) plots and analysis of similarity (ANOSIM) also indicated that the diet composition of mummichogs from the reference site (Lemon Creek) was significantly different from those of the Arthur Kill populations, whereas there were only minor differences among the Arthur Kill populations. As some

polychaete and oligochaete species at the Arthur Kill sites were subsurface deposit-feeders (Chapter 2), which may not be easily accessible to mummichogs, altered abundances of these deposit-feeders may not have had measurable impacts on the diet compositions of mummichogs. Furthermore, high abundances of epibenthic decapods such as *Palaemonetes spp*., which are relatively larger than other potential prey items available in the Arthur Kill, may have ameliorated, to a certain extent, indirect effects of altered prey resources on the diet compositions of mummichogs.

Site-specific relationships between mummichogs and grass shrimp observed in the current study may have been due to altered feeding behaviors induced by chemical pollutants (Smith and Weis, 1997; Weis *et al.*, 2001). The results indicated that only a few individuals in the Main Creek and Neck Creek populations had ingested grass shrimp of sizes similar to those usually found in fish from the other sites. Similarly, Weis *et al.* (2001) have also shown that mummichogs from severely chemically polluted coastal habitats in New York and New Jersey (including the Arthur Kill) ingested a considerably lower proportion of grass shrimp than those from the reference sites. Experimental studies have shown that anthropogenically introduced chemicals (e.g., trace metals) can alter mummichogs' ability to capture epibenthic decapods (Smith and Weis, 1997; Weis *et al.*, 2001). These altered feeding behaviors may ultimately reduce the ingestion of decapods by mummichogs (Smith and Weis, 1997; Weis *et al.*, 2001). In addition to prey availability, altered feeding behaviors may thus also influence the diet compositions of fish in urban coastal habitats.

Mummichogs are a visual (Weisberg *et al.*, 1981) and size-selective predator (Kneib and Stiven, 1978; Kneib *et al.*, 1980; Kneib, 1986), most likely influencing prey

abundance and distribution in tidal salt marshes (Vince *et al.*, 1976; Kneib, 1982b; Kneib and Stiven., 1982; Joyce and Weisberg, 1986; Sardá *et al.*, 1998). Smith and Weis (1997) have shown that chronic exposure to chemical pollutants can alter size-selective feeding by mummichogs. In addition to direct effects of anthropogenic stressors (Warwick and Clarke, 1984), altered size-selective predation pressure may also lead to a shift in size structure of macroinvertebrates (Vince *et al.*, 1976; Kneib and Stiven., 1982; Santiago-Bass *et al.*, 2001). Santiago-Bass et al. (2001) have shown that the body size of the Arthur Kill (Piles Creek, New Jersey) population of grass shrimp is considerably larger than that of a reference site (Tuckerton, New Jersey) population, suggesting that grass shrimp may be more tolerant to chemical pollution than mummichogs (Weis *et al.*, 2000). These species-specific differential responses to chemical pollutants suggest that altered feeding behaviors of predators can have a positive indirect effect (i.e., reduced predation pressure) on their prey and a negative indirect effect on predators themselves (i.e., less available prey) in severely polluted benthic habitats (Weis *et al.*, 1999; Weis *et al.*, 2000; Santiago-Bass *et al.*, 2001).

Altered feeding behaviors and prey availability may also influence ontogenetic diet shifts of mummichogs in urban benthic habitats. In general, large adult mummichogs (> ~70 mm TL) feed on decapods such as fiddler crab (*Uca spp.*) and grass shrimp (*Palaemonetes spp.*) (Kneib and Stiven, 1978; Kneib *et al.*, 1980; Allen *et al.*, 1994), whereas small adults and juveniles (< ~40 mm TL) feed on small crustaceans such as tanaids and copepods (Kneib, 1986; Smith *et al.*, 2000; Able *et al.*, 2008). In the current study, the body size of the dominant prey item, grass shrimp, ingested by mummichogs generally increased with the total length of mummichogs at all sites, while the amount of

other prey categories, especially polychaetes, decreased at most sites. Mummichogs from Main Creek, however, ingested considerably smaller shrimp than those from the other sites, and substituted mainly by an increased ingestion of polychaetes. A frequent ingestion of a moderate amount of insects and gastropods was observed only in the gut of large adult fish from the reference site (Lemon Creek), but not in those from the Arthur Kill sites, which probably reflected the occurrence of these prey items in the environment (Chapter 2). The reduction or disappearance of sensitive invertebrate groups such as many gastropods, bivalves, and crustaceans from benthic macroinfaunal communities is commonly observed in degraded salt marshes (Weston, 1990; Warwick and Clarke, 1994; Warwick, 2001). Although a large number of gastropods were found in benthic macroinfaunal communities at one of the Arthur Kill sites, Mill Creek, a majority of these gastropods were *Illynassa ventriretta* (Chapter 2), which is far larger than the gape size of mummichogs (Vince *et al.*, 1976; Baker-Dittus, 1978; Werme, 1981; Sardá *et al.*, 1998). These gastropods were thus not ingested by mummichogs. Although meiofauna such as nematodes were fairly frequently (6 to 50%) ingested by different sizes of fish from all sites, due to their low contributions by weight (< 1%), their functional importance to adult mummichogs may be negligible (Penczak, 1985b).

Increased abundance and biomass of polychaetes are commonly observed in degraded marine benthic habitats (Pearson and Rosenberg, 1978; Weston, 1990; Warwick and Clarke, 1993; Warwick and Clarke, 1994), including tidal salt marshes in the Arthur Kill (Chapter 2). In the current study, higher relative proportion (by weight) of polychaetes was more frequently observed in the diets of fish from Main Creek, Richmond Creek, and Neck Creek than those from Mill Creek and the reference site

(Lemon Creek). Steimle (2001) has also shown compositional differences in the feeding habits of mummichogs between Mill Creek and the northern Arthur Kill sites, which may be due to the residual impacts from the 1990 oil spill. The most frequently observed polychaete species in the present study was *Nereis spp*., which was also one of the most abundant polychaete species (particularly, *Nereis acuminata*) found in the benthic macroinfaunal communities at those Arthur Kill sites (Chapter 2). As *Nereis spp*. were relatively larger than other polychaete species found in the Arthur Kill sites, they may have been more conspicuous to mummichogs than other abundant, but smaller polychaete species such as *Hobsonia florida* and *Streblospio benedicti*.

Despite their high abundance in urban tidal salt marshes, oligochaetes are rarely found in the gut of mummichogs (Moy and Levin, 1991; Smith *et al.*, 2000; Steimle, 2001). Although it is possible that the rapid digestion of soft-bodied invertebrates (e.g., polychaetes and oligochaetes) may influence their percentage contributions in the diet of mummichogs (Smith *et al.*, 2000), the present study indicated that enhanced abundance and biomass of oligochaetes in the Arthur Kill (Chapter 2) appear to have little or no effect on the foraging habit of mummichogs. Werme (1981) has experimentally shown that mummichogs are much less efficient in foraging on sediment-dwelling prey than another fundulid species, striped killifish (*Fundulus majalis*). Striped killifish often co-occur with mummichogs in tidal salt marshes in the northwest Atlantic coast, competing for prey resources (Baker-Dittus, 1978; Werme, 1981; Weisberg, 1986; Sardá *et al.*, 1998; Lynk, 2003). Unlike striped killifish, however, mummichogs efficiently capture only epibenthic prey on the sediment surface, while striped killifish forage for potential prey items by aggressively disturbing sediments (Werme, 1981; Sardá *et al.*, 1998). As a

result, these fundulid species, despite a high degree of diet overlap, tend to have differential 'preferences' in prey type (Werme, 1981; Weisberg, 1986; Sardá *et al.*, 1998; Lynk, 2003); mummichogs generally 'prefer' relatively mobile prey such as decapods and amphipods in intertidal marsh surface (Kneib and Stiven, 1978; Lynk, 2003), while striped killifish prefer sedentary sediment-associated prey such as gastropods and bivalves (Harvey, 1998; Lynk, 2003; Kim and O'Connor, 2007; Brousseau *et al.*, 2008). Further studies would, however, still require determining the importance of subsurface deposit-feeders to the diet of mummichogs.

Previous studies have suggested that an increased ingestion of detritus may indicate pollution impacts on the feeding habits of mummichogs in urban salt marshes with impoverished prey resources (Smith and Weis, 1997; Steimle, 2001; Weis *et al.*, 2001). In the current study, however, there was no consistent difference in the amount of detritus ingested by mummichogs among sites. A frequent occurrence (~31% to 100%) of detritus with an average of ~20% (by weight) of the total gut content was observed in fish from all study sites. This frequent ingestion of detritus is not uncommon for many benthivorous predators such as mummichogs (Morgan, 1990; Moy and Levin, 1991; Gerking, 1994). It is also highly unlikely for mummichogs to use detritus as a primary food source for their growth or metabolism (Prinslow *et al.*, 1974; Katz, 1975; White *et al.*, 1986). Furthermore, in the current study, a large amount of detritus was often found in the gut content of mummichogs with sediment-dwelling invertebrates such as polychaetes, but not with highly mobile epibenthic prey such as grass shrimp (personal observation). The occurrence of detritus may thus have been due to an accidental ingestion (Kneib and Stiven, 1978; Penczak, 1985b). In highly prey resource-limited

habitats such as urban tidal salt marshes, however, mummichogs may continue to unintentionally ingest detritus in search for sediment-dwelling prey as a short-term strategy (Weisberg and Lotrich, 1986). Altered prey availability in the environment may, therefore, indirectly influence the amount of detritus ingested by mummichogs.

Macroalgae (e.g., *Ulva spp.*) were also frequently found in the gut contents of mummichogs from all study sites in the present study. The frequency of occurrence was slightly higher in fish from the reference site (Lemon Creek) and Mill Creek than the other sites, whereas the relative proportion (by weight) was much larger in fish from the Arthur Kill sites than those from the reference site. Unlike detritus, the ingestion of macroalgae by mummichogs may not be accidental (Fell *et al.*, 1998), though mummichogs may feed on small crustaceans and insects that aggregate around macroalgae (Werme, 1981). The amount of plant material in the gut of some benthivorous fishes in coastal habitats, including mummichogs, is known to increase with their body size (Clements and Livingston, 1983; Smith *et al.*, 2000; Able *et al.*, 2008). In general, larvae and juveniles of these benthivorous fishes in coastal habitats are often primarily carnivorous, feeding mostly on meiofauna and macroinfaunal larvae, while adults become more omnivorous, ingesting a progressively increasing amount of plant material as they grow (Kneib and Stiven, 1978; Clements and Livingston, 1983; Smith *et al.*, 2000). Although the morphology of their digestive tract suggests that mummichogs are not well suited for herbivorous feeding habits (Babkin and Bowie, 1928; Werme, 1981; Weisberg, 1986), Moerland (1985) has experimentally shown that there is a temperature-dependent cellulase activity in the gut of mummichogs. It is thus possible

that when necessary, mummichogs may partially substitute an insufficient invertebrate prey supply with macroalgae.

Studies suggest that non-random (e.g., pollution) perturbations on trophic structures may provide a unique opportunity to elucidate intricate trophic interactions in marine and freshwater ecosystems (Fleeger *et al.*, 2003; Raffaelli, 2005; Woodward *et al.*, 2005). The modified Costello plots in the current study revealed highly flexible nature of the overall feeding strategy of mummichogs in the Arthur Kill as well as Raritan Bay, i.e., that of a generalist, mostly corresponding to a general pattern in benthic macroinfaunal communities (Chapter 2), as suggested by previous studies (Penczak, 1985b; Kneib, 1986; Moy and Levin, 1991). A large amount of decapods (mostly, *Palaemonetes spp.*) frequently appeared in the gut of adult mummichogs may have been due to their high abundance and relatively large body size, resulting in decapods being the most 'preferred' prey item. This feeding habit of mummichogs observed in the current study may also suggest a strong trophic relationship between mummichogs and decapods in this highly urbanized salt marsh ecosystem. At one of the Arthur Kill sites, Main Creek (a site with highly impoverished prey resources), however, mummichogs ingested decapods considerably less frequently than the other sites. This alteration in feeding habit led to a slight shift in feeding strategy toward an individual-level specialization (i.e., certain prey items ingested by only a few individuals, resulting in high heterogeneity within a population), specifically, an increased ingestion of algae and gastropods by some individuals. A population comprised of specialist individuals (i.e., each individual differently feeds on a few select prey items, potentially resulting high diet breadth at the population level) can be indistinguishable from a population comprised of

generalist individuals (i.e., all individuals similarly feed on a variety of prey items) at the population level, but there is an important difference in the degree of within-population heterogeneity between these two types of populations. The results from the present study suggest that the degree of individual-level diet specialization in fish may increase in heterogeneous habitats with low prey diversity such as urban tidal salt marshes.

Conclusions

The present study showed that the feeding habits of mummichogs in urban tidal salt marshes generally reflected altered benthic macroinfaunal assemblages, as previously suggested (Fritz, 1974; Baker-Dittus, 1978; Moy and Levin, 1991). As benthic macroinvertebrates are highly responsive to environmental conditions in urban coastal habitats (e.g., increased chemical pollutants, Chapter 2), the direct trophic relationship with macroinvertebrates may integrate overall anthropogenic impacts on benthic habitats (Kneib, 1997). Furthermore, due to their opportunistic feeding habits, omnivorous predators such as mummichogs can also be an integrative biological surrogate 'sampler' for the assessment of benthic habitat quality (e.g., Rachlin and Warkentine, 1997; Frid and Hall, 1999; Link, 2004; Fjellheim *et al.*, 2007). The predominant prey of adult mummichogs in the present study, grass shrimp, are also among the most productive macroinvertebrate species in tidal salt marshes in the northwest Atlantic coast, and known to feed not only on plant material, but also on a variety of benthic meiofauna and macroinfauna (Bell and Coull, 1978; Morgan, 1980; Kneib, 1985; Gregg and Fleeger, 1998). Partial trophic decoupling between mummichogs and grass shrimp observed at

some of the Arthur Kill sites could, thus, disrupt not only energy transfer to mummichogs (Chapter 6), but also ecosystem functions in these highly urbanized salt marshes.

The importance of integrity of trophic structure to ecosystem functioning is widely recognized (Clements and Newman, 2002). Theoretical and experimental studies have demonstrated a close association between biodiversity and ecosystem functioning; low biodiversity ecosystems (e.g., urban tidal salt marshes) are likely to have low buffering capacity toward anthropogenic disturbances (Loreau and Thébault, 2005; Woodward *et al.*, 2005). Highly urbanized ecosystems with low biodiversity and simplified trophic structures are likely to be at a vulnerable state, potentially facing food chain collapse from a loss of any member of food webs (Clements and Newman, 2002). As a key species in urban salt marshes, monitoring the feeding ecology of mummichogs (e.g., trophic relationships with grass shrimp) is critical in understanding the structural and functional responses to restorations of chronically degraded coastal habitats.

Figure 3-1. A modified Costello feeding strategy plot (Amundsen *et al.*, 1996).

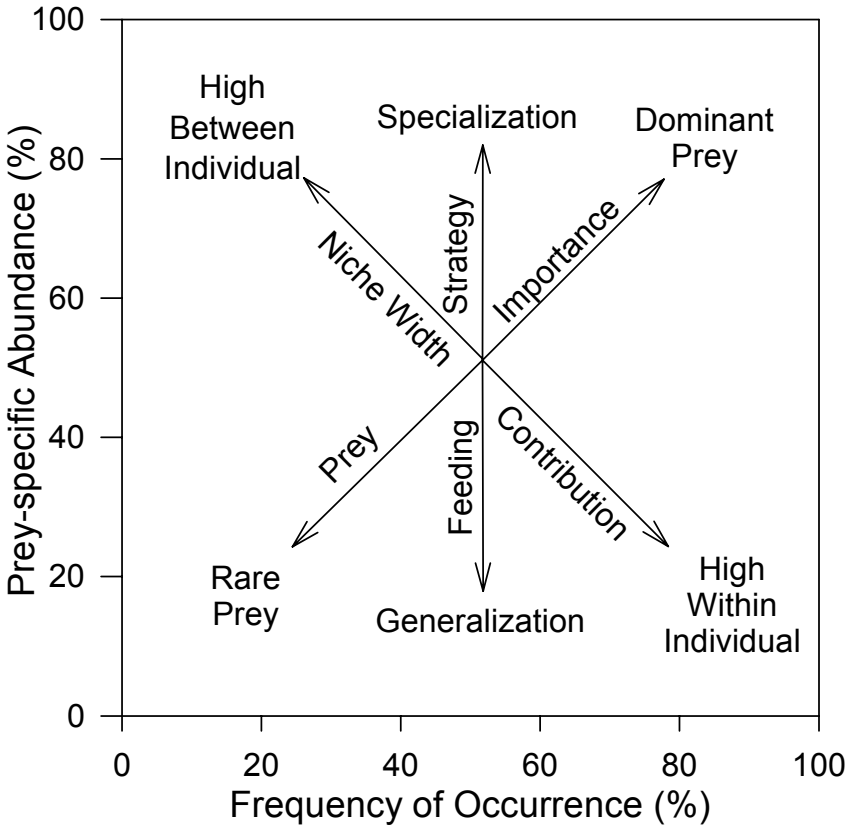


Figure 3-2. Mean values of indices of (a) gut fullness, (b) prey species richness, (c) diet niche breadth, and (d) prey species evenness of the gut contents of mummichogs from Lemon Creek, Mill Creek, Richmond Creek, Main Creek, and Neck Creek. Errors bars indicate ± 1 SE. Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test).

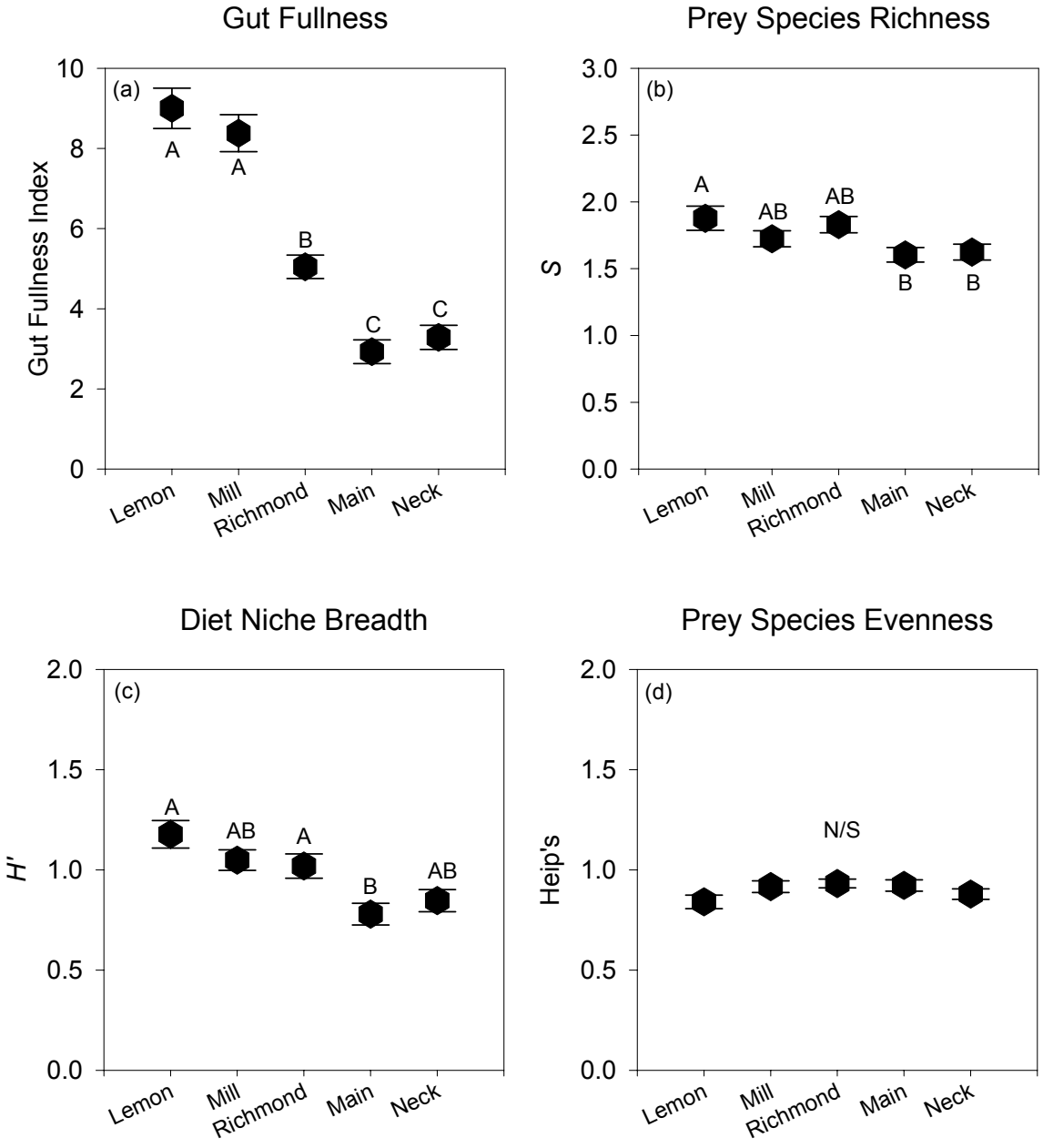


Table 3-1. Length class-specific frequency of occurrence (%) of diet categories in the gut contents of mummichogs from Lemon Creek, Mill Creek, Richmond Creek, Main Creek, and Neck Creek. *n* indicates the number of fish samples analyzed for each length class.

Site-Length class	*n*	Decapoda	Amphipoda	Isopoda	Cirripedia	Polychaeta	Nematoda	Gastropoda	Arachnida	Insecta	Zooplankton	Alga	Detritus
Lemon-40+	12	75.0	0.0	16.7	0.0	33.3	0.0	25.0	16.7	50.0	0.0	16.7	58.3
Lemon-50+	11	90.9	0.0	0.0	9.1	27.3	18.2	18.2	27.3	54.5	9.1	36.4	54.5
Lemon-60+	13	92.3	23.1	30.8	0.0	46.2	46.2	38.5	61.5	61.5	15.4	23.1	61.5
Lemon-70+	6	66.7	0.0	33.3	0.0	33.3	33.3	66.7	0.0	33.3	0.0	16.7	83.3
Lemon-80+	5	100.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	50.0	0.0	0.0	100.0
Mill-60+	6	100.0	16.7	0.0	16.7	0.0	16.7	0.0	0.0	0.0	0.0	33.3	66.7
Mill-70+	18	100.0	11.1	0.0	50.0	16.7	5.6	16.7	0.0	11.1	0.0	33.3	44.4
Mill-80+	13	92.3	0.0	15.4	23.1	7.7	30.8	7.7	0.0	23.1	0.0	23.1	30.8
Mill-90+	5	100.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Richmond-60+	5	75.0	0.0	0.0	50.0	75.0	25.0	0.0	0.0	0.0	0.0	25.0	75.0
Richmond-70+	15	80.0	13.3	6.7	20.0	40.0	26.7	0.0	0.0	13.3	6.7	13.3	53.3
Richmond-80+	30	100.0	3.3	3.3	33.3	53.3	6.7	0.0	0.0	6.7	3.3	3.3	73.3
Richmond-90+	11	100.0	9.1	18.2	9.1	81.8	18.2	9.1	0.0	9.1	0.0	9.1	72.7
Main-40+	9	11.1	0.0	11.1	33.3	66.7	0.0	0.0	0.0	0.0	0.0	0.0	44.4
Main-50+	29	31.0	3.4	0.0	17.2	44.8	13.8	0.0	0.0	10.3	6.9	24.1	58.6
Main-60+	21	47.6	9.5	14.3	38.1	52.4	19.0	0.0	4.8	19.0	19.0	14.3	71.4
Main-70+	5	40.0	0.0	40.0	0.0	80.0	40.0	40.0	0.0	0.0	0.0	20.0	60.0
Main-80+	7	100.0	0.0	20.0	40.0	20.0	20.0	0.0	0.0	0.0	0.0	0.0	40.0
Neck-50+	6	80.0	20.0	0.0	0.0	60.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Neck-60+	26	65.4	38.5	7.7	11.5	30.8	15.4	0.0	0.0	0.0	0.0	23.8	73.1
Neck-70+	35	74.3	37.1	17.1	11.4	45.7	31.4	2.9	0.0	8.6	2.9	17.1	54.3
Neck-80+	9	77.8	0.0	22.2	0.0	66.7	22.2	0.0	0.0	11.1	11.1	22.2	0.0

Figure 3-3. Contributions by count (%) of diet categories (Decapoda, Amphipoda, Isopoda, Cirridedia, Polychaeta, Oligochaeta, Nematoda, Gastropoda, Bivalvia, Arachnida, Insecta, Zooplankton, Osteichthyes, Alga, and detritus) to the length class-specific total diet compositions of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. N/A = samples were not available.

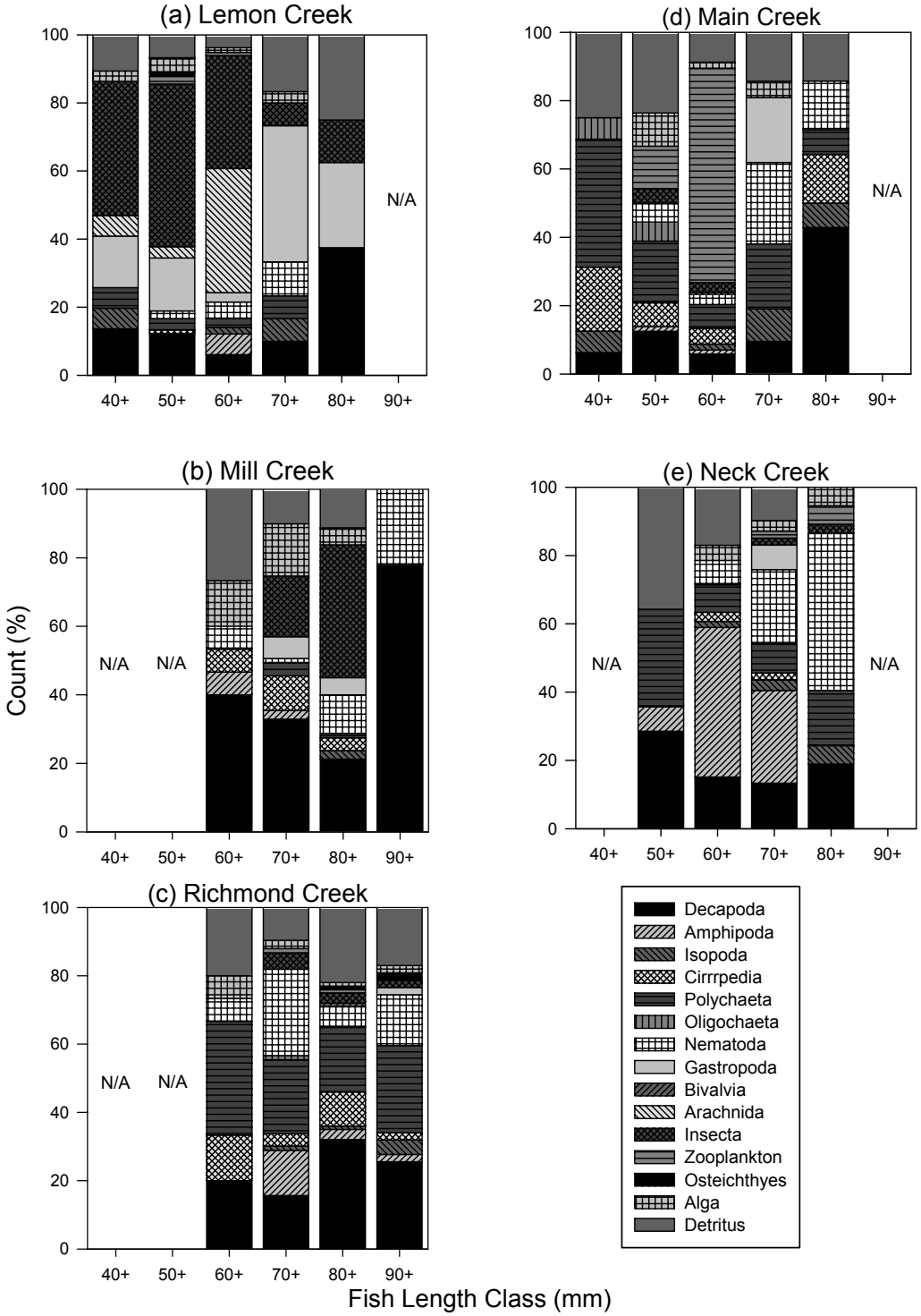


Figure 3-4. Contributions by weight (%) of diet categories (Decapoda, Amphipoda, Isopoda, Cirridedia, Polychaeta, Oligochaeta, Nematoda, Gastropoda, Bivalvia, Arachnida, Insecta, Zooplankton, Osteichthyes, Alga, and detritus) to the length class-specific total diet compositions of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. N/A = samples were not available.

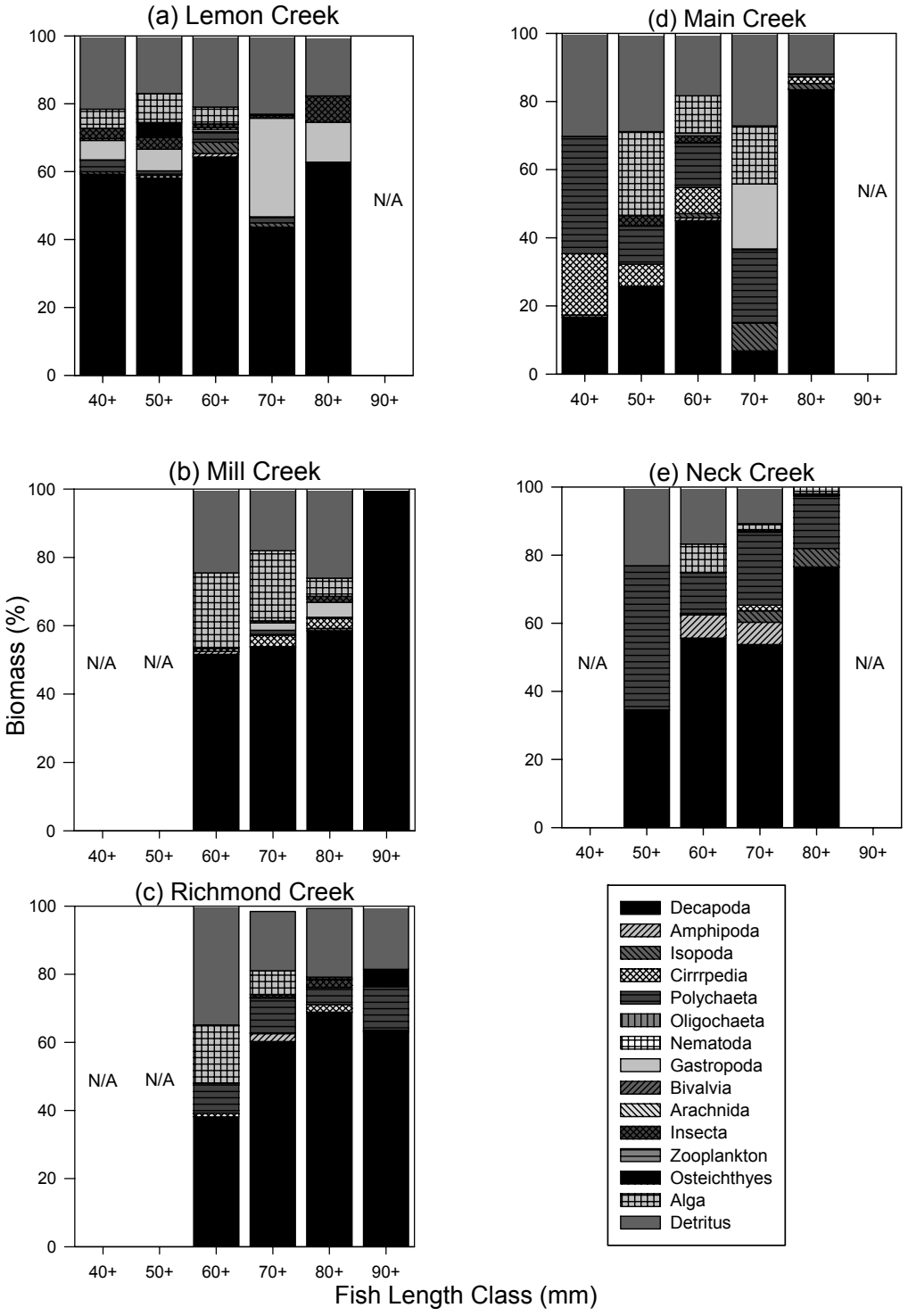


Figure 3-5. Contributions by proportional index of relative importance (*IRI*) (%) of diet categories (Decapoda, Amphipoda, Isopoda, Cirridedia, Polychaeta, Oligochaeta, Nematoda, Gastropoda, Bivalvia, Arachnida, Insecta, Zooplankton, Osteichthyes, Alga, and detritus) to the length class-specific total diet compositions of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. N/A = samples were not available.

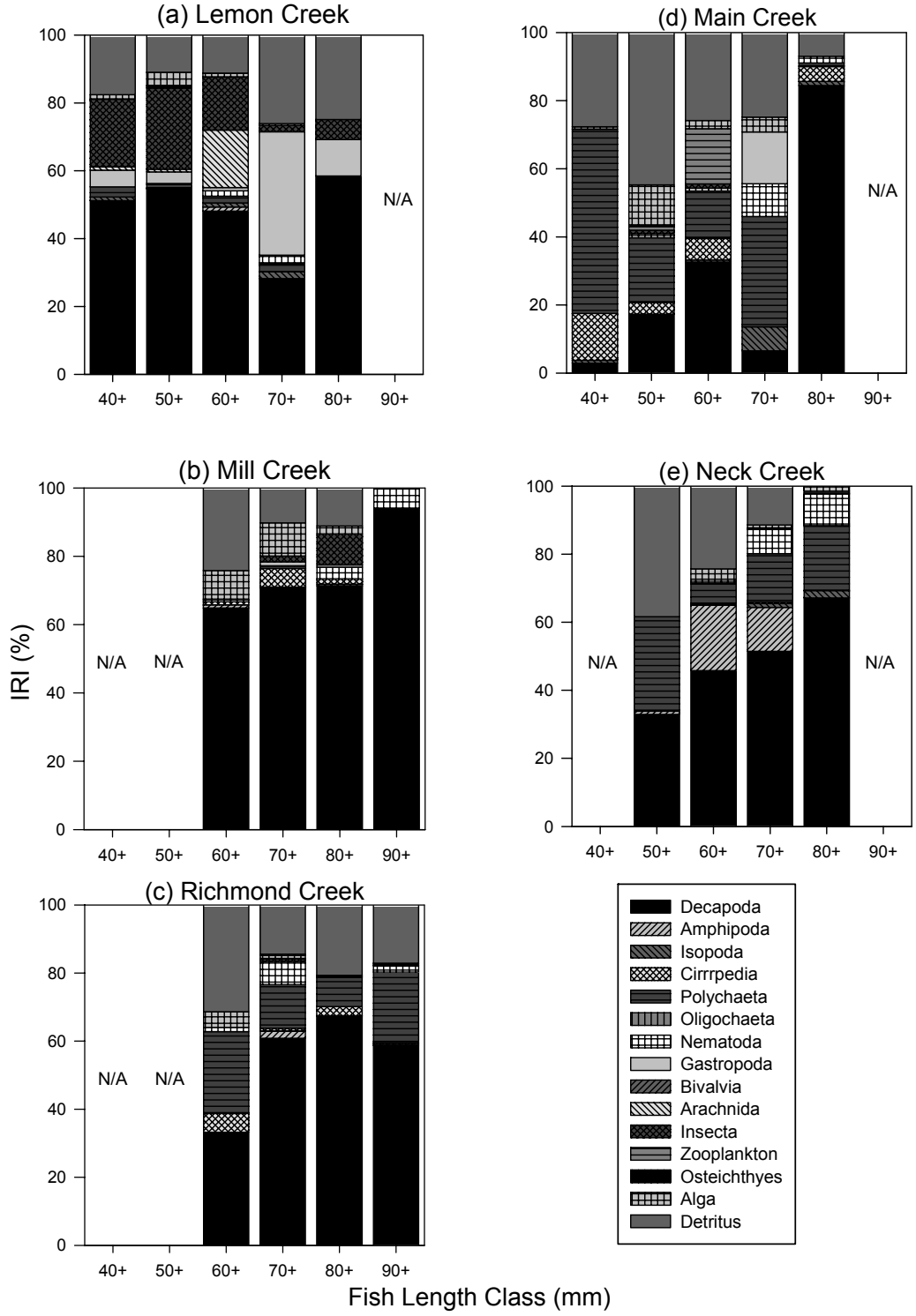


Figure 3-6. Population-specific feeding strategies of mummichogs represented with the modified Costello plots: frequency of occurrence (%) vs. prey-specific abundance (by weight) (%) of the diet compositions (Decapoda, Amphipoda, Isopoda, Cirridedia, Polychaeta, Oligochaeta, Nematoda, Gastropoda, Bivalvia, Arachnida, Insecta, Zooplankton, Osteichthyes, Alga, and detritus) of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. The explanation of the diagrams is provided in (f) (Amundsen *et al.*, 1996).

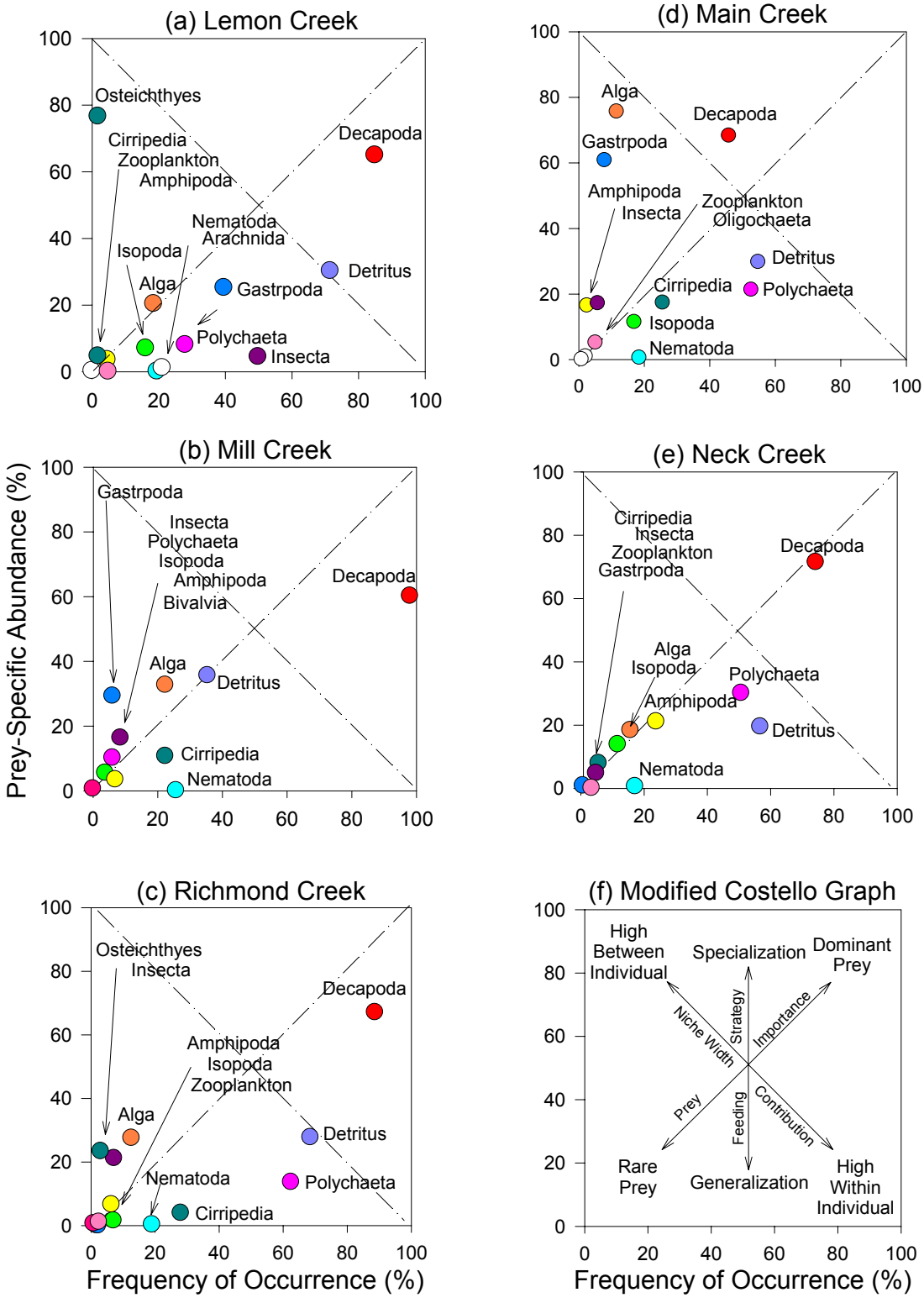

(a) Lemon Creek
Osteichthyes
Cirripedia
Zooplankton
Amphipoda
Decapoda
Nematoda
Arachnida
Isopoda
Alga
Gastrpoda
Detritus
Polychaeta
Insecta
(d) Main Creek
Alga
Decapoda
Gastrpoda
Amphipoda
Insecta
Zooplankton
Oligochaeta
Detritus
Cirripedia
Polychaeta
Isopoda
Nematoda
(b) Mill Creek
Prey-Specific Abundance (%)
Gastrpoda
Insecta
Polychaeta
Isopoda
Amphipoda
Bivalvia
Decapoda
Alga
Detritus
Cirripedia
Nematoda
(e) Neck Creek
Cirripedia
Insecta
Zooplankton
Gastrpoda
Decapoda
Alga
Isopoda
Polychaeta
Amphipoda
Detritus
Nematoda
(c) Richmond Creek
Osteichthyes
Insecta
Decapoda
Amphipoda
Isopoda
Zooplankton
Alga
Detritus
Nematoda
Polychaeta
Cirripedia
Frequency of Occurrence (%)
(f) Modified Costello Graph
High Between Individual
Specialization
Dominant Prey
Niche Width
Strategy
Importance
Prey
Feeding
Contribution
Rare Prey
Generalization
High Within Individual
Frequency of Occurrence (%)

Figure 3-7. Relationships between the total length (mm) of mummichogs and wet weight (g) of *Palaemonetes spp.* in the gut contents of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate a best-fit regression curve.

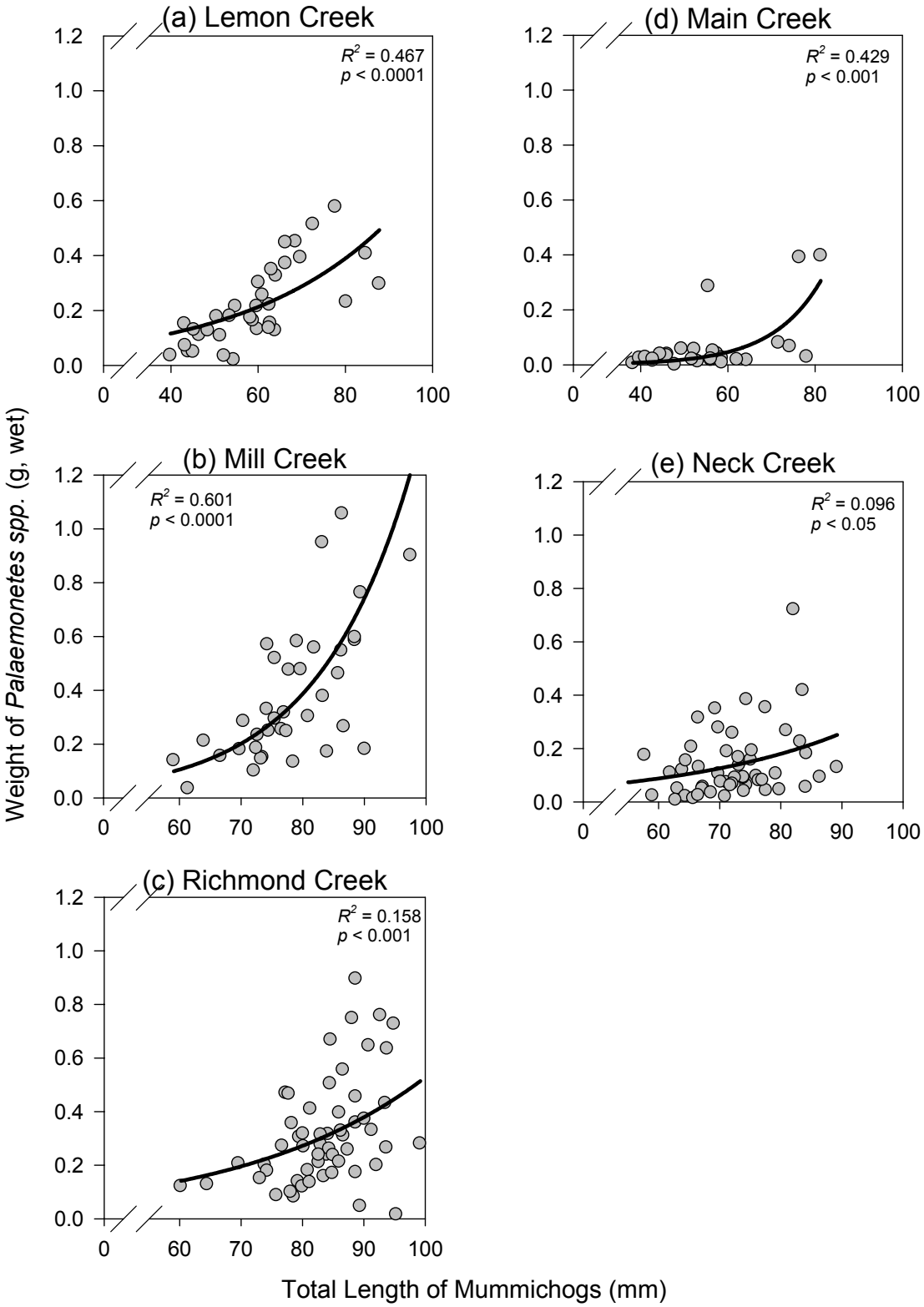


Figure 3-8. 2-dimensional plots of non-metric multidimensional scaling (nMDS) (based on Bray-Curtis similarities of square root-transformed data) of mean contributions (%) by (a) frequency of occurrence, (b) weight, (c) count, and (d) *IRI* of diet categories to the length class-specific total diet compositions of mummichogs from the from Lemon Creek (●), Mill Creek (▼), Richmond Creek (△), Main Creek (■), and Neck Creek (■).

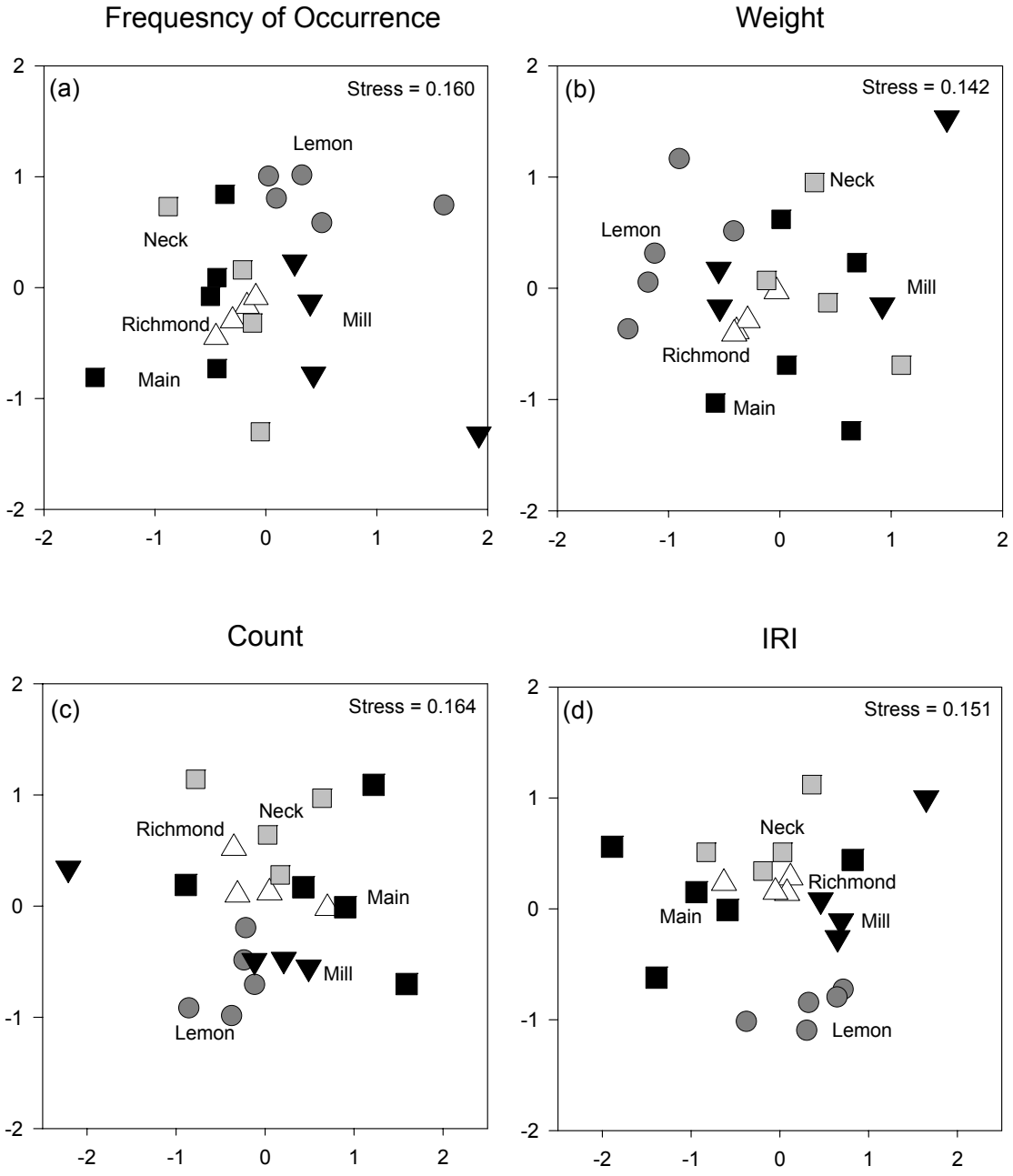
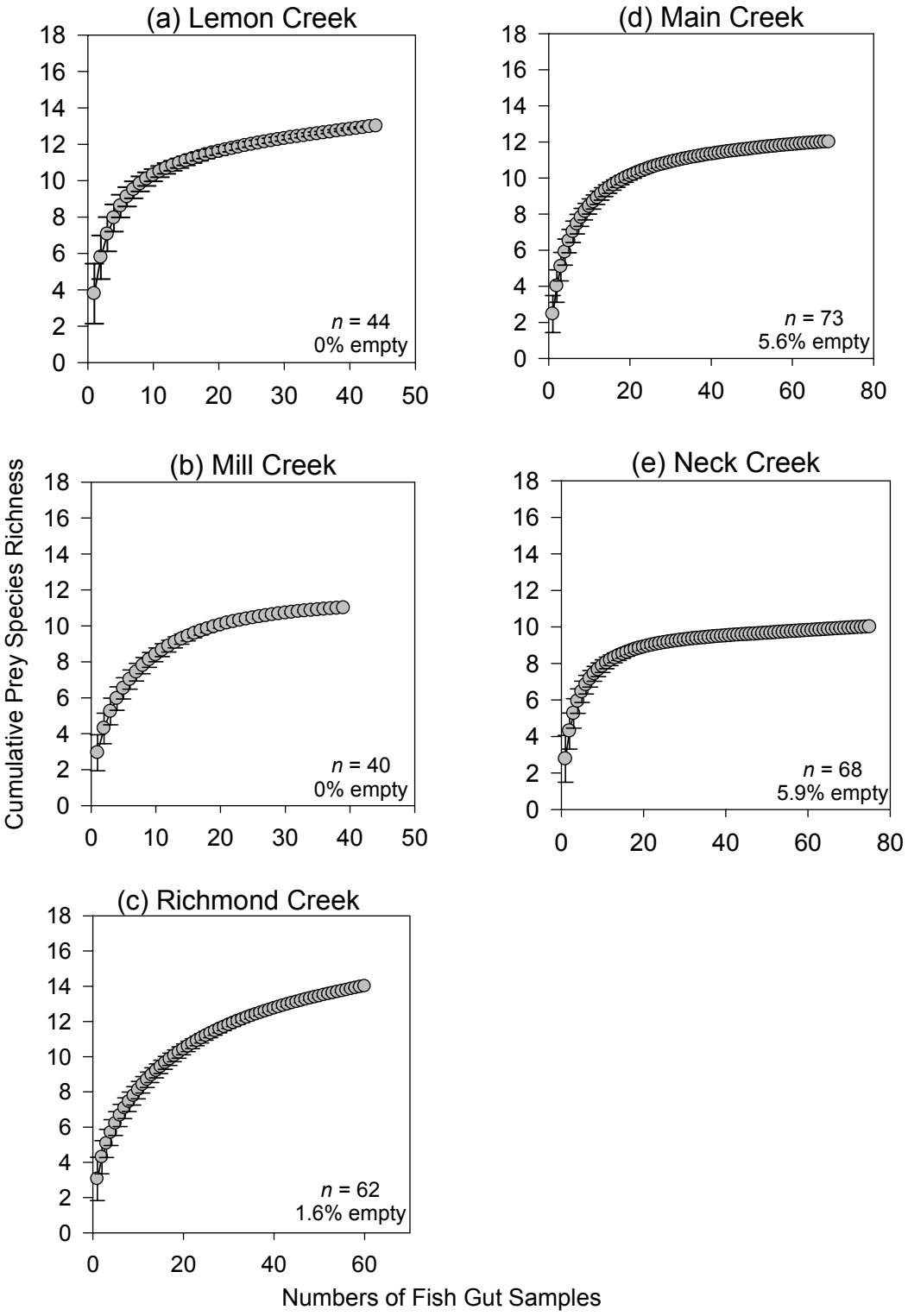


Table 3-2. Results of analysis of similarity (ANOSIM) on diet compositions (by count and weight) of mummichogs among the study sites. Statistically significant differences are indicated in **bold** ($p < 0.05$ or 5%).

	Count		Weight	
Global Tests	*R* Statistic	Significance Level %	*R* Statistic	Significance Level %
Site	0.294	**0.1**	0.268	**0.1**
Length Class	0.043	**3.4**	0.044	**2.9**
Pairwise Tests				
Lemon vs. Mill	0.300	**4.0**	0.244	7.1
Lemon vs. Richmond	0.781	**0.8**	0.569	**1.6**
Lemon vs. Main	0.624	**0.8**	0.492	**0.8**
Lemon vs. Neck	0.581	**0.8**	0.713	**0.8**
Mill vs. Richmond	0.375	**2.9**	0.219	11.4
Mill vs. Main	0.250	5.8	0.063	30.2
Mill vs. Neck	0.188	17.1	0.323	5.7
Richmond vs. Main	-0.056	59.5	0.013	40.5
Richmond vs. Neck	0.083	28.6	0.125	20.0
Main vs. Neck	0	45.2	0.088	26.2

Appendix 3-A. Cumulative prey species richness of the gut contents of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Sample size and % empty gut are provided in each panel. Errors bars indicate ± 1 SE.



Appendix 3-B. Results of analysis of similarity percentages (SIMPER) on contributions by count and weight (%) of dietary categories to total dissimilarity in pairwise comparisons of diet compositions of mummichogs among the study sites. AvDiss = average dissimilarity between sites for each contributing dietary category, Diss/SD = ratio of average dissimilarity divided by standard deviation, Contrib% = contribution (%) to total average dissimilarity by each dietary category, and Cum% = cumulative contribution (%) to total average dissimilarity.

	Count					Weight				
Study site	Species	AvDiss	Diss/SD	Contrib%	Cum%	Species	AvDiss	Diss/SD	Contrib%	Cum%
Lemon vs. Mill	Average dissimilarity = 46.48					Average dissimilarity = 26.81				
	Insecta	6.74	1.58	14.51	14.51	Alga	7	3.7	26.1	26.1
	Gastropoda	5.46	2.81	11.74	26.25	Gastropoda	4.81	1.25	17.95	44.05
	Decapoda	5.23	2.36	11.26	37.51	Cirripedia	3.57	3.08	13.31	57.36
Lemon vs. Richmond	Average dissimilarity = 50.92					Average dissimilarity =31				
	Gastropoda	8.32	1.89	16.34	16.34	Gastropoda	7.84	1.41	25.3	25.3
	Polychaeta	6.91	2.47	13.57	29.91	Polychaeta	4.36	2.94	14.06	39.36
	Cirripedia	5.69	2.86	11.18	41.09	Alga	3.69	2.24	11.91	51.26
Mill vs. Richmond	Average dissimilarity = 40.69					Average dissimilarity = 26.32				
	Polychaeta	8.74	2.19	21.48	21.48	Polychaeta	7.05	1.85	26.77	26.77
	Decapoda	4.47	1.46	10.99	32.47	Detritus	4.68	0.7	17.8	44.57
	Amphipoda	3.93	3.56	9.67	42.14	Decapoda	3.05	1.11	11.58	56.15
Lemon vs. Main	Average dissimilarity = 47.69					Average dissimilarity = 34.11				
	Insecta	8.31	3.38	17.42	17.42	Gastropoda	8.18	1.84	23.96	23.96
	Gastropoda	8.02	2.41	16.81	34.23	Decapoda	6.51	1.62	19.07	43.04
	Zooplankton	5.02	0.94	10.52	44.75	Polychaeta	3.9	1.75	11.43	54.47
Mill vs. Main	Average dissimilarity = 46.11					Average dissimilarity = 38.52				
	Gastropoda	6.97	2.46	15.12	15.12	Decapoda	7.69	1.85	19.96	19.96
	Isopoda	5.81	7.71	12.61	27.73	Gastropoda	7.02	1.58	18.22	38.18
	Alga	5.36	1.62	11.63	39.36	Alga	6.61	0.89	17.16	55.34
Richmond vs. Main	Average dissimilarity = 36.12					Average dissimilarity = 32.58				
	Cirripedia	5.49	2.02	15.2	15.2	Decapoda	5.81	1.89	17.84	17.84
	Isopoda	4.63	2	12.82	28.02	Polychaeta	4.93	3.11	15.12	32.96
	Gastropoda	4.43	0.71	12.26	40.28	Gastropoda	4.9	0.71	15.05	48.01
Lemon vs. Neck	Average dissimilarity = 54.79					Average dissimilarity = 39.46				
	Insecta	7.99	1.37	14.58	14.58	Polychaeta	8.87	2.18	22.49	22.49
	Gastropoda	7.38	2.11	13.47	28.04	Gastropoda	7.44	1.65	18.86	41.35
	Detritus	6.14	1.45	11.2	39.24	Detritus	4.51	0.92	11.43	52.78

Appendix 3-B (Continued).

Mill vs. Neck	Average dissimilarity =36.11					Average dissimilarity = 32.1				
	Amphipoda	4.9	1.12	13.56	13.56	Polychaeta	8.16	14.17	25.43	25.43
	Insecta	4.64	1.02	12.85	26.41	Detritus	5.78	0.92	18.01	43.44
	Polychaeta	4.47	1.9	12.38	38.79	Alga	4.61	1.95	14.35	57.79
Richmond vs. Neck	Average dissimilarity = 34.48					Average dissimilarity = 24.78				
	Amphipoda	6.5	1.06	22.22	22.22	Detritus	6.12	1.17	24.69	24.69
	Cirripedia	3.65	1.38	12.46	34.68	Isopoda	3.19	1.35	12.86	37.55
	Detritus	3.23	0.65	11.02	45.7	Amphipoda	3.1	1.1	12.52	50.07
Main vs. Neck	Average dissimilarity = 45.41					Average dissimilarity = 34.64				
	Amphipoda	8.76	1.82	19.29	19.29	Polychaeta	6.24	1.83	18.02	18.02
	Zooplankton	6.72	0.71	14.81	34.1	Decapoda	5.67	1.29	16.38	34.4
	Gastropoda	4.53	1.05	9.98	44.07	Alga	4.58	1.68	13.22	47.61

CHAPTER 4

Internal partitioning of metals in benthic macroinvertebrates and its relevance to metal trophic transfer to mummichogs (*Fundulus heteroclitus*) in urban tidal salt marshes in New York

CHAPTER SUMMARY

Intracellular partitioning of trace metals is critical to aquatic species tolerance to metals, and may also influence metal trophic transfer in aquatic ecosystems. In the present study, metal (Cd, Cu, Pb, and Zn) handling capacities of mummichogs (*Fundulus heteroclitus*) were assessed along with potential metal transfer from two common prey, decapods (*Palaemonetes spp.*) and polychaetes (*Nereis spp.*), in urban salt marshes in the Arthur Kill (New York, USA) by examining metal intracellular partitioning. Despite the lack of differences in whole body burdens among sites, the intracellular partitioning revealed clear population-specific metal handling in mummichogs. Population-specific metal partitioning in mummichogs was particularly distinct for one of the non-essential metals, Pb. The Arthur Kill populations of mummichogs stored considerably more Pb in metal-rich granules as detoxified forms than the reference populations, which sequestered high percentage of Pb into metal-binding proteins. Furthermore, differential metal partitioning within invertebrate prey was reflected only in non-essential metal bioaccumulation in mummichogs; Cd and Pb partitioned to trophically available cellular components in the invertebrates were strongly associated with whole body burdens in mummichogs, while there was no relationship for Cu and Zn. Despite substantial differences in sediment-associated Cu and Zn among sites, Cu and Zn partitioning in invertebrate prey and mummichogs varied relatively little. These findings suggest that species- and population- specific intracellular partitioning of trace metals in prey and predator may be partially responsible for metal-specific differential biogeochemical cycling in urban coastal ecosystems.

INTRODUCTION

Marine organisms living in urban coastal habitats are exposed to a variety of anthropogenic stressors (Able *et al.*, 1998; Levin *et al.*, 2001). Among these stressors, sediment-associated chemicals such as trace metals have particularly persistent and cumulative effects, potentially inducing various ecological and physiological alterations in marine organisms (Luoma, 1996). In chronically polluted habitats, trace metal pollution can exert selection pressure on aquatic organisms (Luoma, 1977; Klerks and Weis, 1987; Klerks and Levinton, 1989), eliminating local populations of metal-sensitive species and allowing metal-tolerant species to dominate biological communities (Chapter 2; Clements, 1997; Clements and Newman, 2002). Tolerance can develop from physiological acclimation or genetic adaptation to potential toxicity of trace metals (Klerks and Weis, 1987; Klerks and Levinton, 1989; Weis and Weis, 1989). Klerks and Levinton (1989), for instance, have demonstrated that a deposit-feeding oligochaete (*Limnodrilus hoffmeisteiri*) rapidly developed heritable resistance to cadmium in metal-polluted habitats.

Metal-tolerant aquatic species generally possess physiological or biochemical mechanisms that allow them to cope with an elevated level of bioavailable trace metals in the environment (Mason and Jenkins, 1995). These mechanisms include 1) alterations in metal assimilation or elimination rates (Langston and Spence, 1995; Xie and Klerks, 2004), 2) sequestration to metal-binding proteins (e.g., metallothioneins) (Roesijadi, 1992; Mason and Jenkins, 1995), and 3) formation of granular concretions (or metal-rich granules) (Mason and Nott, 1981; Klerks and Bartholomew, 1991; Mason and Jenkins, 1995). In general, assimilated metals usually go through a series of metabolic processes

in organisms, and are subsequently incorporated into various cellular components (O'Connor and Rachlin, 1982; Mason and Jenkins, 1995). The incorporated metals may be initially sequestered to metal-binding proteins induced upon uptake (Petering *et al.*, 1990; Langston *et al.*, 1998; Goto and Wallace, 2007). However, the capacities of these proteins to sequester trace metals are limited (Mason and Jenkins, 1995; Giguere *et al.*, 2003). Some metals that are not bound to metal-binding proteins may be transported to other cellular components such as enzymes and organelles, while others may be sequestered into metal-rich granules in detoxified forms (Brown *et al.*, 1977; Brown and Parsons, 1978). These metals associated with the detoxifying cellular components, metal-binding proteins and metal-rich granules, can be compartmentalized as 'biologically detoxified metals' (BDM), which may indicate species tolerance to metals (Wallace *et al.*, 2003; Cain *et al.*, 2004). Metals that are not sequestered into either metal-binding proteins or metal-rich granules may be incorporated into non-detoxifying cellular components (e.g., enzymes and organelles), which could result in toxicity at various levels of biological organization (Brown and Parsons, 1978; Wallace *et al.*, 2003). Metals associated with these non-detoxifying fractions can be compartmentalized as 'metal-sensitive fractions' (MSF), which may indicate species sensitivity to metals (Wallace *et al.*, 2003; Cain *et al.*, 2004).

In the past few decades, an increasing number of studies have explored ecological and evolutionary implications for intracellular partitioning of trace metals in marine and freshwater organisms in their natural habitats (e.g., Wallace *et al.*, 1998; Cain *et al.*, 2004; Perceval *et al.*, 2004; Martin *et al.*, 2007). Differential tolerance to trace metals among populations or species appears to be related to intracellular metal storage within

aquatic organisms (Cain *et al.*, 2004; Perceval *et al.*, 2004; Buchwalter *et al.*, 2007). A population of a deposit-feeding oligochaete, *Limnodrilus hoffmeisteiri*, living in metal-polluted habitats, for instance, preferentially sequestered cadmium (Cd) to metal-rich granules, whereas a population of *L. hoffmeisteiri* from non-polluted habitats sequestered the majority of Cd into metal-binding proteins (Klerks and Bartholomew, 1991; Wallace *et al.*, 1998). These population-specific differential strategies of Cd detoxification imply that the sequestration into insoluble granules may be more efficient in detoxifying Cd than metal-binding proteins, allowing this oligochaete to tolerate an elevated level of Cd in the environment (Wallace *et al.*, 1998). The preferential sequestration to insoluble granules by metal-tolerant species has also been frequently observed in other marine organisms living in metal-polluted habitats (e.g., Mason and Nott, 1981; Nott and Nicolaidou, 1990; Nott and Nicolaidou, 1994; Berthet *et al.*, 2003; Mouneyrac *et al.*, 2003).

Differential intracellular partitioning of trace metals within marine organisms may also be relevant to biogeochemical cycling of trace metals in ecosystems. Some experimental studies have shown that intracellular partitioning of trace metals in prey can influence metal trophic transfer to their predators (e.g., Wallace and Luoma, 2003; Cheung and Wang, 2005; Seebaugh *et al.*, 2005). An increasing number of studies have demonstrated the importance of dietary ingestion of trace metals as a predominant route for metal bioaccumulation in marine organisms (e.g., Griscom *et al.*, 2002; Wang, 2002; Xu and Wang, 2002; Wang and Wong, 2003). Trace metals accumulated in prey can be transferred to and potentially cause secondary toxic effects in their predators (Ni *et al.*, 2000; Baines *et al.*, 2002; Xu and Wang, 2002). Furthermore, dietary exposure to trace

metals is more likely to cause toxic effects in fish than aqueous exposure (Woodward *et al.*, 1994; Woodward *et al.*, 1995; Farag *et al.*, 1999).

The relevance of intracellular metal distributions within prey to metal trophic transfer results from differential trophic availabilities of trace metals distributed among various cellular components (Wallace and Lopez, 1997; Nott, 1998; Zhang and Wang, 2006). As trace metals bound to organelles and cytosolic proteins (including metal-binding proteins) are readily solubilized by the digestive processes of a predator, metals associated with these cellular components are thought to be more available to a predator than those with other components (Wallace and Lopez, 1997; Zhang and Wang, 2006). Due to their high bioavailabilities to predators, metals associated with cytosolic proteins and organelles within prey may be compartmentalized as 'trophically available metal' (TAM) (Wallace and Luoma, 2003). In contrast, trace metals partitioned to insoluble components such as metal-rich granules within prey are not readily available to many predators, as most granules are not easily solubilized by the digestive processes (Nott and Nicolaidou, 1993; Nott and Nicolaidou, 1994; Wallace and Lopez, 1997; Zhang and Wang, 2006). The majority of trace metals sequestered into granules within prey can pass through the digestive tract of a predator without being assimilated (Nott and Nicolaidou, 1990; Wallace and Lopez, 1997; Rainbow *et al.*, 2004). Determining intracellular partitioning of trace metals within prey may, therefore, be used to 1) understand specific metal trophic pathways and 2) estimate the extent of potential metal trophic transfer efficiency when assessing ecological impacts associated with trace metal pollution. Because of its sensitivity to spatial and temporal metal gradients in the environment,

population- or species-specific intracellular partitioning of trace metals may elucidate the mechanisms involved in biogeochemical cycling of trace metals in aquatic ecosystems.

In the present study, metal-handling capacities of mummichogs, *Fundulus heteroclitus* (Pisces: Cyprinodontidae), in urban tidal salt marshes in the Arthur Kill (New York, USA) were assessed along with potential metal trophic transfer from two common prey, decapods (*Palaemonetes spp.*) and polychaetes (*Nereis spp.*), by examining metal intracellular partitioning. Mummichogs are among the most abundant fishes in tidal creeks and salt marshes in the northwest Atlantic coast (Nixon and Oviatt, 1973; Valiela *et al.*, 1977; Meredith and Lotrich, 1979). Like many benthic predators, mummichogs primarily feed on a variety of benthic macroinvertebrates including *Palaemonetes spp.* and *Nereis spp.* (Chapter 3; Kneib *et al.*, 1980; Steimle, 2001; Weis *et al.*, 2001). Benthic macroinvertebrates are in direct contact with sediments (the main source of trace metals in benthic food chains), and are also an important component of the diet of various benthivorous predators (Adams and Benyi, 2003; Steinberg *et al.*, 2004). Furthermore, mummichogs play an essential role as an intermediate predator linking sediment-associated invertebrates to piscivorous fishes and wading birds using tidal salt marshes and inland wetlands as feeding grounds (Valiela *et al.*, 1977; Kneib, 1986; Kneib and Wagner, 1994). Understanding factors determining the extent of metal trophic transfer to and metal handling by mummichogs (a conduit of trace metal transfer to top predators) would, therefore, provide much needed information on potential ecological impacts of trace metal pollution in urban coastal ecosystems.

MATERIALS AND METHODS

Samplings of Benthic Macroinvertebrates and Mummichogs

Samplings of mummichogs and macroinvertebrate prey (*Palaemonetes spp.* and *Nereis spp.*) were conducted during the summers (June to September) of 2001 and 2004. Specific sampling sites were four tributaries of the Arthur Kill; Richmond Creek, Main Creek, Neck Creek, and Mill Creek and two regional reference sites external to the Arthur Kill; Lemon Creek and Great Kills Harbor (see Chapter 1 for site description). Large adult mummichogs (> 70 mm TL) were collected using a 3.05 x 1.22 m-seine net with 6 mm-polyester mesh or cylindrical minnow trap with 6 mm-mesh. *Nereis spp.* were collected by sieving bulk sediments through a 500 μm-mesh sieve, while adult *Palaemonetes spp.* (> ~25 mm TL) were collected using a D-frame dip net. Mummichogs, *Palaemonetes spp.*, and *Nereis spp.* were then transported on ice to laboratory.

Laboratory Processing of Benthic Macroinvertebrates and Mummichogs

In the laboratory, to minimize measurement errors associated with unassimilated metals in the gut contents, which can introduce considerable variability (Brooke *et al.*, 1996), mummichogs and macroinvertebrates were allowed to depurate gut contents for at least 24 hours in filtered 15‰ seawater. Mummichogs were then immediately euthanized by an overdose of MS222. Macroinvertebrates and mummichogs were stored in a freezer (–80 °C) for subsequent fractionation and metal analyses.

Isolation of TAM Compartment from Benthic Macroinvertebrates

Trace metals associated with the trophically available metal (TAM) compartment were isolated from field-collected *Palaemonetes spp.* and *Nereis spp.* using a centrifugation technique (Wallace and Luoma, 2003). Macroinvertebrates (n = 5) were thawed on ice, dabbed dry, and weighed. Tissues were then transferred into pre-weighed centrifuge tubes and homogenized (under a nitrogen atmosphere) in cold TRIS buffer (20 mM, pH = 7.6) with a Polytron tissue homogenizer (Kinematica, Luzern, Switzerland) (Wallace *et al.*, 2003). The homogenates were fractionated by centrifugation at 1,450 x g for 15 minutes, which produced a pellet containing tissue fragments and cellular debris, and a supernate containing cytosolic proteins and organelles (i.e., TAM) (Wallace and Luoma, 2003). Each fraction was processed for metal analyses, as described below.

Intracellular Partitioning (MSF and BDM) of Metals in Mummichogs

Site-specific intracellular partitioning of trace metals within mummichogs collected in 2004 was examined using the established method by Wallace *et al.* (2003) with minor modifications. This method produces four major fractions, i.e., organelles, heat-stable proteins (HSP), heat-denatured proteins (HDP), and metal-rich granules (MRG), which are grouped as either metal-sensitive fraction (MSF = organelles + HDP), or biologically-detoxified metal (BDM = HSP + MRG) (Wallace *et al.*, 2003).

Previously depurated and frozen mummichogs were thawed on ice and homogenized in cold TRIS buffer (pH = 7.6) with a Polytron tissue homogenizer under a nitrogen atmosphere. Then, subsamples of homogenates were fractionated using differential centrifugation (Wallace *et al.*, 2003) under a nitrogen atmosphere. Briefly, homogenized fish tissues were centrifuged at 1,450 x g for 15 minutes, which produced a

supernate (S1) and a pellet (P1). S1 was further centrifuged at 100,000 x *g* for 60 minutes, which resulted in a supernate (S2) containing cytosol and a pellet (P2) containing organelles. After heat treatment (80 °C) for 1 hour, S2 was fractionated by 10-minute 30,000 x *g* centrifugation into a supernate (S3) containing HSP and a pellet (P3) (= HDP) (Bebianno and Langston, 1992). P2 was centrifuged further at 5,000 x *g* for 10 minutes with sodium hydroxide (1 M) to isolate MRG (P4) from other cellular fragments ("cellular debris") (S4) (Silverman *et al.*, 1983). All fractions were processed for metal analyses as described below.

Analyses of Metals in Benthic Macroinvertebrate Prey and Mummichogs

Resultant supernates and pellets from fractionations as well as homogenized whole body of mummichogs were oven-dried (~70 °C) for 24 to 48 hours and weighed (dry weight). Samples were then digested under reflux with concentrated Trace Metal Grade nitric acid (5 ml) overnight at room temperature (~20 ºC), and subsequently on a hotplate (~80 ºC) for ~48 to 72 hours (Csuros and Csuros, 2002). Once digested, samples were evaporated to dryness, re-suspended in 2% nitric acid (8 ml), and filtered (0.45 μm). Metal concentrations in samples were analyzed with graphite furnace atomic absorption spectrometer for cadmium (Cd), copper (Cu), and lead (Pb), or flame atomic absorption spectrophotometer for zinc (Zn) (Perkin Elmer 3100AAS with AS-60).

As quality assurance, standard reference material (mussel tissue, SRM 2976, National Institute of Standards and Technology, USA) was processed and analyzed for Cd, Cu, Pb, and Zn, as described above. The average recovery rates of Cd, Cu, Pb, and Zn were 95.3, 100.3, 63.5, and 96.3%, respectively. Procedural and reagent blanks were

also analyzed for potential secondary metal contamination. Select calibration standard solutions of each metal were analyzed every 10 samples. When the deviation from the initial values was more than ± 10%, the instrument was recalibrated. The correlation coefficients of calibration curves were maintained > 0.999 for the analysis. All standard solutions and samples were prepared with NANOpure® (reagent-grade) water. All glassware was soaked in 10% hydrochloric acid overnight, rinsed once with deionized water, and rinsed twice with NANOpure® water.

Statistical Analyses

The normality of data was tested using Shapiro-Wilk's *W* test. The homogeneity of variance was tested using Levene's test. Proportional data were arcsine-transformed, and concentration data were $\log_{10}$-transformed before analyses, when necessary. The statistical significance of differences in whole body burdens of mummichogs among study sites was tested using 1-way analysis of variance (ANOVA), which, if significant, was followed by Tukey's honestly significant difference (HSD) test. The relationships between trace metals associated with TAM and whole body burdens in *Palaemonetes spp.* and *Nereis spp.*, were analyzed with model I regression (Sokal and Rohlf, 1995). The relationships between trace metals associated TAM in *Palaemonetes spp.* or *Nereis spp.*, and whole body burdens in mummichogs were analyzed with model II (reduced major axis) regression (Sokal and Rohlf, 1995). All univariate statistical analyses were performed using Statistica 7.1 (Statsoft, Inc®, USA).

Relative dissimilarities in intracellular partitioning of metals in mummichogs (2004) among populations were graphically analyzed using non-metric multidimensional

scaling (nMDS) with Bray-Curtis similarity index on square root-transformed data (Clarke, 1993; Clarke and Gorley, 2006). The reliability of nMDS representations of metal intracellular partitioning among sites was assessed with the stress value; stress < 0.2 was considered to be acceptable (Clarke and Warwick, 2001). The statistical significance of differences in metal intracellular partitioning among populations was tested using 1-way analysis of similarity (ANOSIM) with randomization permutation (n = 9999) at the significance level of 5%, which, if significant, was followed by pairwise comparisons (Clarke, 1993; Clarke and Gorley, 2006). Then, 1-way analysis of similarity percentages (SIMPER) was used to identify intracellular fractions contributing to dissimilarities among sites (Clarke, 1993; Clarke and Warwick, 1994). All analyses of nMDS, ANOSIM, and SIMPER were performed using PRIMER v6.1.9 (PRIMER-E Ltd, Plymouth, UK).

RESULTS

Intracellular Partitioning of Trace Metals to the TAM Compartment in Prey

Metal partitioning patterns in prey were highly species- and metal- specific. The concentration of Cd partitioned to the TAM compartment (TAM-[Cd]) was significantly correlated with Cd whole body burden in *Palaemonetes spp.* in both 2001 and 2004 (2001: $R^2 = 0.96$, $p < 0.001$, Fig. 4-1a; 2004: $R^2 = 0.85$, $p < 0.001$, Fig. 4-2a). In 2001, TAM-[Cd] in *Palaemonetes spp.* was lowest at Great Kills Harbor and Lemon Creek (~0.05 $\mu g \cdot g^{-1}$) and highest at Richmond Creek (0.22 $\mu g \cdot g^{-1}$) (Fig. 4-1a). In 2004, TAM-[Cd] in *Palaemonetes spp.* was lowest at Great Kills Harbor (0.03 $\mu g \cdot g^{-1}$) and highest at Richmond Creek (0.05 $\mu g \cdot g^{-1}$) (Fig. 4-2a). In 2001, although there was a significant

correlation between the proportion of Cd associated with the TAM compartment (TAM-Cd%) and the Cd whole body burden in *Palaemonetes spp.* ($R^2 = 0.34$, $p < 0.05$), TAM-Cd% in *Palaemonetes spp.* was approximately 40% of the Cd whole body burden at all study sites (Fig. 4-1c). In contrast, in 2004, there was no relationship between TAM-Cd% and the Cd whole body burden in *Palaemonetes spp.* (Fig. 4-2c).

In *Nereis spp.*, there was a significant correlation between TAM-[Cd] and Cd whole body burden in both 2001 and 2004 (2001: $R^2 = 0.47$, $p < 0.001$, Fig. 4-1b; 2004: $R^2 = 0.64$, $p < 0.001$, 4-2b) with a disproportionately low TAM-[Cd] at Main Creek (0.30 $\mu g \cdot g^{-1}$) in 2001 (Fig. 4-1b). In 2001, TAM-Cd% in *Nereis spp.* varied from 26.9% at Main Creek to 74.8% at Great Kills Harbor, and was negatively correlated with the Cd whole body burden ($R^2 = 0.76$, $p < 0.001$, Fig. 4-1d). In 2004, however, there was no relationship between TAM-Cd% and Cd whole body burden in *Nereis spp.* (Fig. 4-2d).

The concentration of Pb in the TAM compartment (TAM-[Pb]) in *Palaemonetes spp.* was significantly correlated with the Pb whole body burden in both 2001 and 2004 (2001: $R^2 = 0.49$, $p < 0.001$, Fig. 4-3a; 2004: $R^2 = 0.37$, $p < 0.001$, Fig. 4-4a). In 2001, TAM-[Pb] in *Palaemonetes spp.* was lowest at Great Kills Harbor (0.04 $\mu g \cdot g^{-1}$) and highest at Main Creek and Mill Creek (~0.13 $\mu g \cdot g^{-1}$) (Fig. 4-3a). In 2004, TAM-[Pb] in *Palaemonetes spp.* was lowest at Lemon Creek (0.25 $\mu g \cdot g^{-1}$) and highest at Great Kills Harbor (0.43 $\mu g \cdot g^{-1}$) (Fig. 4-4a). In contrast, the proportion of Pb in the TAM compartment (TAM-Pb%) in *Palaemonetes spp.* was negatively correlated with the Pb whole body burden in both 2001 and 2004 (2001: $R^2 = 0.33$, $p < 0.001$, Fig. 4-3c; 2004: $R^2 = 0.42$, $p < 0.001$, Fig. 4-4c). In 2001, TAM-Pb% in *Palaemonetes spp.* varied from ~25% at Neck Creek and Richmond Creek to 63.86% at Great Kills Harbor (Fig. 4-3c),

while in 2004, TAM-Pb% in *Palaemonetes spp.* varied from 34.8% at Mill Creek to ~52% at Lemon Creek, Richmond Creek, and Great Kills Harbor (Fig. 4-4c).

In *Nereis spp.*, both TAM-[Pb] and TAM-Pb% were significantly correlated with the Pb whole body burden in 2001 (TAM-[Pb]: $R^2 = 0.33$, $p < 0.001$, Fig. 4-3b; TAM-Pb%: $R^2 = 0.57$, $p < 0.01$, Fig. 4-3d), but due to large variability, these relationships were much less clear than those in *Palaemonetes spp*. (Fig. 4-3b and 4-3d). Despite its high whole body burden, TAM-[Pb] and TAM-Pb% in *Nereis spp.* at Main Creek were disproportionately lower than those at the other sites. In 2004, both TAM-[Pb] and TAM-Pb% were also significantly correlated with the whole body burden (TAM-[Pb]: $R^2 = 0.56$, $p < 0.01$, Fig. 4-4b; TAM-Pb%: $R^2 = 0.52$, $p < 0.05$, Fig. 4-4d), but varied relatively little among sites.

Significant correlations were observed between the concentration of Cu in the TAM compartment (TAM-[Cu]) and the Cu whole body burden in *Palaemonetes spp.* in both 2001 and 2004 (2001: $R^2 = 0.42$, $p < 0.01$, Fig. 4-5a; 2004: $R^2 = 0.87$, $p < 0.001$, Fig. 4-6a). In 2001, TAM-[Cu] in *Palaemonetes spp.* was lowest at Lemon Creek and Mill Creek (~65 $\mu g \cdot g^{-1}$) and highest at Neck Creek and Main Creek (~98 $\mu g \cdot g^{-1}$) (Fig. 4-5a), while TAM-[Cu] in *Palaemonetes spp.* varied relatively little in 2004 (~110 to 130 $\mu g \cdot g^{-1}$) (Fig. 4-6a). The proportion of Cu associated with the TAM compartment (TAM-Cu%) in *Palaemonetes spp.* remained relatively constant (~80%) across the sites in 2001, with the exception of Mill Creek (~60%), resulting in no relationship with the whole body burdens (Fig. 4-5c). Similarly, although TAM-Cu% was significantly correlated with the whole body burden in *Palaemonetes spp.* in 2004 ($R^2 = 0.22$, $p < 0.05$), it generally remained approximately 80% at all sites, except for Mill Creek (~60%) (Fig. 4-6c).

In *Nereis spp.*, TAM-[Cu] was significantly correlated with the Cu whole body burden in both 2001 and 2004 (2001: $R^2 = 0.43$, $p < 0.001$, Fig. 4-5d; 2004: $R^2 = 0.56$, $p < 0.001$, Fig. 4-6d), but TAM-[Cu] at Main Creek in 2001 was disproportionately low (Fig. 4-5d). In both 2001 and 2004, there was no clear relationship between TAM-Cu% and whole body burden in *Nereis spp.* (Fig. 4-5d and 4-6d).

Both the concentration and proportion of Zn associated with the TAM compartment (TAM-[Zn] and TAM-Zn%, respectively) were significantly correlated with the Zn whole body burden in *Palaemonetes spp.* in 2001 (TAM-[Zn]: $R^2 = 0.33$, $p < 0.01$, Fig. 4-7a; TAM-Zn%: $R^2 = 0.33$, $p < 0.01$, Fig. 4-7c). However, both TAM-[Zn] and TAM-Zn% in *Palaemonetes spp.* were highly similar among sites (40 to 60 $\mu g \cdot g^{-1}$ and ~60%, respectively) (Fig. 4-7a and 4-7c).

In *Nereis spp.*, TAM-[Zn] was significantly correlated with the Zn whole body burden (100 to 180 $\mu g \cdot g^{-1}$) in 2001 ($R^2 = 0.49$; $p < 0.001$, Fig. 4-7c). TAM-[Zn] in *Palaemonetes spp.* was lowest at Richmond Creek (60.5 $\mu g \cdot g^{-1}$) and highest at Lemon Creek (98.5 $\mu g \cdot g^{-1}$) (Fig. 4-7c). In contrast, TAM-Zn% in *Nereis spp.* remained relatively constant (~60%) across sites (Fig. 4-7d).

Metal Bioaccumulation in Mummichogs

In 2001, there were significant differences in whole body burdens of Cd, Pb, Cu, and Zn in mummichogs among sites (1-way ANOVA, $p < 0.05$, Fig. 4-8a through 4-8d). The whole body burdens of Cd varied from 0.03 $\mu g \cdot g^{-1}$ at Richmond Creek to 0.10 $\mu g \cdot g^{-1}$ at Great Kills Harbor (Fig. 4-8a). The whole body burdens of Pb varied from ~0.25 $\mu g \cdot g^{-1}$ at Great Kills Harbor and Richmond Creek to ~0.90 $\mu g \cdot g^{-1}$ at Neck Creek, Main Creek,

and Mill Creek (Fig. 4-8b). The whole body burdens of Cu were similar among sites (~8 $\mu g \cdot g^{-1}$), except for Neck Creek (18.5 $\mu g \cdot g^{-1}$) (Fig. 4-8c). The whole body burdens of Zn varied from ~140 $\mu g \cdot g^{-1}$ at Lemon Creek, Main Creek, and Richmond Creek to 193.7 $\mu g \cdot g^{-1}$ at Neck Creek (Fig. 4-8d).

In 2004, there was no significant difference in the bioaccumulation of metals in mummichogs among sites (Cd: ~0.04 $\mu g \cdot g^{-1}$, Fig. 4-9a; Cu: ~10 $\mu g \cdot g^{-1}$, Fig. 4-9c; Zn: ~166 $\mu g \cdot g^{-1}$, Fig. 4-9d), except for Pb. The Pb whole body burden in mummichogs from Mill Creek was significant higher (1.3 $\mu g \cdot g^{-1}$) than those from the other sites (~0.7 $\mu g \cdot g^{-1}$) (Tukey's HSD test, $p < 0.05$) (Fig. 4-9b).

Relationship between TAM in Prey and Metal Bioaccumulation in Mummichogs

Significant relationships with the whole body burdens in mummichogs were observed only for *Palaemonetes spp.* TAM-[Pb] in 2001 and TAM-[Cd] in 2004 (TAM-[Pb]: $y = 6.42x + 0.11$, $R^2 = 0.63$, $p < 0.01$, Fig. 4-10; TAM-[Cd]: $y = 0.97x + 7.05$, $R^2 = 0.81$, $p < 0.01$, Fig. 4-11). In both of these cases, the Pb and Cd whole body burdens in *Palaemonetes spp.* were randomly distributed without any consistent relationship with the whole body burdens in mummichogs (Fig. 4-10 and 4-11).

Intracellular Partitioning of Metals in Mummichogs

The 2-dimensional representation of nMDS on population-specific metal intracellular partitioning in mummichogs showed that the data points in all the nMDS plots for Cd, Cu, and Zn were generally interspersed with each other (Fig. 4-12a through

4-12d). In contrast, the nMDS plot for Pb showed the intracellular partitioning in mummichogs from Great Kills Harbor and Mill Creek were clearly distinguishable from the other sites (Fig. 4-12b). The stress levels of all the nMDS plots were less than 0.2, indicating reasonable representations for the relative similarity among populations (Fig. 4-12a through 4-12d).

The results of nMDS corresponded to 1-way ANOSIM on the metal intracellular partitioning data. Although the intracellular partitioning of Cd and Zn were significantly different among sites (Cd: p = 1.9%, Zn: p = 0.05%), the global R values for the among-site comparisons (Cd: R = 0.116, Zn: R = 0.207) were much lower than that for Pb (R = 0.671, p = 0.05%). There was no significant difference in Cu partitioning among sites (R = 0.059, p = 11%). The *post-hoc* pairwise comparisons indicated that a significant difference in Cd partitioning was observed only between Great Kills Harbor and Main Creek (R = 0.246, p = 1.5%), Lemon Creek and Neck Creek (R = 0.263, p = 1.4%), and Neck Creek and Mill Creek (R = 0.241, p = 4.7%). For Pb, with an exception of a comparison between Neck Creek and Richmond Creek (R = 0.121, p = 11.1%), all pairwise comparisons were significant (R = 0.252 to 1.000, p = 0.02 to 3.2%). The Zn partitioning in mummichogs from Lemon Creek was significantly different from that in fish from Neck Creek (R = 0.498, p = 0.2%), Richmond Creek (R = 0.508, p = 0.4%), and Main Creek (R = 0.422, p = 0.4%), while the Zn partitioning in mummichogs from Great Kills Harbor was significantly different only from that in fish from Neck Creek (R = 0.354, p = 0.3%).

The intracellular partitioning patterns of trace metals in mummichogs were highly metal- and population-specific (Fig. 4-13 through 4-16). The proportions of Cd

partitioned to biologically-detoxified metals (BDM% = heat-stable proteins or HSP% + metal-rich granules or MRG%) varied considerably among populations (26% at Neck Creek to 40.8% at Mill Creek) (Fig. 4-13). In contrast, the proportions of Cd partitioned to metal-sensitive fractions (MSF% = organelles % + heat-denaturable proteins or HDP%) in mummichogs were fairly similar among populations (~21%), except for the Lemon Creek population (30.5%) (Fig. 4-13). With an exception of mummichogs from Great Kills Harbor, the majority of Pb (46.2 to 63.1%) was generally stored in the BDM compartment (Fig. 4-14). Furthermore, more than 50% of Pb in mummichogs from Mill Creek was partitioned to MRG, whereas only ~8% was stored in the MSF compartment (Fig. 4-14). In contrast, a relatively higher proportion of Pb in mummichogs from Great Kills Harbor (20.1%) was stored in HSP than fish from the other sites (5.1 to 15.5%) (Fig. 4-14). Mummichogs stored a large proportion of Zn (37.4 to 45.9%) in the BDM compartment, particularly MRG (35.0 to 43.1%) at all sites (Fig. 4-16).

The analyses of 1-way SIMPER indicated that the difference in Cd partitioning between Great Kills Harbor and Main Creek was due to metals partitioned to organelles and MRG (relative % contributions to dissimilarity = 33.24 and 32.87, respectively), while MRG and HSP were responsible for the differences between Lemon Creek and Neck Creek (relative % contributions to dissimilarity = 31.31 by MRG and 29.28 by HSP), and Neck Creek and Mill Creek (relative % contributions to dissimilarity = 30.63 by MRG and 26.06 by HSP). For Pb, significant differences among populations were mostly due to MRG (relative % contributions to dissimilarity = 27.52 to 49.83). However, the Pb partitioning in mummichogs from Lemon Creek was different from Main Creek, Neck Creek, and Richmond Creek, due to the differences in organelles and

HDP (relative % contributions to dissimilarity = ~40.5 by organelles and ~43.5 by HDP). Similarly, the Pb partitioning in mummichogs from Main Creek was different from Richmond Creek and Neck Creek due to the differences in organelles and HDP (relative % contributions to dissimilarity = ~30.2 by organelles and ~38.5 by HDP). The significant differences in Zn partitioning were all attributed to the differences in HDP (relative % contributions to dissimilarity = 39.68 to 52.63).

DISCUSSION

The relevance of intracellular partitioning of trace metals to metal tolerance has been increasingly recognized for various marine and freshwater organisms in metal-polluted habitats (e.g., Klerks and Bartholomew, 1991; Cain and Luoma, 1998; Mouneyrac *et al.*, 2003; Campbell *et al.*, 2005). However, secondary implications of metal intracellular partitioning in prey to their predators in the field setting have not been fully explored. Some studies have demonstrated that metal detoxification strategies by prey can influence metal trophic transfer (e.g., Wallace *et al.*, 1998; Rainbow *et al.*, 2004; Rainbow *et al.*, 2006b). Although there have been many field studies on metal pollution impacts on fish (e.g., metal bioaccumulation and toxicity) in marine and freshwater ecosystems, these studies often focus on whole body burdens (e.g., Clements and Rees, 1997; Farag *et al.*, 1998; Farag *et al.*, 1999). Whole body burdens are, however, often not informative in understanding metal pollution impacts on fishes and shellfishes (O'Connor and Rachlin, 1982; Clements and Rees, 1997; Draves and Fox, 1998; Farag *et al.*, 1999). Farag et al. (1999) have, for example, demonstrated that metal bioaccumulation and toxic effects on feeding, growth, and survival of cutthroat trout (*Oncorhynchus clarki*) fed with

benthic macroinvertebrate prey from metal-polluted habitats (Coeur d'Alene River, Idaho, USA) did not correspond to whole body burdens in prey. Metals in macroinvertebrate prey from an intermediately polluted site were more bioavailable and subsequently caused stronger toxic effects in trout than those from a highly polluted site (Farag *et al.*, 1999).

The results from the current study indicated that metal intracellular partitioning in an omnivorous decapod *Palaemonetes spp.* and a deposit-feeder *Nereis spp.* in the Arthur Kill were highly species- and metal- specific. Although sediment-associated cadmium (Cd) levels in the Arthur Kill sites were relatively low (~2 to 5 $\mu g \cdot g^{-1}$) in 2001, a clear gradual shift in Cd intracellular partitioning in *Nereis spp.* was observed among sites. At one of the reference sites, Great Kills Harbor, for instance, nearly 80% of Cd whole body burden in the polychaetes was partitioned to the trophically available metal (TAM) compartment, whereas only 30% was partitioned to TAM at one of the Arthur Kill sites, Main Creek, resulting in a similar concentration of Cd associated with TAM (0.2 to 0.3 $\mu g \cdot g^{-1}$) at these sites. This site-specific differential partitioning suggests that *Nereis spp.* from the reference and less polluted sites may primarily rely on metal-binding proteins (part of TAM) for detoxification, while *Nereis spp.* from more polluted sites may sequester more Cd into insoluble granules (not part of TAM). Similar results were also observed in other annelid species [e.g., a deposit-feeding oligochaete *Limnodrilus hoffmeisteiri* (Wallace *et al.*, 1998) and polychaete *Hediste diversicolor* (Berthet *et al.*, 2003)]. This exposure-dependent 'detoxification strategy shift' from metal-binding proteins to metal-rich granules in benthic invertebrates may reflect levels of bioavailable metals in sediments (Ballan-Dufrançais *et al.*, 2001; Berthet *et al.*, 2003; Cain *et al.*,

2004). Since metal-rich granules are more durable and less likely to be recycled during cellular cycling than metal-binding proteins (Nott and Nicolaidou, 1996; Wallace *et al.*, 1998; Rainbow *et al.*, 2004), granules may be more efficient in detoxification in chronically metal-polluted habitats.

In contrast, the proportions of Cd partitioned to the TAM compartment were fairly uniform (~40%) in *Palaemonetes spp.* across sites, and Cd concentration in TAM consistently increased with Cd whole body burden in 2001, corresponding to a Cd concentration gradient in sediments. This differential intracellular partitioning between *Nereis spp.* and *Palaemonetes spp.* may be the result of the difference in feeding mode between these invertebrates (a deposit-feeder vs. an omnivore). As a deposit-feeder, *Nereis spp.* are likely to ingest a considerable amount of sediments to extract sufficient organic carbon (Cammen, 1979; Lopez and Levinton, 1987). As a result, these polychaetes may have been exposed to more sediment-bound Cd than *Palaemonetes spp.* in the Arthur Kill; Cd whole body burdens in *Nereis spp.* were more than twice as much as those in *Palaemonetes spp.* at most of the study sites. *Palaemonetes spp.* may ingest sediments along with animal or plant materials, but their exposure to sediment-bound metals is likely to be lower than that to deposit-feeding polychaetes.

Although there have been several studies on the effects of metal detoxification in prey on metal trophic transfer to predators in metal-polluted habitats (e.g., Nott and Nicolaidou, 1994; Wallace *et al.*, 1998; Rainbow *et al.*, 2004; Rainbow *et al.*, 2006b), it is unclear if detoxification strategies used by predators can simultaneously influence metal trophic transfer. Through the chronic exposure to trace metals, both prey and predators living in metal-polluted habitats are likely to independently develop

detoxification strategies. In general, many fishes are known to efficiently eliminate a large amount of Cd ingested with the diet (e.g., Pentreath, 1977; Weis, 1988; Harrison and Klaverkamp, 1989; Harrison and Curtis, 1992; Baines *et al.*, 2002; Seebaugh *et al.*, 2005). Feeding experiments using the reference population (Lemon Creek) have shown that mummichogs are able to eliminate more than 90% of ingested Cd in *Palaemonetes pugio* (Seebaugh *et al.*, 2005). It is thus not surprising that the populations of mummichogs from chronically Cd-polluted habitats can also eliminate the majority of trophically available Cd in ingested prey.

In the current study, despite considerable differences in Cd trophic availability from invertebrate prey species among sites, Cd bioaccumulation in mummichogs varied surprisingly little in 2001. The results from 2004, however, indicated that Cd whole body burden in mummichogs was strongly associated with the trophically available fraction of Cd (i.e., TAM-[Cd]) in *Palaemonetes spp.* (incidentally, sediment-bound Cd as well as *Palaemonetes spp*. TAM-[Cd] in 2004 were more than 50% lower than those in 2001 at most of the sites). This relationship between Cd intracellular partitioning in *Palaemonetes spp.* and Cd bioaccumulation in mummichogs may provide some useful insights into Cd trophic availability to mummichogs in the Arthur Kill. For example, despite a similar Cd whole body burden in *Palaemonetes spp.* from Mill Creek, Richmond Creek, and Main Creek, there was a substantial difference in TAM-Cd% among these sites (46.8%, 59.1% and 73.1%, respectively). This difference was clearly reflected in the Cd bioaccumulation in mummichogs at these sites.

Cadmium intracellular partitioning in mummichogs also revealed their population-specific differential Cd handing in the Arthur Kill. Although it was not apparent in the

whole body burdens, Cd intracellular partitioning in mummichogs clearly indicated that the Mill Creek population was able to store a higher proportion of Cd in the biologically-detoxified metal (BDM) compartment (especially metal-rich granules), suggesting its better capacity to handle Cd, than the other Arthur Kill as well as reference populations.

Many experimental studies on metal trophic transfer to marine and freshwater organisms are often conducted using a pulse-chase feeding technique with radioisotopes (e.g., Reinfelder and Fisher, 1994; Wallace and Lopez, 1997; Wang and Fisher, 1999). As there is no usable radioisotope available for lead (Pb), however, its trophic transfer efficiency is not fully explored for many organisms. Pb is often inefficiently transferred from prey to predators (e.g., Ward *et al.*, 1986; Chen and Folt, 2000; Chen *et al.*, 2000; Besser *et al.*, 2001; Mikac *et al.*, 2001). However, a potential cause of low Pb trophic transfer has not been well understood. Rainbow *et al.* (2006a) have experimentally demonstrated that benthic invertebrate predators (*Nereis virens* and *Palaemonetes varians*) accumulated a considerably low amount of Pb from a deposit-feeding polychaete (*Nereis diversicolor*) from highly metal-polluted creeks in southwest England. This low Pb trophic transfer efficiency may be the result of its high affinity to insoluble granules (not part of TAM) in prey (Rainbow *et al.*, 2006a). A few studies have also shown that metal-tolerant aquatic insects living in metal-polluted habitats sequester a substantial amount of Pb (more than 95% of whole body burdens) into an insoluble cellular component (Cain and Luoma, 1998; Cain *et al.*, 2000). In the present study, similar results were also observed for both marine benthic invertebrate species. Although there were considerable differences in Pb whole body burdens between *Palaemonetes spp.* and *Nereis spp.* in both 2001 and 2004, in general, the proportion of Pb associated

with TAM (TAM-Pb%) in both species gradually decreased from low to high Pb-polluted sites (i.e., a reduction in Pb trophic availability to mummichogs). For example, despite the highest Pb whole body burden, TAM-Pb% in *Nereis spp.* from Main Creek was the lowest among sites in 2001.

The Pb bioaccumulation in mummichogs, however, reflected the differential Pb intracellular partitioning (i.e., TAM-[Pb]) only in *Palaemonetes spp.* in 2001. This relationship between TAM-[Pb] in *Palaemonetes spp.* and Pb whole body burden in mummichogs may explain certain differential Pb bioaccumulation patterns in mummichogs. For example, despite their similar Pb whole body burdens (~0.23 $\mu g \cdot g^{-1}$), TAM-Pb% in *Palaemonetes spp.* from Main Creek was twice as much as that in shrimp from Richmond Creek (53.7% vs. 27.2%, respectively). This differential Pb intracellular partitioning in *Palaemonetes spp.* was clearly reflected in Pb bioaccumulation in mummichogs from these sites (Main Creek: 0.94 $\mu g \cdot g^{-1}$ vs. Richmond Creek: 0.21 $\mu g \cdot g^{-1}$). A cause of this differential Pb intracellular partitioning in *Palaemonetes spp.* between these sites (both tributaries of Fresh Kill Complex) is not clear, as the concentrations of sediment-bound Pb at these sites were also similar (~60 $\mu g \cdot g^{-1}$) in 2001.

Despite the lack of difference in Pb whole body burden in mummichogs among sites (except for Mill Creek) in 2004, there was a substantial population-specific difference in Pb intracellular partitioning. The majority of Pb in the Arthur Kill populations of mummichogs was stored in metal-rich granules of the BDM compartment, whereas the reference populations sequestered more Pb into metal-binding proteins as well as metal-sensitive fractions (MSF = organelles and enzymes) than the Arthur Kill populations. These differential partitioning patterns suggest that mummichogs from the

Arthur Kill sites (especially Mill Creek) may be able to tolerate trophically available Pb from prey by sequestering it into the detoxifying cellular components, without exhibiting any sublethal effect (e.g., bioenergetics, Chapter 5).

Intracellular partitioning of essential metals, copper (Cu) and zinc (Zn), in both invertebrate prey species varied relatively little among sites. Despite substantially elevated levels of these metals in sediments at one of the Arthur Kill sites, Mill Creek (Zn: 3 to 5-fold and Cu: 4 to 16-fold more than the other sites), the variability in metals associated with the TAM compartment in both *Palaemonetes spp.* and *Nereis spp.* was generally low among sites. This low variability among sites as well as relatively high TAM-Cu% and TAM-Zn% suggest that these macroinvertebrates may be able to regulate or at least tolerate elevated levels of these metals more than non-essential metals in the Arthur Kill. Similar results have also been observed in other marine and freshwater organisms (e.g., Cain and Luoma, 1998; Cain *et al.*, 2000; Mouneyrac *et al.*, 2001; Berthet *et al.*, 2003). Furthermore, high TAM-[Cu] in *Palaemonetes spp.* observed in the current study, compared to that in *Nereis spp.*, is likely to be due to the requirement of Cu in haemocyanin by crustaceans (White and Rainbow, 1985; Depledge and Bjerregaard, 1989; Rainbow, 1993; Abdennour, 1997).

With an exception of Cu in fish from Neck Creek in 2001, Cu and Zn bioaccumulations in mummichogs were also fairly similar among sites (~10 μg $Cu \cdot g^{-1}$ and ~150 μg $Zn \cdot g^{-1}$, respectively). Furthermore, there was no difference in Cu intracellular partitioning in mummichogs among sites. In spite of a highly elevated potential dietary exposure (i.e., TAM-[Cu]) from *Palaemonetes spp.*, the majority of ingested Cu may have been efficiently eliminated from mummichogs. Weis and Weis

(1999) have also demonstrated in a field transplant experiment that, compared to crustaceans such as *Palaemonetes pugio*, mummichogs accumulated substantially lower Cu after 3 months. In contrast, both the Arthur Kill and reference populations of mummichogs accumulated a substantial amount of Zn in both 2001 and 2004. Compared to other metals including Cu, a large amount of Zn in mummichogs is usually deposited in calcified structures such as scales (Sauer and Watabe, 1984; 1989). In the present study, a substantial proportion of Zn was stored in the BDM compartment, particularly insoluble granules, within both the Arthur Kill and reference populations of mummichogs, suggesting that the temporary deposition of excess Zn in calcified structures may be a detoxification strategy for fish.

Experimental studies on metal trophic transfer are often conducted using a naïve population of predators that have not been exposed to elevated levels of trace metals in their natural habitats (e.g., Reinfelder and Fisher, 1994; Wang and Wong, 2003). As both prey and predators are chronically exposed to trace metals in metal-polluted habitats, they are likely to independently develop differential detoxification strategies. It may thus be misleading to directly extrapolate a relationship based on laboratory experiments to predict metal trophic transfer and bioaccumulation in the field setting. There is an urgent need to synthesize experimental findings and field observations to understand mechanisms involved in trace metal pollution in coastal ecosystems. The results of the present study suggest that metal intracellular partitioning within prey may be partially responsible for metal trophic transfer to a predator in metal-polluted habitats. However, there was also evidence that some predator-dependent processes (e.g., digestive processes) may have offset differential trophic availabilities from prey (e.g., Cd

bioaccumulation in mummichogs in 2001). Further studies still need to be conducted to understand the importance of both prey- and predator- dependent processes to assess trace metal pollution in coastal ecosystems (Clements and Newman, 2002; Wang, 2002; Rainbow *et al.*, 2007; Wallace *et al.*, 2008).

Table 4-1. Mean concentrations of metals ($\mu g \cdot g^{-1}$) in sediments collected from Lemon Creek, Great Kills Harbor, Mill Creek, Richmond Creek, Main Creek, and Neck Creek in 2001 and 2004†.

Trace Metals (μg/g)	Study Sites											
	Lemon Creek		Great Kills Harbor*		Mill Creek		Richmond Creek		Main Creek		Neck Creek	
	2001	2004	2001	2004	2001	2004	2001	2004	2001	2004	2001	2004
Cd	2.4	1.2	–	1.1	6.0	2.9	5.7	1.6	5.2	2.9	2.8	1.1
Cu	91.3	124.8	–	92.2	1483.5	911.5	266.9	99.7	294.4	216.5	238.8	152.5
Pb	27.5	83.9	–	98.7	402.8	655.5	63.8	91.9	58.0	171.3	80.4	214.7
Zn	107.8	220.5	–	188.4	555.9	1193.3	293.0	289.0	336.7	410.9	165.8	339.0

†Sources of the data: Ward (2002) for 2001 and Chapter 2 for 2004.
*Sediment samples from Great Kills Harbor were not available in 2001.

Figure 4-1. Relationships between Cd whole body burdens ($\mu g \cdot g^{-1}$) and concentrations of Cd ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Cd]) in (a) *Palaemonetes spp*. or (b) *Nereis spp*.; relationships between Cd whole body burdens ($\mu g \cdot g^{-1}$) and percentages of Cd associated with TAM (TAM-Cd%) in (c) *Palaemonetes spp*., or (d) *Nereis spp*. in 2001. Errors bars indicate ± 1 SE. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.

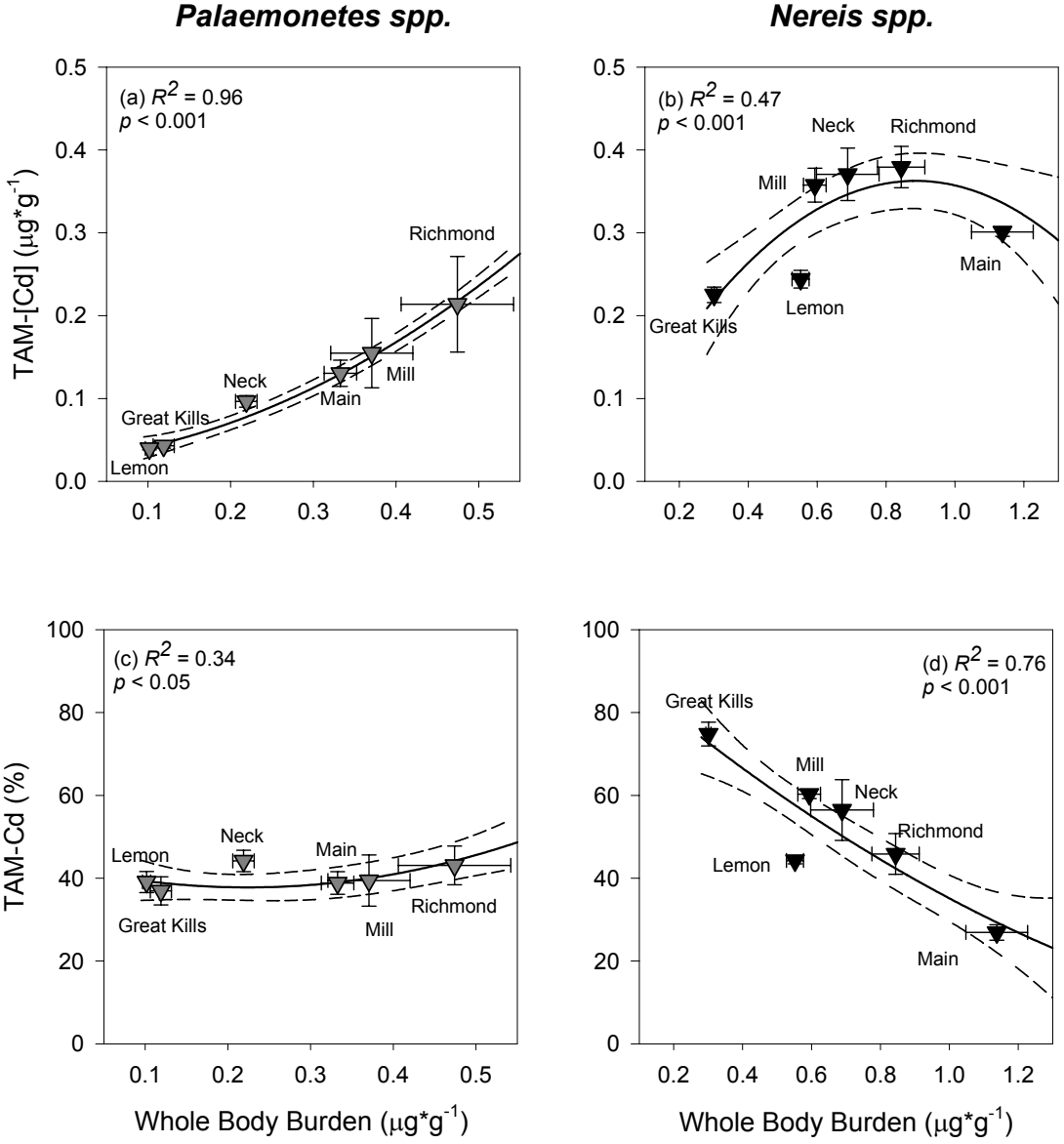


Figure 4-2. Relationships between Cd whole body burdens ($\mu g \cdot g^{-1}$) and concentrations of Cd ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Cd]) in (a) *Palaemonetes spp*. or (b) *Nereis spp*.; relationships between Cd whole body burdens ($\mu g \cdot g^{-1}$) and percentages of Cd associated with TAM (TAM-Cd%) in (c) *Palaemonetes spp*., or (d) *Nereis spp*. in 2004. Errors bars indicate ± 1 SE. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.

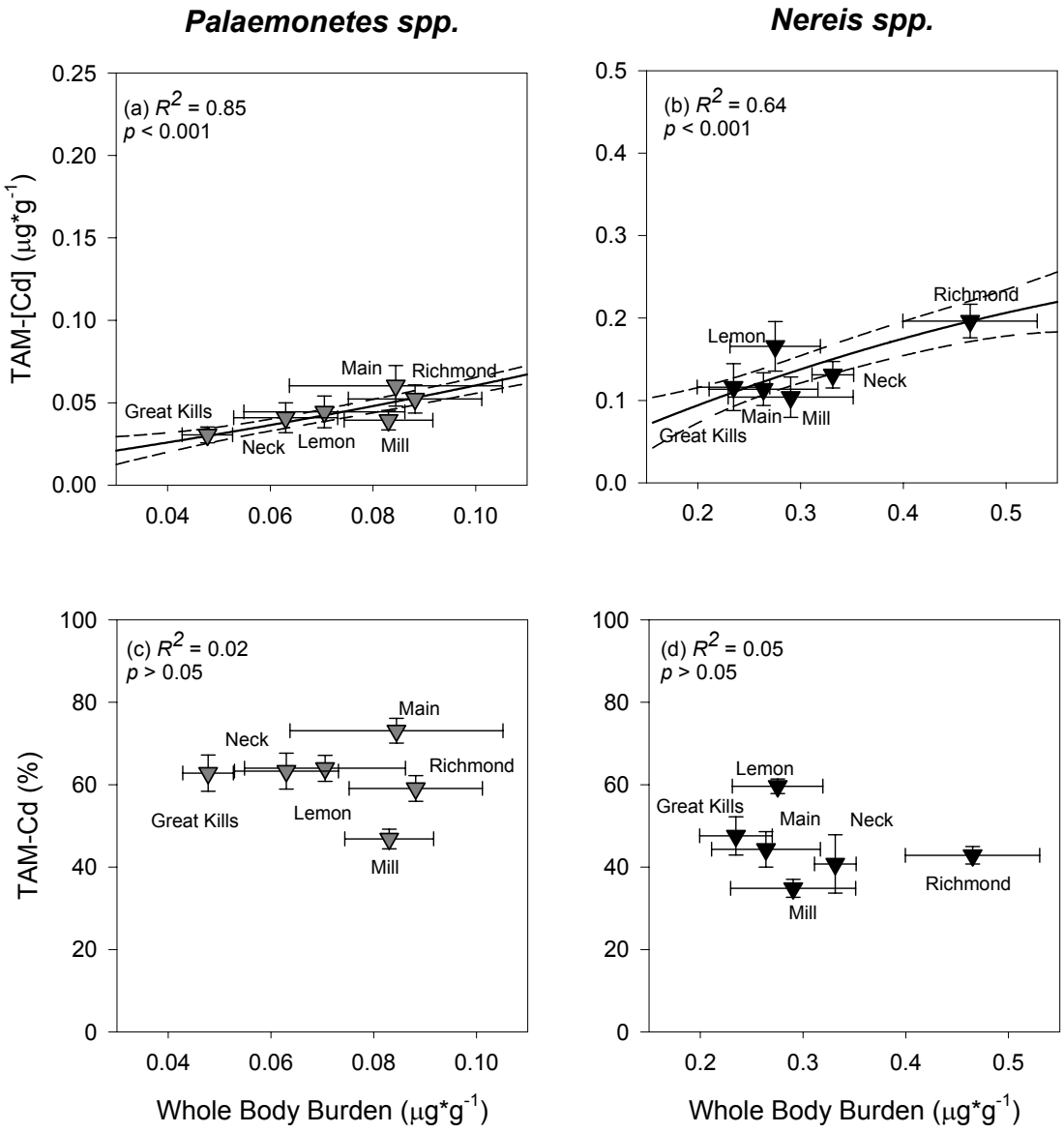


Figure 4-3. Relationships between Pb whole body burdens ($\mu g \cdot g^{-1}$) and concentrations of Pb ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Pb]) in (a) *Palaemonetes spp*. or (b) *Nereis spp*.; relationships between Pb whole body burdens ($\mu g \cdot g^{-1}$) and percentages of Pb associated with TAM (TAM-Pb%) in (c) *Palaemonetes spp*., or (d) *Nereis spp*. in 2001. Errors bars indicate ± 1 SE. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.

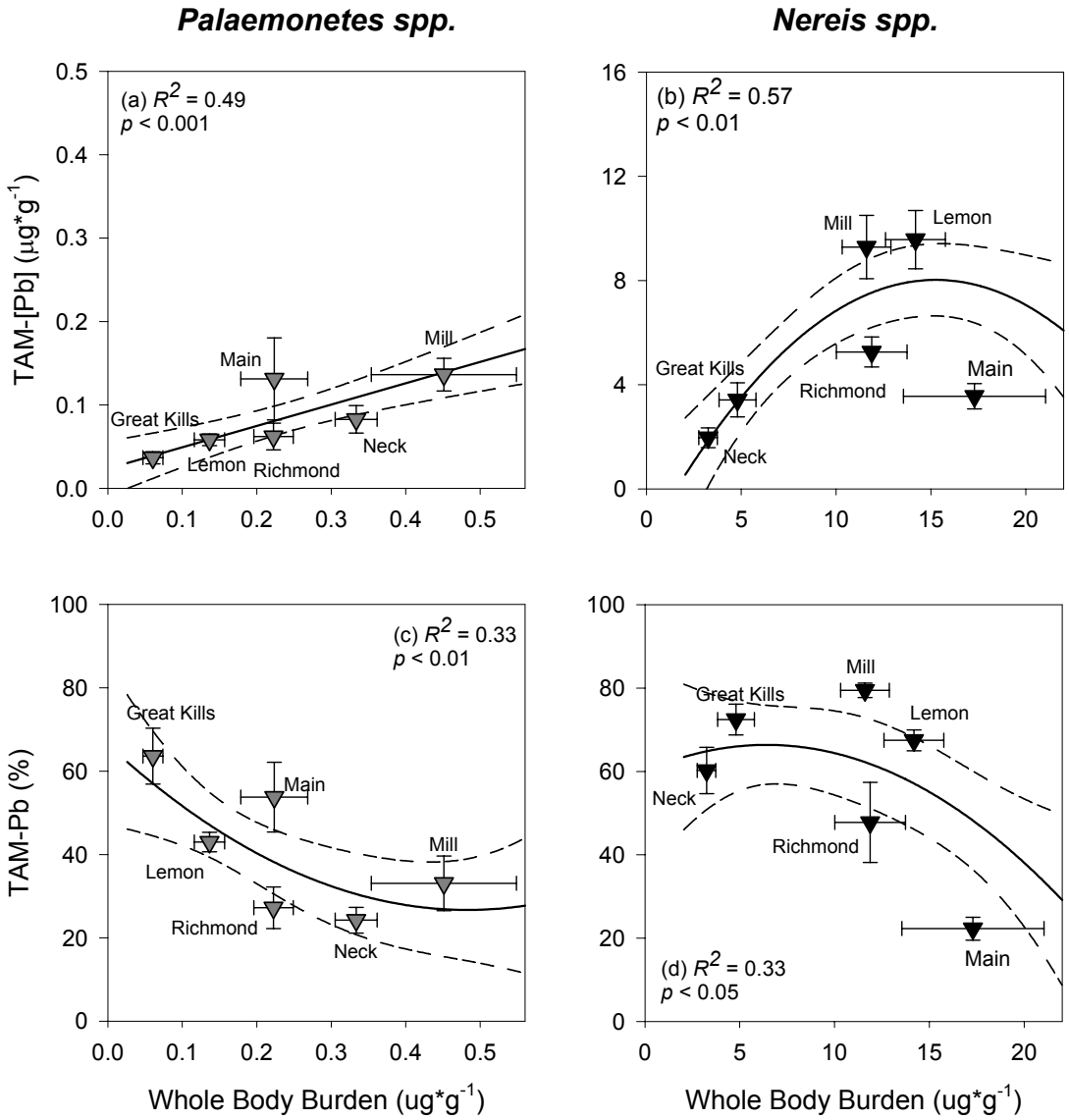


Figure 4-4. Relationships between Pb whole body burdens ($\mu g \cdot g^{-1}$) and concentrations of Pb ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Pb]) in (a) *Palaemonetes spp*. or (b) *Nereis spp*.; relationships between Pb whole body burdens ($\mu g \cdot g^{-1}$) and percentages of Pb associated with TAM (TAM-Pb%) in (c) *Palaemonetes spp*., or (d) *Nereis spp*. in 2004. Errors bars indicate ± 1 SE. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.

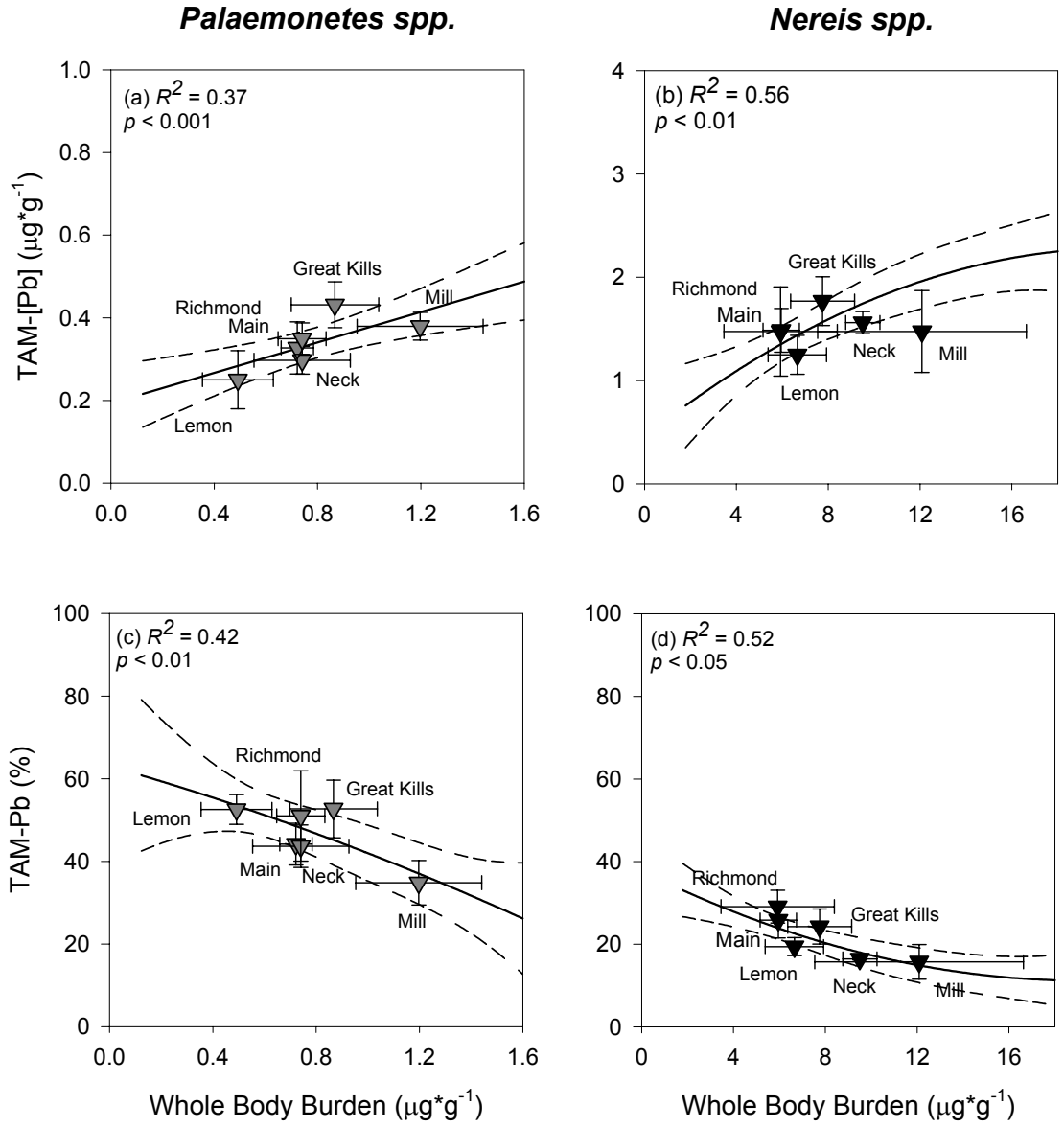


Figure 4-5. Relationships between Cu whole body burdens ($\mu g \cdot g^{-1}$) and concentrations of Cu ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Cu]) in (a) *Palaemonetes spp*. or (b) *Nereis spp*.; relationships between Cu whole body burdens ($\mu g \cdot g^{-1}$) and percentages of Cu associated with TAM (TAM-Cu%) in (c) *Palaemonetes spp*., or (d) *Nereis spp*. in 2001. Errors bars indicate ± 1 SE. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.

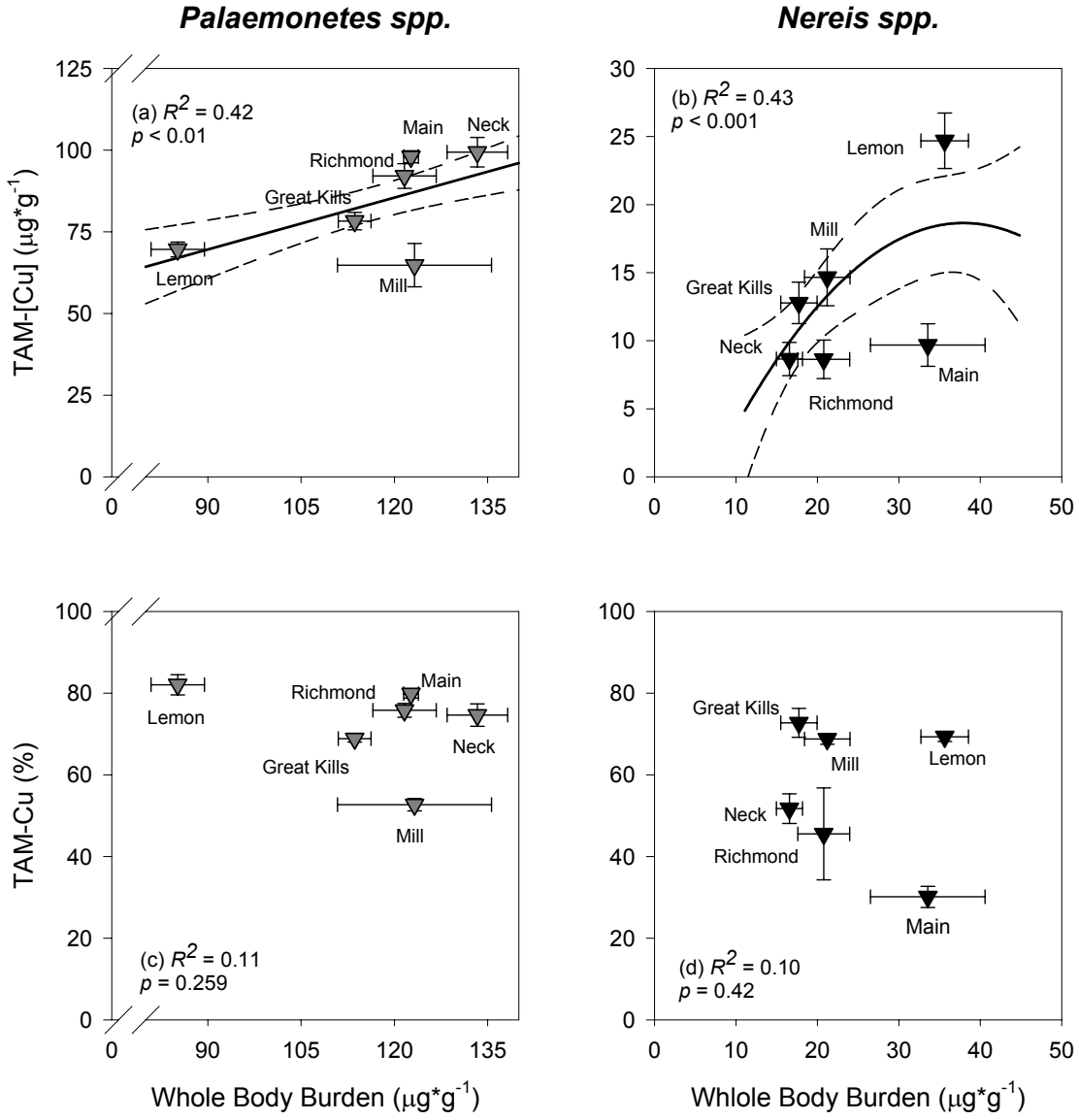


Figure 4-6. Relationships between Cu whole body burdens ($\mu g \cdot g^{-1}$) and concentrations of Cu ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Cu]) in (a) *Palaemonetes spp*. or (b) *Nereis spp*.; relationships between Cu whole body burdens ($\mu g \cdot g^{-1}$) and percentages of Cu associated with TAM (TAM-Cu%) in (c) *Palaemonetes spp*., or (d) *Nereis spp*. in 2004. Errors bars indicate ± 1 SE. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.

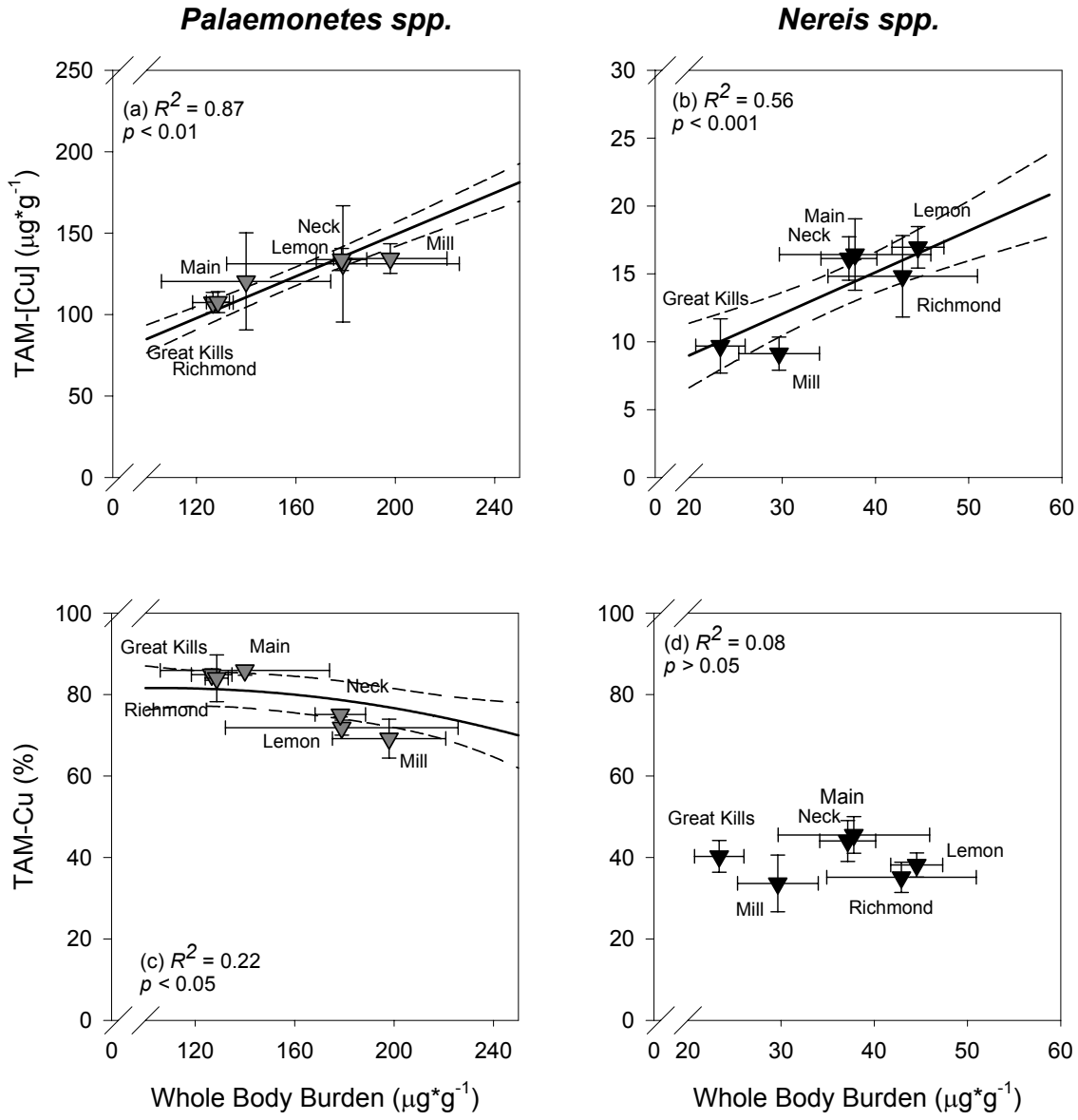


Figure 4-7. Relationships between Zn whole body burdens ($\mu g \cdot g^{-1}$) and concentrations of Zn ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Zn]) in (a) *Palaemonetes spp*. or (b) *Nereis spp*.; relationships between Zn whole body burdens ($\mu g \cdot g^{-1}$) and percentages of Zn associated with TAM (TAM-Zn%) in (c) *Palaemonetes spp*., or (d) *Nereis spp*. in 2001. Errors bars indicate ± 1 SE. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.

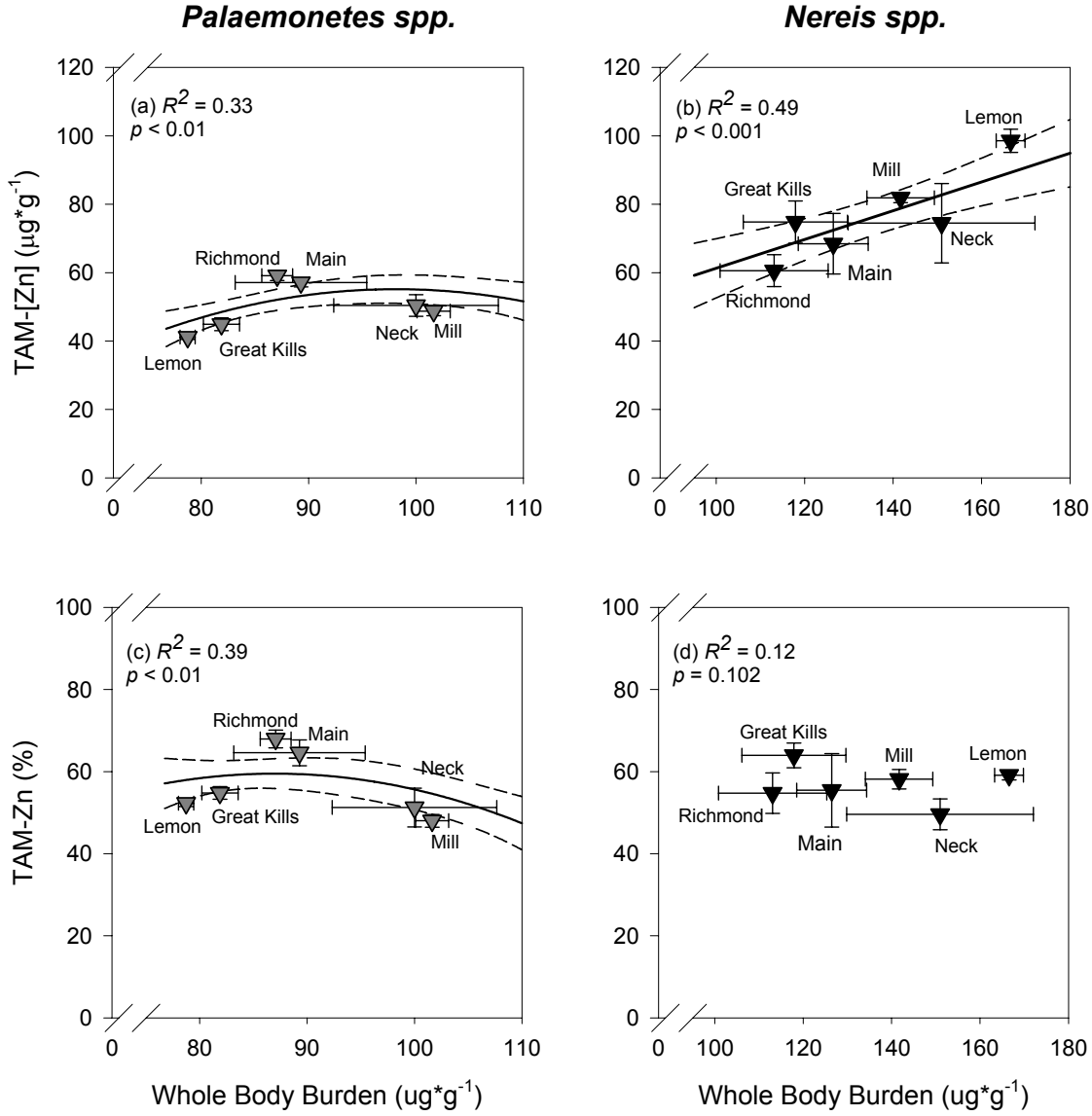


Figure 4-8. Concentrations ($\mu g \cdot g^{-1}$) of (a) Cd, (b) Pb, (c) Cu, and (d) Zn whole body burdens in mummichogs from Great Kills Harbor, Lemon Creek, Neck Creek, Main Creek, Richmond Creek, and Mill Creek in 2001. Errors bars indicate ± 1 SE. Different letters indicate statistically significant difference in whole body burdens in mummichogs among sites (1-way ANOVA followed by Tukey's HSD test).

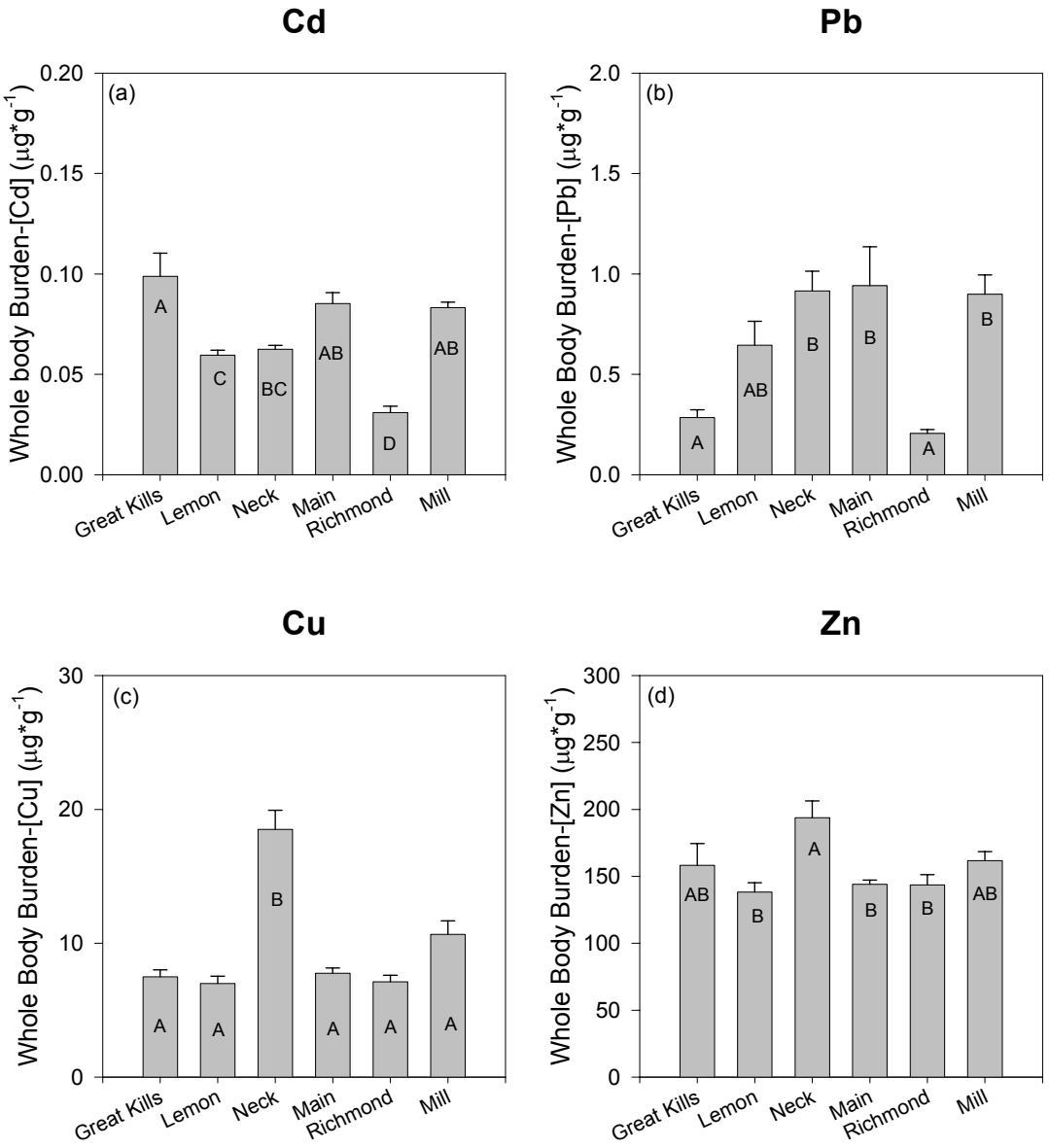


Figure 4-9. Concentrations ($\mu g \cdot g^{-1}$) of (a) Cd, (b) Pb, (c) Cu, and (d) Zn whole body burdens in mummichogs from Great Kills Harbor, Lemon Creek, Neck Creek, Main Creek, Richmond Creek, and Mill Creek in 2004. Errors bars indicate ± 1 SE. Different letters indicate statistically significant difference in whole body burdens in mummichogs among sites (1-way ANOVA followed by Tukey's HSD test). N/S = not significant.

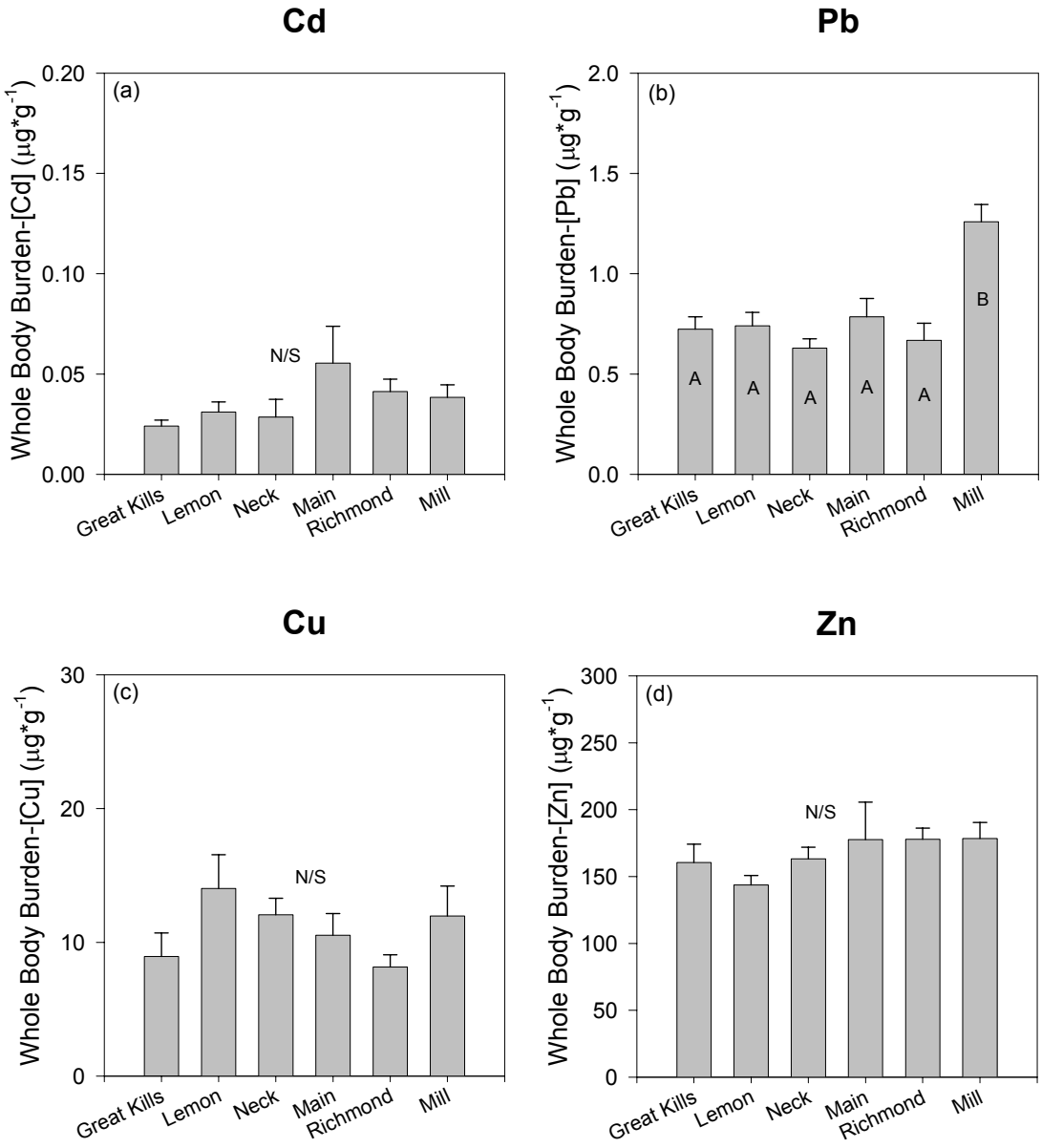


Figure 4-10. Relationships between Pb whole body burdens ($\mu g \cdot g^{-1}$) in mummichogs and concentrations of Pb ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Pb]) in *Palaemonetes spp.* (▼), or Pb whole body burdens in *Palaemonetes spp*. (●) in 2001. The solid line indicates least squares regression between TAM-[Pb] in *Palaemonetes spp*. and Pb whole body burdens in mummichogs.

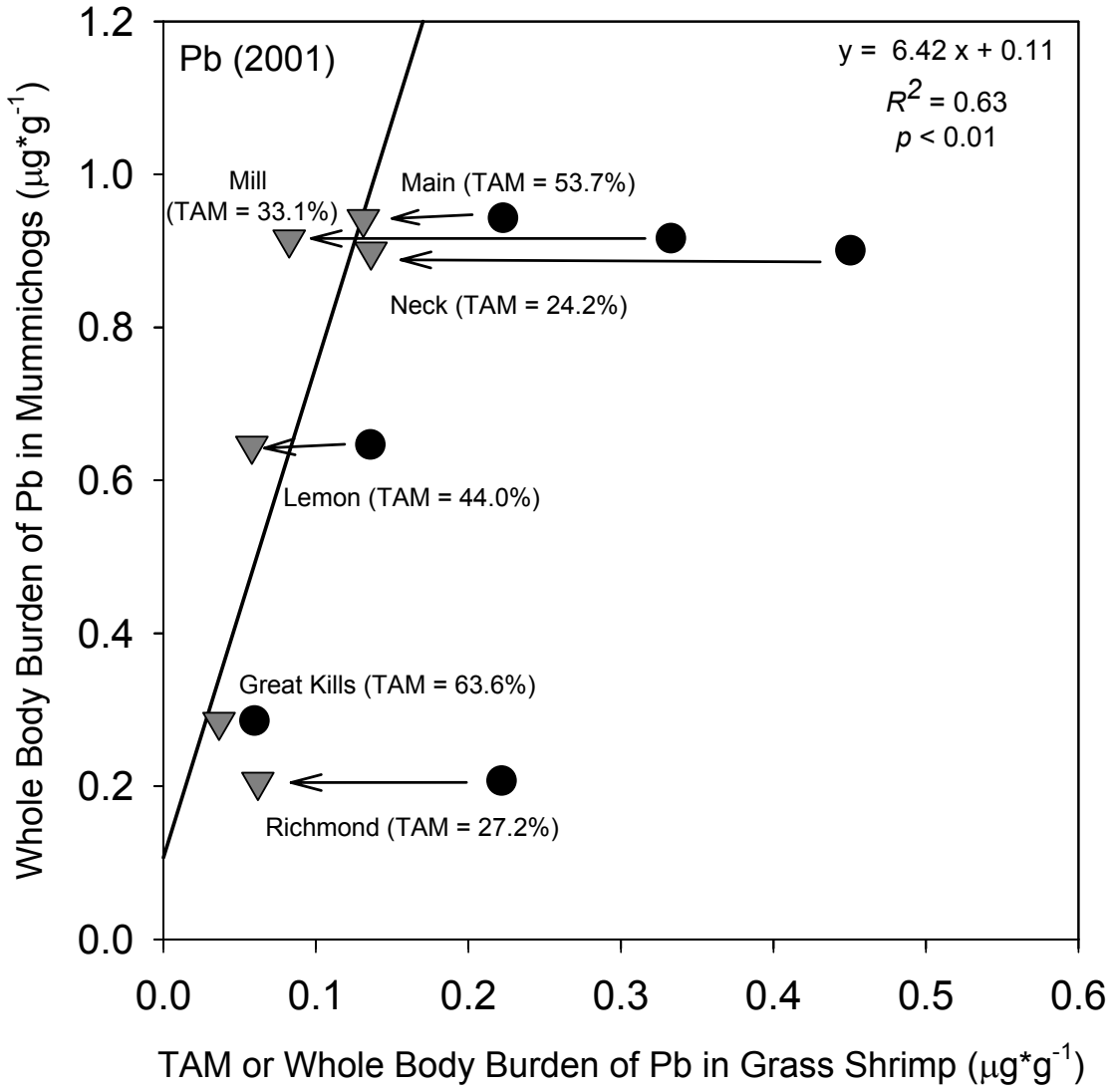


Figure 4-11. Relationships between Cd whole body burdens ($\mu g \cdot g^{-1}$) in mummichogs and concentrations of Cd ($\mu g \cdot g^{-1}$) associated with TAM (TAM-[Cd]) in *Palaemonetes spp*. (▼), or Cd whole body burdens in *Palaemonetes spp*. (●) in 2004. Solid line indicates least squares regression between TAM-[Cd] in *Palaemonetes spp*. and Cd whole body burdens in mummichogs.

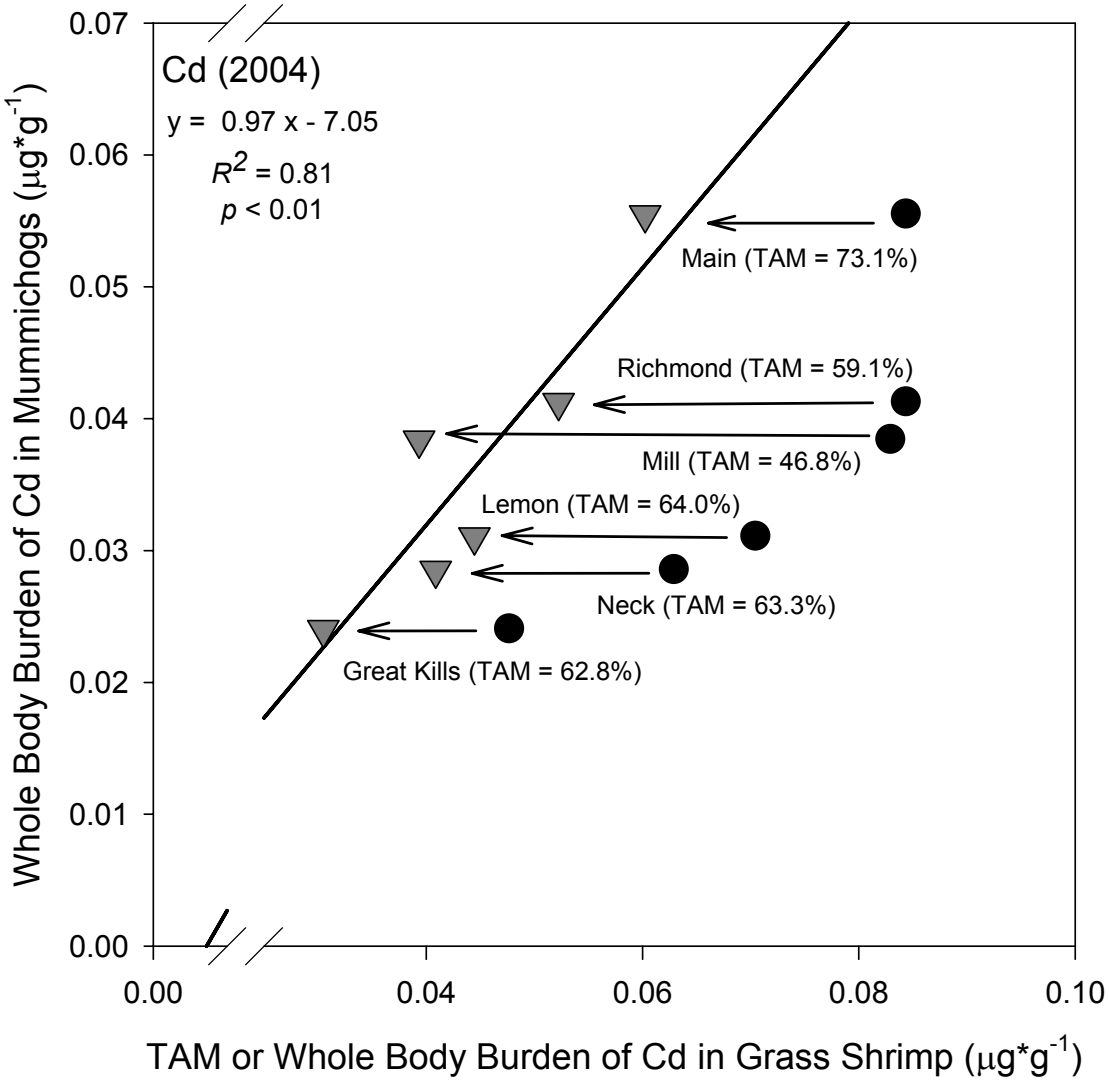


Figure 4-12. 2-dimensional plots of non-metric multidimensional scaling (nMDS) ordination on the intracellular partitioning of (a) Cd, (b) Pb, (c) Cu, and (d) Zn in mummichogs collected from Great Kills Harbor (○), Lemon Creek (●), Mill Creek (▼), Richmond Creek (△), Main Creek (■), and Neck Creek (■) in 2004.

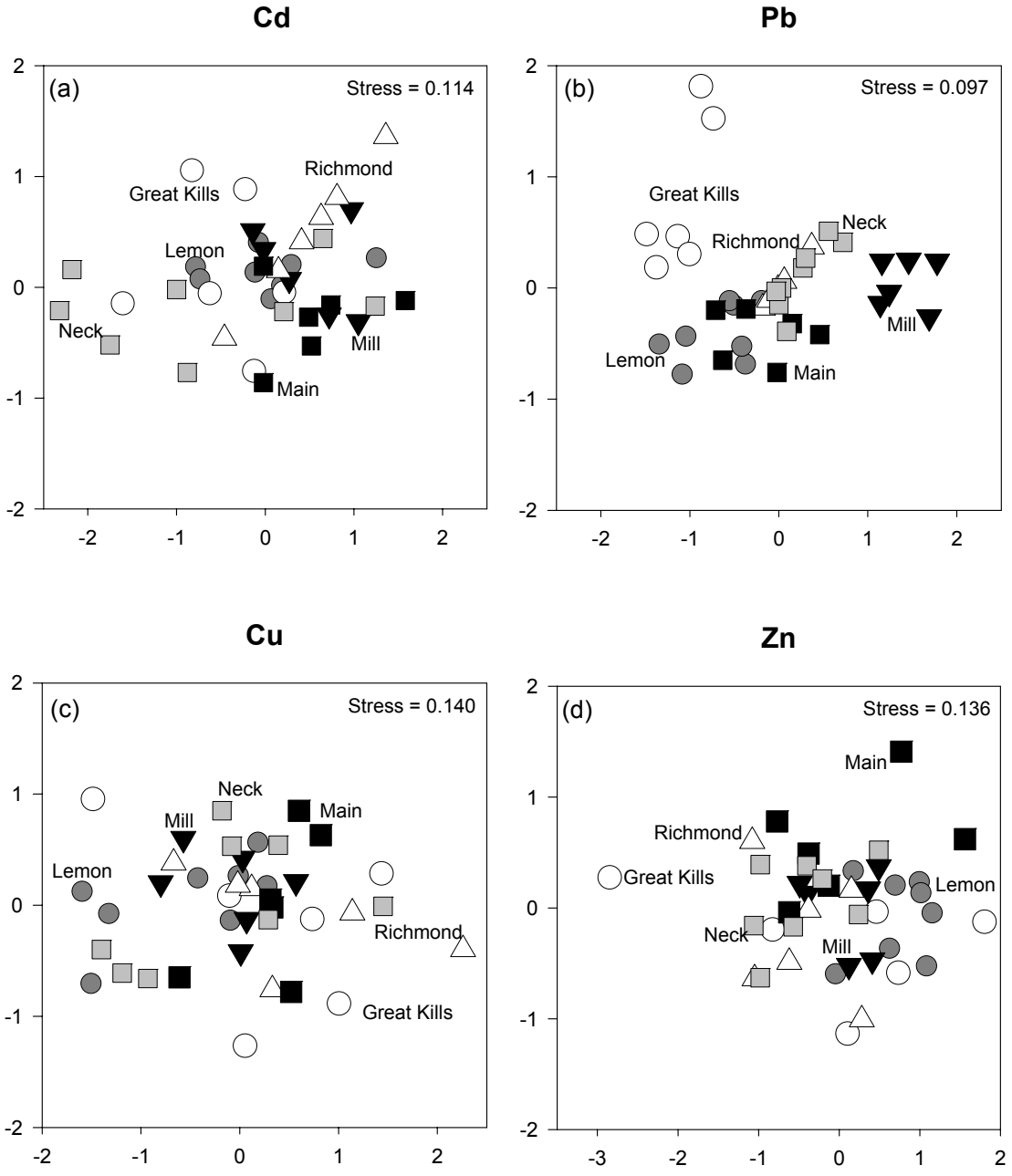


Figure 4-13. Intracellular partitioning (%) of Cd to heat-denatured proteins (HDP), organelles, heat-stable proteins (HSP), and metal-rich granules (MRG) in mummichogs collected from (a) Great Kills Harbor, (b) Lemon Creek, (c) Neck Creek, (d) Mill Creek, (e) Richmond Creek, and (f) Main Creek in 2004. HDP + organelles = metal-sensitive fractions (MSF). HSP + MRG = biologically detoxified metals (BDM).

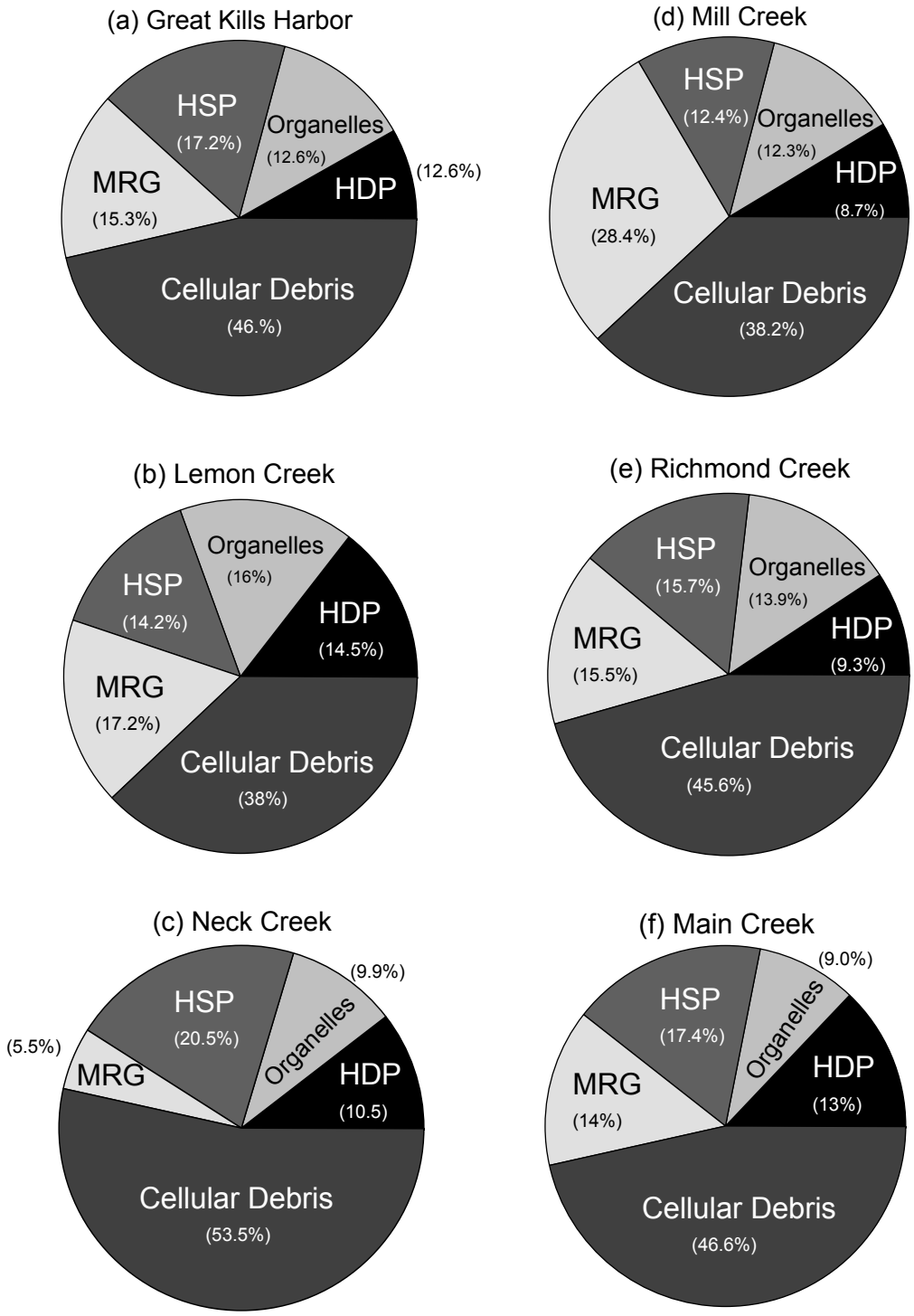


Figure 4-14. Intracellular partitioning (%) of Pb to heat-denatured proteins (HDP), organelles, heat-stable proteins (HSP), and metal-rich granules (MRG) in mummichogs collected from (a) Great Kills Harbor, (b) Lemon Creek, (c) Neck Creek, (d) Mill Creek, (e) Richmond Creek, and (f) Main Creek in 2004. HDP + organelles = metal-sensitive fractions (MSF). HSP + MRG = biologically detoxified metals (BDM).

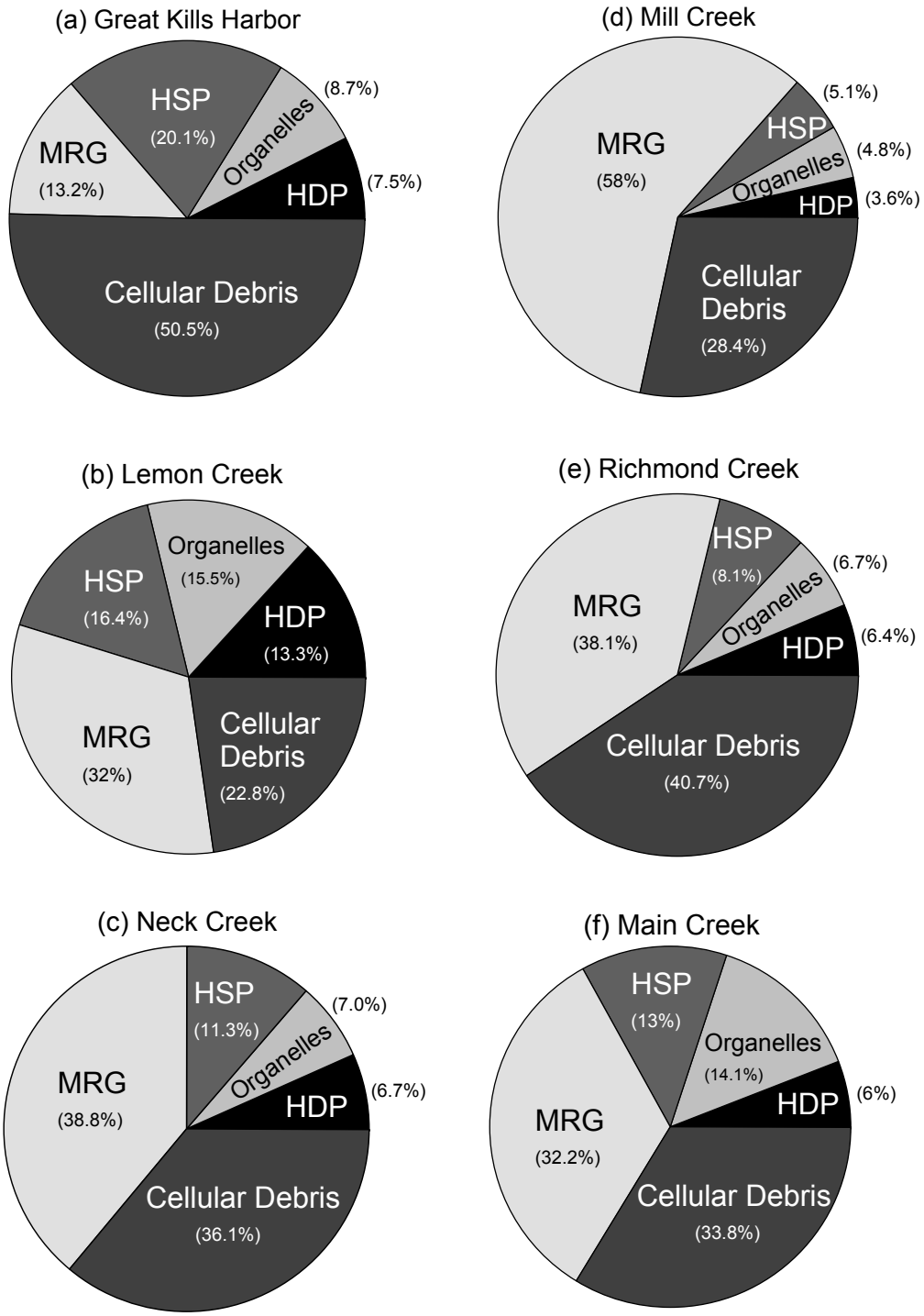


Figure 4-15. Intracellular partitioning (%) of Cu to heat-denatured proteins (HDP), organelles, heat-stable proteins (HSP), and metal-rich granules (MRG) in mummichogs collected from (a) Great Kills Harbor, (b) Lemon Creek, (c) Neck Creek, (d) Mill Creek, (e) Richmond Creek, and (f) Main Creek in 2004. HDP + organelles = metal-sensitive fractions (MSF). HSP + MRG = biologically detoxified metals (BDM).

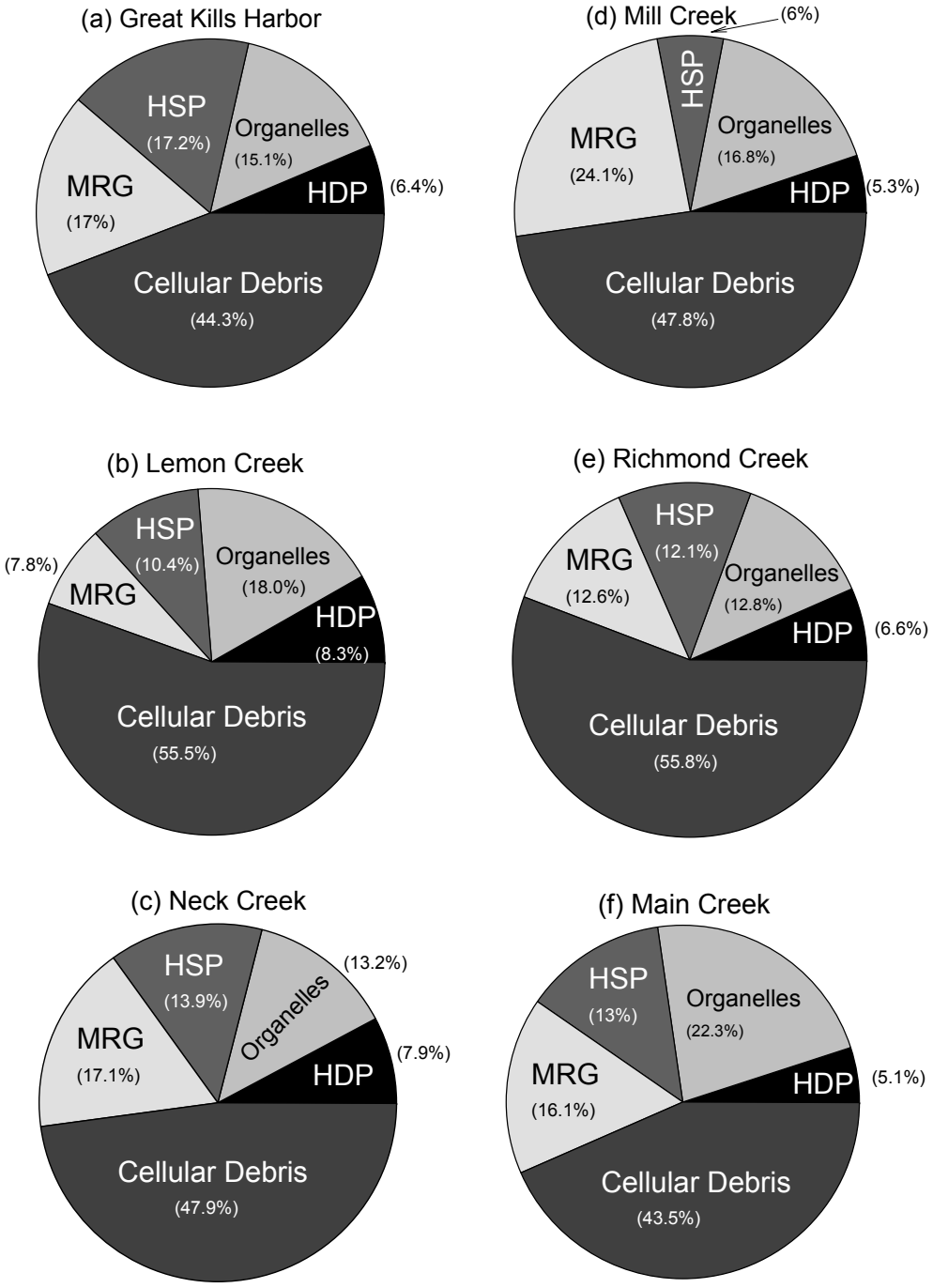
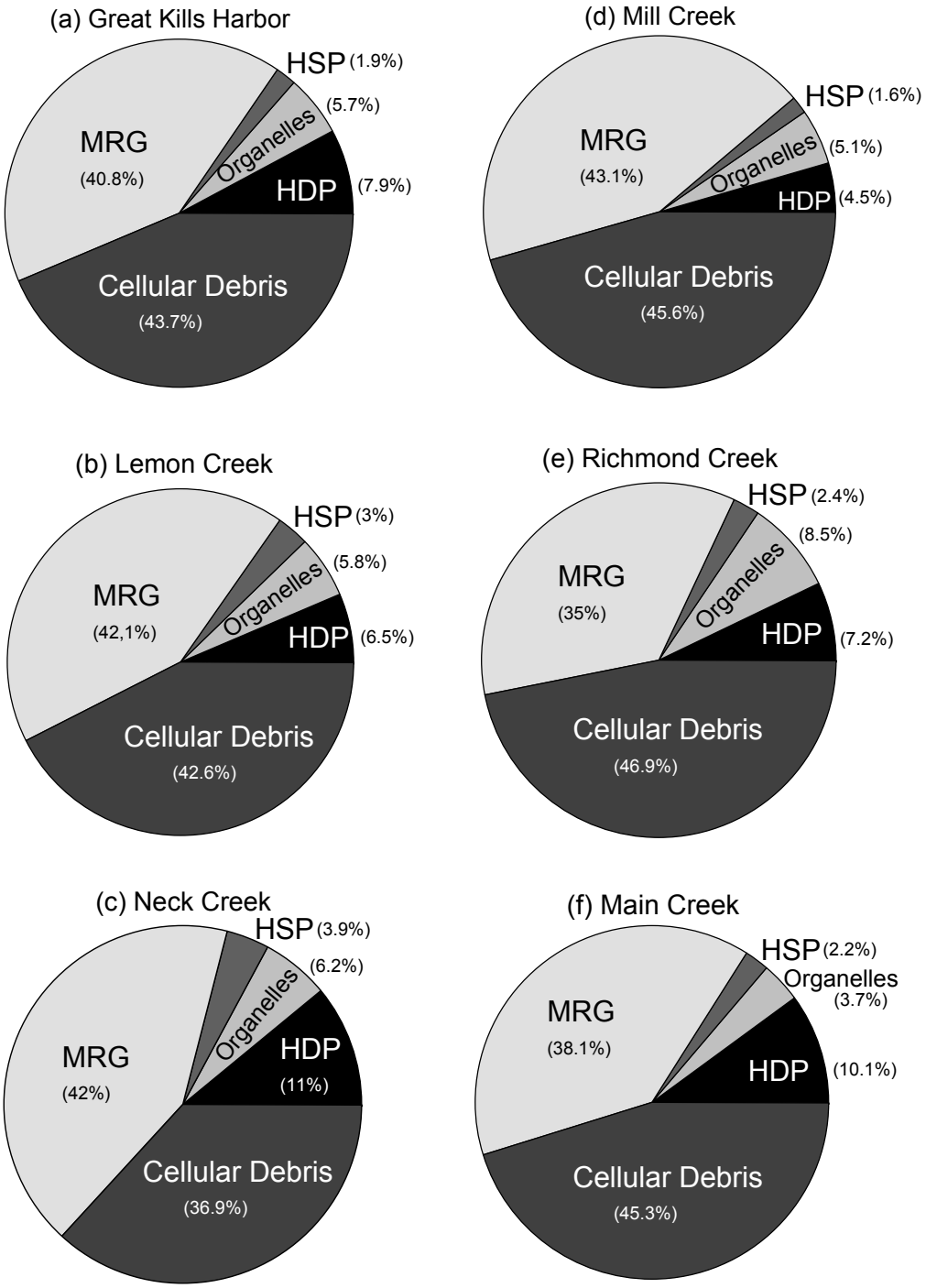


Figure 4-16. Intracellular partitioning (%) of Zn to heat-denatured proteins (HDP), organelles, heat-stable proteins (HSP), and metal-rich granules (MRG) in mummichogs collected from (a) Great Kills Harbor, (b) Lemon Creek, (c) Neck Creek, (d) Mill Creek, (e) Richmond Creek, and (f) Main Creek in 2004. HDP + organelles = metal-sensitive fractions (MSF). HSP + MRG = biologically detoxified metals (BDM).



CHAPTER 5

Disruption in coastal energy flow: Alteration in bioenergetics of mummichogs (*Fundulus heteroclitus*) in urban tidal salt marshes in New York

CHAPTER SUMMARY

Degradation of habitat quality in urban tidal salt marshes can adversely affect resident fishes, potentially disrupting trophic connectivity and energy flow in coastal ecosystems. In this study, by incorporating *in situ* field-based food consumption estimates with the mercury mass balance model, bioenergetics of mummichogs (*Fundulus heteroclitus*) was evaluated in highly urbanized tidal salt marshes in the Arthur Kill (New York, USA), where benthic macroinfaunal communities (prey resource of mummichogs) were severely impoverished. Both age 2+ and 3+ fish from most of the Arthur Kill sites had significantly elevated total metabolic costs, suggesting degraded habitat conditions in the Arthur Kill may have induced an increase in metabolic activities. However, both age 2+ and age 3+ fish from these Arthur Kill sites also had ~2 to 3-fold higher food consumption rates than those from the reference site, suggesting that the Arthur Kill populations of mummichogs may have increased food consumption to offset elevated metabolic costs. Furthermore, only age 2+ females from the Arthur Kill sites had significantly reduced growth rates, whereas there was little among-site difference for age 3+ fish, indicating that these fish may have compensatory mechanisms (e.g., increased food consumption) to maintain growth. Both age 2+ and age 3+ fish from most of the Arthur Kill sites, however, had substantially (up to 80%) reduced growth conversion efficiency. This reduction in growth/energy conversion efficiency at the individual level may cascade through trophic chains, potentially resulting in 'energetic bottlenecks' at the community level. Altered salt marsh trophic structures and their resultant impacts on mummichog bioenergetics, therefore, have important implications for ecosystem functioning of urban tidal salt marshes in the Arthur Kill.

INTRODUCTION

Tidal salt marshes are a highly productive environment (Kneib, 2000; Levin *et al.*, 2001), supporting adjacent coastal ecosystems (Nixon and Oviatt, 1973; Deegan *et al.*, 2000; Mitsch and Gosselink, 2000). As an interface of terrestrial, freshwater, and saltwater environments, a substantial amount of land- and ocean- originated materials and energy are transported through salt marsh ecosystems (Snelgrove *et al.*, 2000; Levin *et al.*, 2001; Martinetto *et al.*, 2006). Salt marshes provide an essential habitat for resident estuarine fish and shellfish species (Kneib, 1986; Rountree and Able, 1992; Kneib and Wagner, 1994; Kneib, 1997), as well as nursery and foraging grounds for migrant species (Kneib and Wagner, 1994; Nemerson and Able, 2003; Weis, 2005; Dittel *et al.*, 2006). Tidal migrations and trophic interactions of the nekton within salt marshes are thus likely to contribute to the connectivity of spatially heterogeneous ecological landscapes ("ecoscapes"), facilitating material and energy cycling (Kneib, 1994; Kneib and Wagner, 1994; Secor and Rooker, 2000; Ray, 2005).

It has been suggested that the movement of salt marsh production to open coastal environments may be mediated through trophic pathways (Kneib and Wagner, 1994; Kneib, 1997; 2000). Kneib (1997) hypothesized that the spatial movement of marsh production toward open coastal habitats is intimately associated with energy flow through trophic interactions between resident and migrant species, as well as tidal migrations of the nekton ("trophic relay") (Kneib, 1997; 2000). Benthic invertebrates, and resident and migrant nekton all play crucial roles in facilitating this movement of materials and energy in salt marsh ecosystems (Kneib, 1997; 2000). In addition to biogeochemical cycling of materials and remobilizing primary production (i.e., vascular plant detritus and algae)

(Levin *et al.*, 2001; Somerfield *et al.*, 2006), benthic invertebrates are an essential part of salt marsh food webs as prey for a variety of benthivorous predators (Sardá *et al.*, 1995; Levin *et al.*, 2001). Resident nekton feeding primarily on sediment-associated invertebrates can thus be an integrator of marsh production incorporated by these invertebrates. As resident nekton also temporarily share a common habitat (i.e., "intertidal-subtidal corridors") with juvenile and adult migrant nekton feeding on resident nekton (Kneib and Wagner, 1994; Kneib, 2000; Levin *et al.*, 2001), marsh production is likely to be transported to adjacent coastal habitats through these trophic pathways (Kneib, 1997; 2000).

The connectivity of salt marsh ecoscapes is important for trophic interrelationships among resident and migrant nekton (Kneib and Wagner, 1994; Kneib, 2000; Levin *et al.*, 2001). This connectivity may, however, be disrupted in urban coastal habitats due to anthropogenically induced degradation of habitat quality (e.g., chemical pollution, dredging, eutrophication, and overfishing) (Boesch, 1982; Able *et al.*, 1998; Levin *et al.*, 2001). Altered physicochemical properties of the environment can effect a considerable shift in biological assemblages (Pearson and Rosenberg, 1978; Weston, 1990; Able *et al.*, 1998; Warwick, 2001). Tidal migrations of nekton in heterogeneous coastal habitats may be disrupted by man-made structures such as impoundments and bulkheads (Able *et al.*, 1998; Duffy-Anderson *et al.*, 2003; Kneib, 2003; Able and Duffy-Anderson, 2006). The disruption in nekton movements could subsequently prevent trophic interactions (e.g., resident prey-migrant predator relationships) in salt marshes (Kneib, 2000; Levin *et al.*, 2001; Ray, 2005; Able and Duffy-Anderson, 2006). Furthermore, chemical pollution is also widespread in urban coastal habitats, and anthropogenically introduced chemicals

may indirectly alter habitat use by migrant nekton, which is in turn likely to disrupt the trophic links with marsh resident nekton (Boesch, 1982; Levin *et al.*, 2001). These alterations in movements of key nekton species (e.g., tidal migrations) and interspecific interactions among them (e.g., prey-predator relationship) can disrupt trophic relay processes (Kneib and Wagner, 1994; Kneib, 1997; 2000; Kneib, 2003), which may in turn disrupt cycling of materials with terrestrial, freshwater, and marine origins (Boesch, 1982; Levin *et al.*, 2001).

Alterations in benthic macroinfaunal assemblages can also indirectly affect the feeding habits of their predators in marine and estuarine ecosystems (e.g., Chapter 3; Steimle *et al.*, 1993; Duffy-Anderson and Able, 2001; Hinz *et al.*, 2005; Powers *et al.*, 2005). Since sediment-associated invertebrates have species-specific differential tolerance levels to anthropogenic stressors, habitat degradation in urban salt marshes can also alter the availability of potential prey resources to benthivorous resident and migrant nekton (Chapter 2; Boesch, 1982). The impacts of anthropogenic stressors on macroinvertebrates can thus disrupt benthic food chains, affecting trophic connectivity (e.g., benthic invertebrate prey-benthivorous predators) in urban salt marshes (Jeffree and Williams, 1980; Boesch, 1982; Clements and Livingston, 1983).

Altered feeding habits may influence energetic performances of fish (e.g., elevated metabolism) (Livingston, 1984; Pihl, 1994; Rose, 2000; Eby *et al.*, 2005). Decoupling of trophic links in salt marshes can affect energy conversion efficiencies and productivities of resident and migrant nekton. Since resident nekton can be a conduit of marsh production transport (Kneib and Wagner, 1994), alterations in bioenergetics of resident

nekton can have further implications for energy transport within coastal ecosystems, as well as habitat use and production of migrant nekton (Kneib, 2000; Kneib, 2003).

There is, however, a limited understanding of the underlying mechanisms of how altered food web structures influence functional responses of nekton in urban coastal habitats (Clements and Livingston, 1983; Livingston, 1984; Rose, 2000). Anthropogenic stressors often cascade through food chains (Clements and Rees, 1997; Farag *et al.*, 1999; Chen *et al.*, 2000), potentially resulting in a variety of biologically adverse effects in fish (Campbell *et al.*, 2002; Hammerschmidt *et al.*, 2002; Farag *et al.*, 2003), including disruption in energetic balance (Sherwood *et al.*, 2000; Campbell *et al.*, 2003; Coghlan and Ringler, 2005). Some fishes living in degraded habitats are, however, capable of compensating for additional energetic costs incurred by anthropogenic stressors (e.g., pollutants and hypoxia) (Levin *et al.*, 2001; Campbell *et al.*, 2002). For instance, chronic exposure to anthropogenically introduced chemicals through the diet can induce physiological stresses in fish, which may be compensated for through metabolic processes such as sequestration and detoxification of chemicals (Calow, 1991; Handy *et al.*, 1999; Campbell *et al.*, 2002). Since energy allocation to metabolism precedes that to growth and/or reproduction, stress-induced metabolic activities can indirectly affect growth and reproduction of fish (Priede, 1985; Health, 1995; Berntssen and Lundebye, 2001; Hammerschmidt *et al.*, 2002; Brown *et al.*, 2003). Furthermore, a reallocation of available energy to additional metabolic costs in fish may also affect energy reserves for routine energy-demanding activities such as foraging and predator avoidance (Handy *et al.*, 1999; Campbell *et al.*, 2002). These altered energy allocations may reduce the fitness of fish and could ultimately lead to mortality (Campbell *et al.*, 2002).

Individual-level impacts (e.g., reduced growth rates) of habitat degradation on fish may also lead to population-level impacts, including changes in recruitment, productivity, and age/size structure (Carlisle, 2000; Sherwood *et al.*, 2000). Increased energetic demands from anthropogenic stressors can reduce energy conversion efficiency in fish (Stoner and Livingston, 1978; Sherwood *et al.*, 2000), which may in turn reduce reproductive output (e.g., fewer spawning events) (Moiseenko, 2002). Furthermore, this stress-induced reduction in energy conversion efficiency may also cascade through trophic chains (e.g., reduced trophic efficiency), resulting in 'energetic bottlenecks' at the community level (Nisbet *et al.*, 1997; Carlisle, 2000; Sherwood *et al.*, 2000) and potential loss of apex predators (Clements and Newman, 2002).

Mummichogs, *Fundulus heteroclitus* (Pisces: Cyprinodontidae), are one of the most abundant and productive fishes in tidal salt marshes in the northwest Atlantic coast (Nixon and Oviatt, 1973; Valiela *et al.*, 1977; Meredith and Lotrich, 1979). Due to their strong site fidelity (Lotrich, 1975; Teo and Able, 2003; McMahon *et al.*, 2005; Skinner *et al.*, 2005) and ontogenetic tidal migration within salt marshes (Teo and Able, 2003; Able *et al.*, 2006), this resident fish plays an important role in energy flow in coastal wetland ecosystems (Kneib, 1997; 2000). Tidal salt marshes in the northwest Atlantic coast are also frequently used as feeding grounds by juvenile and adult migrant nekton species such as blue crab (*Callinectus sapidus*), white perch (*Morone americana*), striped bass (*Morone saxatilis*), and bluefish (*Pomatomus saltatrix*), which are potential competitors as well as predators of mummichogs (Kneib, 1982; Peters and Schaaf, 1991; Weis, 2005; Dittel *et al.*, 2006). Tidal migration of mummichogs between intertidal marsh surface and subtidal creeks can, therefore, couple spatially semi-compartmentalized trophic levels

(i.e., benthic invertebrates in intertidal marshes and migrant nekton in subtidal creeks) (Valiela *et al.*, 1977; Weisberg *et al.*, 1981; Kneib, 1997). Furthermore, as an intermediate predator in salt marsh food webs, this cyprinodontid fish acts as a 'stepping stone' in marsh production transport (i.e., trophic relay), integrating a large portion of marsh production incorporated by benthic invertebrates and transferring it to piscivorous nekton (Valiela *et al.*, 1977; Kneib and Wagner, 1994; Kneib, 1997; Smith *et al.*, 2000). These piscivorous predators would subsequently transport marsh production assimilated by mummichogs to open coastal ecosystems (Valiela *et al.*, 1977; Kneib *et al.*, 1980; Kneib, 2000).

Due to their relatively high tolerance to anthropogenic stressors, mummichogs can usually thrive in severely polluted coastal habitats (Weis *et al.*, 1999; Weis, 2002; Wirgin and Waldman, 2004; Schulte, 2007). Anthropogenic stressors such as chemical pollutants can, however, alter foraging and predator-avoidance behaviors of mummichogs in these polluted habitats (Smith and Weis, 1997; Zhou and Weis, 1999; Weis *et al.*, 2001). These altered behaviors are, in addition to altered prey availability (e.g., local extinction of sensitive benthic invertebrate species), most likely one of factors that disrupt trophic coupling in urban tidal salt marshes (Chapter 3; Kneib, 2003; McMahon *et al.*, 2005). This decoupling of trophic chains may affect local ecosystem functions such as biogeochemical cycling of materials and energy flow (Clements and Newman, 2002; McCann *et al.*, 2005; Woodward *et al.*, 2005). The functional responses of mummichogs to altered habitat conditions can, therefore, be highly relevant to structural and functional recovery of restored tidal salt marshes (Moy and Levin, 1991; Allen *et al.*, 1994; James-Pirri *et al.*, 2001; Steimle, 2001).

The main objective of the present study was to investigate how altered benthic trophic structures (Chapters 2 and 3) affected bioenergetics of mummichogs in highly urbanized tidal salt marshes in the Arthur Kill (New York, USA), part of the New York/New Jersey (NY/NJ) Harbor Estuary system. Due to chronic pollution (e.g., chemical discharges from industrial facilities and sewage treatment plants), the water quality of the NY/NJ Harbor Estuary has been severely degraded for more than a century (Crawford *et al.*, 1994; Wakeman and Themelis, 2001; Steinberg *et al.*, 2004). As a result, many fishes and shellfishes in the NY/NJ Harbor Estuary are directly or indirectly exposed to a variety of anthropogenic stressors. As various areas in the NY/NJ Harbor Estuary are the subject of current and future restoration (Bain *et al.*, 2007), it is critical to understand the effects of altered trophic dynamics in benthic habitats on energy flow in evaluating the success of remediation, including energy/production transport and coastal fisheries productivity.

MATERIALS AND METHODS

Field Sampling

Samplings of mummichogs (*Fundulus heteroclitus*) and their macroinvertebrate prey were conducted at a subtidal creek area of four tributaries of the Arthur Kill; Richmond Creek, Main Creek, Neck Creek, and Mill Creek, and a regional reference site near Raritan Bay; Lemon Creek (see Chapter 1 for site description) during the summer (July to September) of 2004. Adult mummichogs were collected using a 3.05 x 1.22 m-seine net with 6 mm-polyester mesh or unbaited cylindrical minnow trap with 6 mm-mesh. The sampling was continued until a representative size of fish population at each

site (n = 100 to 200) were captured. Captured fish were immediately placed on ice, and subsequently transported to laboratory.

Sediment-dwelling macroinvertebrate prey were collected by sieving bulk sediments through a 500 µm-mesh sieve and transferred to an acid-washed glass jar. Epibenthic macroinvertebrate prey (e.g., *Palaemonetes spp.*) were collected using a D-frame dip net. Both sediment-dwelling and epibenthic macroinvertebrates were then transported on ice to laboratory.

Laboratory Sample Processing

In the laboratory, sediment-dwelling macroinvertebrates were sorted from detritus and identified under a stereo microscope (4x or 16x), using species keys from the literature (Fauchald, 1977; Weiss, 1995; Merritt and Cummins, 1996; Pollock, 1998). Then, to minimize measurement errors associated with unassimilated mercury in the gut contents, which can introduce large variability (Brooke *et al.*, 1996), both mummichogs and macroinvertebrates were allowed to depurate gut contents for at least 24 hours in filtered 15‰ seawater. Mummichogs were then euthanized by an overdose of MS222, and then each fish was sexed, measured (total length ± 0.01 mm), and weighed (wet weight ± 0.01 g). 10 to 20 scale samples were taken from the area behind the operculum and above the lateral line of each fish for the determination of age (Valiela *et al.*, 1977; DeVries and Frie, 1996). Macroinvertebrates and mummichogs were then stored in a freezer (–80 °C) for mercury analyses.

Food Consumption Rate Estimation

Overview of the mercury mass balance model

Annual average daily food consumption rates of mummichogs were estimated using the mercury mass balance method (Trudel *et al.*, 2000). Mercury (Hg) is one of the most globally widespread trace elements and readily accumulates in fish. In this mass balance method, Hg is used as a chemical tracer to estimate *in situ* food consumption rates of predators in the field setting (Trudel *et al.*, 2000). The majority of Hg accumulated in many fishes is predominantly taken up through dietary sources (Hall *et al.*, 1997; Wang and Wong, 2003), while the uptake of Hg in the dissolved form from water or sediment-associated Hg is negligible in the natural environment (Weis *et al.*, 1986; Trudel and Rasmussen, 2001; Trudel and Rasmussen, 2006). Therefore, the trophic cycling of Hg can be used to indirectly estimate food consumption rates of predators by quantifying growth rate, daily Hg turnover rates in predators (Hg assimilation and elimination rates), and Hg body burdens in field-collected prey and predators (Trudel *et al.*, 2000). In the current study, specific daily food consumption rates (C, $g \cdot g^{-1} \cdot day^{-1}$) of mummichogs were estimated using the following mass balance model, interpolating fish body size (g, wet weight) and Hg whole body burden in mummichogs ($ng \cdot g^{-1}$) between adjacent age classes (Trudel *et al.*, 2000);

$$(1) \qquad C = \frac{(Hg_{t+\Delta t} - Hg_t \cdot e^{-(E + G + Hg_g) \cdot \Delta t}}{AE \cdot Hg_d \cdot [1 - e^{-(E + G + Hg_g) \cdot \Delta t}]} (E + G + Hg_g)$$

where $Hg_{t+\Delta t}$ and Hg_t = Hg body burdens in mummichogs ($ng \cdot g^{-1}$) at time $t+\Delta t$ and t (days), respectively;

Hg_g = Hg in gonads released at spawning ($ng \cdot g^{-1} \cdot day^{-1}$);

Hg_d = Hg in prey ($ng \cdot g^{-1}$);

AE = Hg assimilation efficiency from prey;

E = Hg elimination rate ($ng \cdot g^{-1} \cdot day^{-1}$);

G = specific growth rate ($g \cdot g^{-1} \cdot day^{-1}$).

Parameterization of the Hg mass balance model

Analyses of Hg in mummichogs

As the majority of Hg accumulated in fish, including mummichogs (Weis, 1984), is in the form of organic Hg (mainly, methyl mercury) (Bloom, 1992), total Hg content in fish was analyzed. Previously frozen fish samples were thawed at room temperature and then homogenized with a Polytron tissue homogenizer (Kinematica, Switzerland) in NANOpure® (reagent-grade) water (Santoro and Koepp, 1986). Homogenized samples were oven-dried (~60 °C) for 24 to 48 hours (Weis and Ashley, 2007). Subsamples (~0.5 g dry) were weighed and transferred into an acid-washed 60 ml-BOD bottle. Samples were then digested in a mixture (1:4 v/v) of concentrated Trace Metal Grade nitric and sulfuric acids (10 ml) in a water bath (60 ºC) for ~3 hours, and then cooled in a refrigerator (USEPA, 1992). Samples were oxidized with 5% potassium permanganate (10 ml) and 5% potassium persulfate (5 ml) at room temperature overnight (USEPA, 1992). The digested samples were transferred into a 100 ml-volumetric flask, and 12% sodium chloride-hydroxylamine sulfate was added to the samples to reduce excess potassium permanganate. Samples were then brought to final volume with NANOpure® water, filtered (0.45 µm), and refrigerated (for < 2 to 3 days) or analyzed immediately

with cold vapor atomic absorption spectrometer (Perkin Elmer Flow Injection Mercury System, FIMS 100, USA) using stannous chloride as a reducing reagent. Population-specific relationships between fish body size (g, wet) and total Hg whole body burden were modeled using regression, which was fitted by the Levenberg-Marquardt least squares algorithm (Appendix 5-A and 5-B). Then, the total Hg whole body burden for back-calculated body size was estimated for each individual fish, which allowed an estimation of individual food consumption rates (Tucker and Rasmussen, 1999).

Analyses of organic Hg in prey

As organic Hg content in aquatic invertebrates is often much lower than total Hg content (Malley *et al.*, 1996), organic Hg was first extracted from macroinvertebrates by acid leaching with methylene chloride and hexane (Malley *et al.*, 1996; Wagemann *et al.*, 1997). Previously frozen samples were thawed in an acid-washed 50 ml-glass centrifuge tube, homogenized in NANOpure® water, and then oven-dried (~60 °C) for 24 to 48 hours (Weis and Ashley, 2007). Dried samples were weighed and homogenized in a mixture of 30% sodium bromide (in 4N sulfuric acid, 5 ml) and 2.5% copper sulfate (in 4N sulfuric acid, 7.5 ml) for 1 minute (Wagemann *et al.*, 1997). Then, a mixture (3:2 v/v) of methylene chloride and hexane (10 ml) was added to the sample homogenates (Wagemann *et al.*, 1997). Samples were vigorously shaken on an orbital shaker for at least 12 hours, and then allowed to stand until the samples settled. An aliquot (5 ml) of the resultant organic layer was pipetted out and transferred into an acid-washed 60 ml-BOD bottle. Samples were then digested in a mixture (1:4 v/v) of concentrated Trace Metal Grade nitric and sulfuric acids (5 ml) on a hot plate (~60 ºC), which eliminated the

solvents (methylene chloride and hexane) (Wagemann *et al.*, 1997). Hg content in the resultant aqueous solution was subsequently processed and analyzed as described above for fish samples (Appendix 5-C).

Quality assurance/quality control

Mercury calibration standard solutions (0.1, 0.5, 1.0, 2.5, and 5.0 $\mu g \cdot l^{-1}$), method and reagent blanks, and samples of the certified reference material (dogfish muscle tissue, DORM-2, a reported certified values of 4.64 ± 0.26 $\mu g \cdot g^{-1}$ for total Hg and 4.47 ± 0.32 $\mu g \cdot g^{-1}$ for methyl mercury, National Research Council Canada) were analyzed with each batch of samples. The calibration standard solution of 2.5 $\mu g \cdot l^{-1}$ was analyzed every 10 samples; when the deviation from the initial value was more than ± 10%, the instrument was recalibrated. The correlation coefficients of calibration curves were maintained > 0.999. Samples with the relative standard deviation between replicates > 15% were reanalyzed. The recovery rates of total Hg and organic (methyl) Hg from the DORM-2 samples were 93.5 to 97.3%, and 96.3 to 100.6%, respectively. All standard solutions and samples were prepared with NANOpure® water. All glassware was soaked in 25% nitric acid overnight, rinsed once with deionized water, and rinsed twice with NANOpure® water.

Hg assimilation efficiencies

Methyl mercury (CH_3Hg) assimilation efficiency in the Hg mass balance model is frequently assumed to be 0.8 for carnivorous fishes (Borgmann and Whittle, 1992; Post *et al.*, 1996; Trudel *et al.*, 2000; Trudel and Rasmussen, 2001). Food consumption rates

estimated by the Hg mass balance model are, however, fairly sensitive to the error associated with the assimilation efficiency (Trudel *et al.*, 2000). In the present study, therefore, prey-specific assimilation efficiencies of dietary CH_3Hg in mummichogs were experimentally estimated, except for that of mollusks, which was derived from the literature (Pentreath, 1976).

Assimilation efficiencies (AEs) of CH_3Hg in mummichogs from prey were estimated through a series of pulse-chase feeding experiments (Wang and Fisher, 1999). *Palaemonetes spp.* was used for the estimation of the AE for decapods, *Nereis virens* for polychaetes, *Gammarus mucronatus* and *Leptochirus plumulosus* for amphipods, and *Chironomus dilutus* for aquatic insect larvae. Each prey species was radiolabeled with $CH_3{}^{203}Hg$, which was synthesized using a method by Rouleau and Block (1997). Prey organisms were exposed to a trace amount of $CH_3{}^{203}Hg$ in filtered 15‰ (or 2.5‰ for *C. dilutus*) seawater (~20 °C) for 96 hours. Following exposure, prey organisms were rinsed with filtered seawater twice and then assayed for radioactivity with a gamma counter (Wallac 1480 Wizard, Finland).

Feeding experiments were conducted in glass aquaria filled with aerated filtered 15‰ seawater (~20 °C). Mummichogs (TL = 70 to 80 mm; n = 6 per prey species) were anesthetized with MS222 (150 $mg \cdot l^{-1}$) in filtered 15‰ seawater for 5 minutes and force-fed radiolabled prey (Rouleau *et al.*, 1998). Once mummichogs were fed, they were immediately assayed for radioactivity with a gamma counter. This initial radioactivity (t = 0) represent 100% of ingested $CH_3{}^{203}Hg$ in fish. Following this initial radioanalysis, fish were transferred to 38 l-depuration aquaria where they were individually housed in a 11.5 x 11.5 x 10.5 cm-unit (Super Breeder™, International Pet Supplies and Distribution,

Inc., USA), and fed with commercial freeze-dried krill (a ration of 5% of fish body weight per day). To prevent recycling of excreted radioisotopes, aquarium water was filtered through a submersible power filter at ~200 l hour^{-1} flow (Duetto 50™, Aquarium Systems, Inc., USA), and fecal materials were physically separated from fish within each unit. Periodical sampling of water from aquarium tanks indicated that leaching of radioisotopes from fecal materials and excretion were below detection. The assimilation efficiencies of ingested $CH_3{}^{203}Hg$ was calculated at t = 24 hours (h) using the ratio of retained isotope activity at t = 24 h to that at t = 0 h (Wang and Wong, 2003; Seebaugh *et al.*, 2005; Rainbow *et al.*, 2006). Assimilation efficiencies obtained from the feeding experiments (Appendix 5-D) and literature (for mollusks) were then incorporated into the Hg mass balance model (Table 5-1).

Dietary Hg uptake

Weighted averages of dietary Hg uptake (AE $\cdot Hg_d$, ng$\cdot$g^{-1}) were estimated using population-specific pooled dietary data for each age class of mummichogs (from Chapter 3), prey-specific AEs, and site-specific organic Hg content in each prey, as following;

$$\text{AE} \cdot Hg_d = \sum p_i \cdot \text{AE}_i \cdot Hg_{di} \quad (7)$$

where p_i = the proportion of the i th prey category in the diet by weight (Chapter 3);

AE_i = the assimilation efficiency of Hg from the i th prey category (Table 5-1);

Hg_{di} = the organic Hg concentration in the i th prey category (ng$\cdot$g^{-1}, Appendix 5-C).

Hg elimination rates

In estimating the daily elimination rate of Hg by fish in the field setting, the effect of the initial rapid loss of unassimilated Hg through egestion on Hg bioaccumulation is negligible (Trudel and Rasmussen, 1997). Thus, only the slow component of Hg loss through excretion was incorporated into the mass balance model (Trudel and Rasmussen, 1997). Hg elimination (E) can be estimated by an empirical model that is independent of species or Hg whole body burden (Trudel and Rasmussen, 1997) as following;

(4) $$E = \varphi \cdot W^{\beta} \cdot e^{\gamma T}$$

where W = fish body size (g);

T = water temperature (°C), which was modeled with a Gaussian function;

φ, β, and γ = empirically derived constants (Table 5-1).

Hg loss through spawning

Annual average daily Hg loss through spawning (K) by adult mummichogs was estimated by the following model (Trudel *et al.*, 2000);

(5) $$K = Q \cdot \mathrm{GSI}/\Delta t$$

where Q = the ratio of Hg in gonads ($ng \cdot g^{-1}$) to Hg whole body burden ($ng \cdot g^{-1}$);

GSI = gonadosomatic index ($g \cdot g^{-1}$) (Table 5-1);

Δt = 365 (days).

In general, the amount of Hg released through spawning by fish including mummichogs is substantially low, as gonadal Hg is a small fraction of Hg whole body burden (Toppin *et al.*, 1987; Hammerschmidt *et al.*, 1999; Baker Matta *et al.*, 2001; Johnston *et al.*, 2001). Furthermore, the errors associated with the estimates of Q or GSI introduce little uncertainty (< 5%) to the estimates of food consumption rates (Trudel *et al.*, 2000). In the current study, therefore, the concentration of Hg in gonads was estimated from Hg whole body burden using the empirical models derived from the relationship between Hg in gonads (Hg_g, ng·g^{-1} dry) and Hg whole body burden (Hg_t, ng·g^{-1} dry) from previous studies; $Hg_g = 7.66 \times 1.00^{Hgt}$ for females (Hammerschmidt *et al.*, 1999) and $Hg_g = 21.50 \times 1.00^{Hgt}$ for males (Rennie, 2003).

Age Determination and Growth Rate Estimation

Age of mummichogs was determined using scales obtained from the area behind the operculum and above the lateral line (Valiela *et al.*, 1977). Scale samples were first cleaned by soaking in a diluted detergent for a few minutes and rinsing with warm water. Then, each scale was mounted on a glass slide and aged by counting annuli under a stereomicroscope (40x) (DeVries and Frie, 1996). All regenerated and distorted scale samples were discarded. Once age was determined, the image of each scale was captured using a digital microscope camera (Moticam 1000, Motic®) mounted on a stereomicroscope, and the distance between the focus and each annulus at the anterio-lateral section was measured (± 0.001 mm) (DeVries and Frie, 1996) with digital imaging software (Motic Images Plus 2.0 ML, Motic®). To increase precision, at least 3 scale

samples per fish were aged and measured, and average radii were used for growth estimation. The relationship between age and total length was back-calculated using the Fraser-Lee method (DeVries and Frie, 1996);

(6) $$L_i = (L_c - a)\ (S_i/S_c) + a$$

where L_i = back-calculated fish total length at the i th annulus (cm);

L_c = fish total length at capture (cm);

S_i = scale radius to the i th annulus (mm);

S_c = total scale radius at capture (mm);

a = the Fraser-Lee correction factor (= the intercept of regression between the fish total length at capture and total scale radius at capture) (Appendix 5-E and 5-F).

Weight-at-age of mummichogs was estimated by length (L)-weight (W) relationships determined for each population; $W = aL^b$, where a and b are constants. The parameters, a and b, were iteratively estimated using the Levenberg-Marquardt least squares algorithm (Appendix 5-G and 5-H). Then, specific growth rate (G, $g \cdot g^{-1} \cdot day^{-1}$) of an individual fish was determined using the following nonlinear equation (Ricker, 1975);

(7) $$G = ln(W_{t+\Delta t}/W_t) \cdot 1/\Delta t$$

where $W_{t+\Delta t}$ and W_t = weight (g) of mummichogs at time t+Δt and t (days), respectively.

Population-specific growth trajectories in length were also estimated from length-at-age data using the von Bertelanffy growth model (von Bertalanffy, 1938);

(8) $$L_t = L_\infty [1 - \exp(-K(t - t_0))]$$

where L_t and L_∞= total length at age t and the asymptotic average maximum total length, respectively;

K = a growth rate coefficient;

t_0 = the hypothetical age at which $L = 0$.

The parameters, L_∞, K, and t_0, were iteratively estimated using the Levenberg-Marquardt least squares algorithm. Then, population-specific length-weight relationships (Appendix 5-G and 5-H) were used to estimate growth trajectories in weight.

Estimation of Growth Conversion Efficiency

Annual average growth conversion efficiency (GCE) (% of energy allocated to growth) of mummichogs was estimated by the following equation;

(9) $$\%\text{GCE} = 100 \cdot G/C$$

where G and C are the growth and food consumption rate estimates of field-collected mummichogs (above), respectively.

Estimation of Total Metabolic Costs

The total metabolic cost (M_T), which includes standard metabolism, activity cost, and specific dynamic action (energy expended for food digestion and assimilation), were estimated using the following bioenergetics model (Hewett and Johnson, 1992);

$$C = M_T + G + F + U \quad (10)$$

where C = daily food consumption rate;

G = growth rate;

F = egestion;

U = excretion.

All components in the bioenergetics model are expressed in g $\cdot g^{-1} \cdot day^{-1}$ (Kitchell *et al.*, 1977). This equation was solved for M_T by incorporating observed estimates of growth and food consumption, and literature-derived estimates of egestion and excretion for mummichogs (F = 12.75% and U = 11.72% of the consumed energy, Weisberg and Lotrich, 1982b) into the bioenergetics model;

$$M_T = C - (G + F + U) \quad (11)$$

All the parameters in the bioenergetics model ($g \cdot g^{-1} \cdot day^{-1}$) were then converted to $kJ \cdot g^{-1} \cdot day^{-1}$ using literature-derived energy densities for each prey category; 4.60 $kJ \cdot g\ wet^{-1}$ for decapods, 1.70 $kJ \cdot g\ wet^{-1}$ for amphipods, 4.58 $kJ \cdot g\ wet^{-1}$ for polychaetes, 2.28 kJ·g

wet^{-1} for gastropods (Steimle and Terranova, 1985), and 2.74 kJ·g wet^{-1} for insects (Cummins and Wuycheck, 1971).

Error Estimation and Statistical Analyses

To account for propagated errors associated with measured parameters of growth rates, food consumption rates, growth conversion efficiencies, and total metabolic rates, standard errors associated with the means of these parameters were estimated using Monte Carlo simulations with n = 1000 (Trudel and Boisclair, 1993; Manly, 2007);

(10) $$P^* = P + (SE_p \cdot RN)$$

where P^* = a pseudo-value of a given parameter;

P = an observed value of a given parameter;

SE_p = the standard error of an observed parameter value,

RN = a random number generated from a normal distribution (mean = 0 and standard deviation = 1).

Statistical significance of differences in mean specific growth rates ($g \cdot g^{-1} \cdot day^{-1}$), specific food consumption rates ($g \cdot g^{-1} \cdot day^{-1}$), growth conversion efficiencies (%), and total metabolic rates ($kJ \cdot g^{-1} \cdot day^{-1}$) of age 2+ and 3+ mummichogs were tested by 2 (site x sex)-way analysis of variance (ANOVA) at the significance level of $p < 0.05$. The relationship between growth rate and food consumption rate was tested using 2-way analysis of covariance (ANCOVA) with food consumption rate as a covariable

(Sherwood *et al.*, 2000). Prior to analyses, data were $\log_{10}$- or arcsine- (for % data) transformed, where necessary (Sokal and Rohlf, 1995). Among-site differences were tested separately for females and males using planned contrast at the significance level of $p < 0.05$ (Sokal and Rohlf, 1995). All statistical analyses were performed with STATISTICA v7.1 (StatSoft®, Inc., USA) and Monte Carlo simulations were performed with MATLAB v7.0.1.15 (The MathWorks®, Inc., USA).

RESULTS

Food Consumption Rates

Two-way ANOVA showed that there were significant differences in specific daily food consumption rates of both age 2+ and 3+ mummichogs among sites (age 2+: $F_{4, 69} = 988.2$, $p < 0.001$; age 3+: $F_{4, 61} = 214.7$, $p < 0.001$, Table 5-2), but the effect of sex was significant only for age 3+ fish (age 2+: $F_{4, 69} = 1.00$, $p = 0.31$; age 3+: $F_{4, 61} = 18.1$, $p < 0.001$, Table 5-2). The interaction between site and sex was significant for both age 2+ and 3+ fish (age 2+: $F_{4, 69} = 43.9$, $p < 0.001$; age 3+: $F_{4, 61} = 10.7$, $p < 0.001$, Table 5-2).

A planned comparison showed that the specific food consumption rates of age 2+ female fish from Lemon Creek (0.072 $g \cdot g^{-1} \cdot day^{-1}$) were slightly higher than those from Mill Creek (0.065 $g \cdot g^{-1} \cdot day^{-1}$), but significantly lower than those from Richmond Creek (0.114 $g \cdot g^{-1} \cdot day^{-1}$) and Neck Creek (0.129 $g \cdot g^{-1}$ day^{-1}) (Fig. 5-1a). The specific food consumption rates of Main Creek female fish (0.067 $g \cdot g^{-1} \cdot day^{-1}$) were not significantly different from those of either Lemon Creek or Mill Creek fish (Fig. 5-1a). A similar trend was also observed for age 2+ males; the highest food consumption rates were observed at Neck Creek (0.147 $g \cdot g^{-1} \cdot day^{-1}$), which was followed by Richmond Creek (0.120 $g \cdot g^{-}$

^{1}·day^{-1}) > Main Creek (0.080 g·g^{-1}·day^{-1}) > Lemon Creek = Mill Creek (~0.058 g·g^{-1}·day^{-1}) (Fig. 5-1b). The specific food consumption rates of both age 3+ females and males from Lemon Creek and Mill Creek were similar to those of age 2+ fish from the corresponding sites (~0.06 to 0.07 g·g^{-1}·day^{-1}), while age 3+ fish from Richmond Creek, Neck Creek, and Main Creek had slightly lower food consumption rates (~0.09 to 0.10 g·g^{-1}·day^{-1}) than age 2+ fish (Fig. 5-1c and 5-1d).

Growth Rates and Fish Body Sizes

The effects of site and sex on specific growth rates of age 2+ and 3+ mummichogs were both significant (age 2+: site-$F_{4, 69}$ = 7.43, $p < 0.001$, sex-$F_{4, 69}$ = 13.05, $p < 0.001$; age 3+: site-$F_{4, 61}$ = 3.44, $p < 0.05$, sex-$F_{4, 61}$ = 13.8, $p < 0.001$, Table 5-2). The interactions between site and sex were also significant for both age 2+ and 3+ fish (age 2+: $F_{4, 69}$ = 25.4, $p < 0.001$; age 3+: $F_{4, 61}$ = 3.59, $p < 0.05$, Table 5-2).

A planned comparison showed that the specific growth rates of age 2+ females from Lemon Creek (0.0037 g·g^{-1}·day^{-1}) were significantly higher than those from other sites (~0.0013 g·g^{-1}·day^{-1} at Neck Creek and Main Creek to 0.0030 g·g^{-1}·day^{-1} at Mill Creek) (Fig. 5-2a). In contrast, age 2+ males from Lemon Creek had slightly lower specific growth rates than those from Neck Creek and Main Creek, while the growth rates of the Mill Creek and Richmond Creek males were not significantly different from any of the other age 2+ males (Fig. 5-2b). The specific growth rate of age 3+ females from Lemon Creek (0.0009 g·g^{-1}·day^{-1}) was slightly lower than those of the other age 3+ females (~0.0014 g·g^{-1}·day^{-1}) (Fig. 5-2c), while there was no difference for age 3+ males among sites (~0.0009 g·g^{-1}·day^{-1}) (Fig. 5-2d).

The length-at-age of mummichogs varied little among sites (Fig. 5-3a), while there were significant differences in weight-at-age among sites (age 2+: $F_{4, 52} = 7.18$, $p < 0.001$; age 3+: $F_{4, 107} = 10.6$, $p < 0.001$, Fig. 5-3b). Age 2+ females from Richmond Creek and age 2+ males from Neck Creek are considerably larger (in weight) than those from the other sites (Fig. 5-3b). Age 3+ fish from both Lemon Creek and Main Creek were considerably smaller than those from Richmond, Mill, and Neck Creeks (Fig. 5-3b).

Growth Conversion Efficiency

Two-way ANOVA showed that the growth conversion efficiencies of age 2+ and 3+ mummichogs were significantly different among sites (age 2+: $F_{4, 69} = 28.1$, $p < 0.001$; age 3+: $F_{4, 61} = 51.6$, $p < 0.001$, Table 5-2), while the significant effect of sex was observed only for age 3+ fish (age 2+: $F_{4, 69} = 2.86$, $p = 0.095$; age 3+: $F_{4, 61} = 7.92$, $p < 0.01$, Table 5-2). The results of 2-way ANCOVA with food consumption rate as a covariable also showed that the relationships between growth rates and food consumption rates were significant for both age 2+ and 3+ fish (age 2+: $F_{4, 68} = 5.09$, $p < 0.001$; age 3+: $F_{4, 60} = 3.47$, $p < 0.001$, Table 5-3 and Fig. 5-4a through 5-4e). The interaction between site and sex in 2-way ANOVA was significant only for age 2+ fish (age 2+: $F_{4, 69} = 3.27$, $p < 0.05$; age 3+: $F_{4, 61} = 2.11$, $p = 0.09$, Table 5-2), while the interaction between site and sex in 2-way ANCOVA was significant for both age 2+ and 3+ fish (age 2+: $F_{4, 68} = 14.0$, $p < 0.001$; age 3+: $F_{4, 60} = 3.60$, $p < 0.05$, Table 5-3).

A planned comparison showed that the conversion efficiencies of age 2+ females from Lemon Creek and Mill Creek (~4.8%) were more than 2-fold higher than those of Richmond Creek, Main Creek (~2.0%), and Neck Creek females (1.1%) (Fig. 5-5a). The

conversion efficiencies of age 2+ males from Lemon Creek, Mill Creek, and Main Creek (~3.8%) were approximately 2-fold higher than those of Richmond Creek and Neck Creek males (~2.3%) (Fig. 5-5b). Age 3+ females from Lemon Creek (1.4%) had a slightly lower conversion efficiency than those from Richmond Creek (1.9%), Main Creek (2.0%), and Mill Creek (2.4%) (Fig. 5-5c), while the conversion efficiencies of age 3+ males from Lemon Creek and Mill Creek (~2.2%) were ~2-fold higher than those of Richmond Creek, Neck Creek, and Main Creek males (~0.93%) (Fig. 5-5d).

Total Metabolic Costs

Assuming that the proportions of energy lost through egestion and excretion were constant (~24.5% of the consumed energy) across the populations, the estimates of specific total metabolic costs (= standard metabolism + active metabolism + specific dynamic action) of age 2+ and 3+ mummichogs were significantly different among sites (age 2+: $F_{4, 69} = 21.3$, $p < 0.001$; age 3+: $F_{4, 61} = 29.3$, $p < 0.001$, Table 5-2). The effect of sex was not significant for either age 2+ or 3+ fish (age 2+: $F_{4, 69} = 0.83$, $p = 0.37$; age 3+: $F_{4, 61} = 2.57$, $p = 0.11$, Table 5-2), while the interaction between site and sex was significant for only age 3+ fish (age 2+: $F_{4, 69} = 1.69$, $p = 0.16$; age 3+: $F_{4, 61} = 3.03$, $p < 0.05$, Table 5-2). With the exception of males and females from Lemon Creek and males from Neck Creek, there was a significant relationship between total metabolic cost ($kJ \cdot day^{-1}$) and body size (g); the metabolic costs increased exponentially with body size (Fig. 5-6a through 5-6e).

A planned comparison showed that the specific total metabolic rate of age 2+ females from Neck Creek ($0.326\ kJ \cdot g^{-1} \cdot day^{-1}$) was more than 2-fold higher than those of

the other females (0.142 $kJ \cdot g^{-1} \cdot day^{-1}$) (Fig. 5-7a). The specific total metabolic rates of age 2+ males from Lemon Creek and Mill Creek (~0.123 $kJ \cdot g^{-1} \cdot day^{-1}$) were significantly lower than those of Richmond Creek and Neck Creek males (~0.323 $kJ \cdot g^{-1} \cdot day^{-1}$), while the specific total metabolic rates of age 2+ males from Main Creek (0.169 $kJ \cdot g^{-1} \cdot day^{-1}$) was significantly lower than those of Neck Creek males only (Fig. 5-7b). The specific metabolic rates of both age 3+ males and females from Richmond Creek and Neck Creek (~0.28 $kJ \cdot g^{-1} \cdot day^{-1}$) were significantly higher than those of Lemon Creek and Mill Creek fish (~0.13 $kJ \cdot g^{-1} \cdot day^{-1}$), while only age 3+ females from Main Creek (0.119 $kJ \cdot g^{-1} \cdot day^{-1}$) had a significantly lower total metabolic rate than those from Richmond Creek and Neck Creek (Fig. 5-7c and 5-7d).

DISCUSSION

Energetic expenditures of fish living in chronically degraded habitats tend to be elevated, partly due to increased metabolic activities induced by physiological impairments (Berntssen and Lundebye, 2001; Campbell *et al.*, 2002; Rajotte and Couture, 2002; Couture and Kumar, 2003). Many aquatic organisms including fish use a variety of physiological and biochemical processes to ameliorate adverse effects of anthropogenic stressors (e.g., the induction of detoxifying proteins for trace metals, Chapter 4; Mason and Jenkins, 1995) that can increase metabolism (Douben, 1989; Calow, 1991; Moiseenko, 2002). Elevated metabolism is also frequently associated with behavioral activities of fish (Ryan and Harvey, 1980; Barlaup *et al.*, 1989; Tucker and Rasmussen, 1999; Sherwood *et al.*, 2000). Anthropogenic stressors such as chemical pollutants can directly affect fish foraging behaviors (i.e., energy intake) (Smith and Weis, 1997; Weis

et al., 2001), and indirectly influence fish energetics (Handy *et al.*, 1999; Campbell *et al.*, 2002). Weis et al. (2001) have, for instance, demonstrated that the capacity of mummichogs to capture decapods (*Palaemonetes pugio*) was considerably compromised in chemically polluted salt marshes in northwest Atlantic coast. It is thus possible that the Arthur Kill populations of mummichogs may have been forced to use a feeding strategy that is energetically inefficient, i.e., foraging for prey that are small but relatively easy to capture (e.g., isopods) (= low predator-prey body size ratio) (Chapter 3; Boisclair and Rasmussen, 1996; Pazzia *et al.*, 2002).

In the current study, the proportions (%) of energy allocated to total metabolism (= standard metabolism + active metabolism + specific dynamic action) of age 2+ and 3+ mummichogs were fairly similar among sites, i.e., 69 to 75%, which were also strikingly similar to the estimates (69%) obtained in a laboratory study by Weisberg and Lotrich (1982). However, due to substantial differences in food consumption rates, mummichogs from the northern Arthur Kill sites (Richmond Creek, Main Creek, and Neck Creek) consistently had 2 to 3-fold higher total metabolic rate ($kJ \cdot g^{-1} \cdot day^{-1}$) than those from the reference site (Lemon Creek). On the other hand, mummichogs from the southern Arthur Kill site, Mill Creek, had a similar total metabolic rate to those from the reference site. Incidentally, Vitaliano and Bejda (2001) have also shown a clear difference in the status of ribbed mussels (*Geukensia demissa*) between the northern Arthur Kill salt marshes (many of which were substantially damaged by the 1990 oil spill) and Mill Creek. Ribbed mussels from Mill Creek (a non-oil-damaged site) had a considerably higher growth rate, larger body size, and better conditions (e.g., higher body-weight to shell-weight ratio)

than those from the northern Arthur Kill sites (heavily oil-damaged sites) (Vitaliano and Bejda, 2001).

In highly urbanized habitats, some fishes can compensate for elevated energy expenditures using several adaptive strategies, including a reduction in behavioral activities (Handy *et al.*, 1999), a reallocation of stored energy (e.g., lipids and carbohydrates) (Campbell *et al.*, 2002; Levesque *et al.*, 2002), and an increase in food consumption (Beyers and Rice, 2002). Previous studies have suggested that reduced activities of stressed fish are a compensatory mechanism for elevated standard metabolism (Handy *et al.*, 1999; Campbell *et al.*, 2002). Handy et al. (1999) have, for instance, indicated that a decrease in behavioral activities (e.g., swimming) by rainbow trout (*Oncorhynchus myskiss*) exposed to dietary copper may be resulted from increased metabolic costs and decreased liver lipid reserves, suggesting energy reallocations may be partly associated with altered behavioral activities. Smith and Weis (1997) have also experimentally shown that mummichogs from polluted salt marshes reduced attempts to capture prey, which may be considered as an adaptive strategy to reduce energy expenditure. Energy expended for foraging activities is often directly related to consumed energy as well as stored energy (Handy *et al.*, 1999; Campbell *et al.*, 2002). As foraging activities can be energetically costly, the cost associated with increasing foraging activities (e.g., an increase in metabolism) may eventually surpass the benefits (i.e., energy gain). Actively foraging fishes such as mummichogs may thus require balancing energy gained from food consumption and energy expended for foraging activities to maximize energy conversion efficiency and perhaps maintain growth rate (Handy *et al.*, 1999; Campbell *et al.*, 2002).

In general, assimilated energy from food is allocated to growth (somatic and/or gonadal) after accounting for essential metabolic activities (Hanson *et al.*, 1997). Due to its sensitivity to external (e.g., physicochemical properties of the environment) as well as internal (e.g., metabolism) conditions, individual growth of fish is an ecologically relevant, integrative indicator that is frequently used in the assessment of fish habitat quality (Ryan and Harvey, 1980; Barlaup *et al.*, 1989; Conover, 1990; Weatherly, 1990; Beyers and Rice, 2002). Examining how habitat degradation influences potential energy available to growth may thus reveal the mechanisms underlying alterations in fish life history traits (Beyers *et al.*, 1999a; Beyers *et al.*, 1999b). In the current study, age 2+ female mummichogs from the Arthur Kill sites had substantially (> 60%) reduced specific growth rates. Since these growth rates include both somatic and gonadal growth, the among-site differences in age 2+ females may also reflect negative impacts not only on somatic but also on gonadal growth of the Arthur Kill populations of mummichogs. Toppin et al. (1987) have suggested that negative growth observed in female adult mummichogs living in chemically polluted habitats may be associated with their investment in embryonic resistance to chemical pollutants. Furthermore, Sherwood *et al.* (2000) have also indicated that increased energy requirement due to chemically induced metabolic costs (e.g., detoxification of chemical pollutants) is likely to be compensated for by a reallocation of energy that is potentially available to growth. Collvin (1985) has experimentally demonstrated that when food consumption was controlled, the growth rate of copper-exposed Eurasian perch (*Perca fluviatilis*) was considerably lower than that of the control fish. These differential growth rates suggest that some assimilated energy that

could have been allocated to growth may have been reallocated to offset increased metabolic costs incurred by the detoxification of excess copper.

In certain cases, however, the allocation of energy available to growth may be indirectly maintained by flexible foraging habits (Calow, 1991; Health, 1995). Growth of tolerant fishes with a flexible feeding habit appears to be influenced little by alterations in prey resources in urban habitats (e.g., reduced abundance or disappearance of sensitive species) (Jeffree and Williams, 1980; Steimle, 1994; Clements and Rees, 1997; Clements and Newman, 2002). This flexible feeding habit may thus be considered as an adaptive strategy (trophic plasticity) to acquire sufficient energy to maintain growth, accommodating to fluctuations in prey availability (Jeffree and Williams, 1980; Gerking, 1994; Elser and Hessen, 2005; Woodward *et al.*, 2005). In the current study, despite their elevated metabolism, individual growth rates of age 2+ males, and age 3+ females and males of the Arthur Kill populations of mummichogs were similar to or slightly higher than those of the reference (Lemon Creek) population. Furthermore, population-specific individual growth trajectories of mummichogs also indicated that there was little difference in average total length-at-age among sites, while average weight-at-age of some of the Arthur Kill populations was considerably higher than that of the reference population. Growth enhancement has been previously observed in some fishes living in degraded habitats, most likely as a result of indirect ecological responses to altered trophic structures (e.g., reduced competitions and increased tolerant prey availabilities) (McFarlane and Franzin, 1978; Ryan and Harvey, 1980; Barlaup *et al.*, 1989; Henshel *et al.*, 2006). In urban habitats, tolerant fishes such as mummichogs may thus benefit from

reduced exploitative competition as well as increased tolerant prey abundance (Chapter 2; Ryan and Harvey, 1980; Barlaup *et al.*, 1989).

Growth of mummichogs can also be influenced by inter- as well as intra-specific competitions (Kneib, 1981; Dunson and Rowe, 1996), which influence the accessibility to potential prey resources (Weisberg, 1986; Dunson and Rowe, 1996; Sardá *et al.*, 1998). In the present study, though nekton communities were not quantitatively assessed, there was a considerable qualitative difference in nekton community assemblages between the Arthur Kill and reference (Lemon Creek) sites. At the reference site, there were a number of nekton species including blue crab (*Callinectus sapidus*), summer flounder (*Paralichthys dentatus*), bluefish (*Pomatomus saltatrix*), American shad (*Alosa sapidissima*), sheepshead minnows (*Cyprinodon variegatus*), and striped killifish (*Fundulus majalis*), while at the Arthur Kill sites, only a large number of mummichogs and a relatively small number of Atlantic silversides (*Menidia menidia*) and striped killifish were observed (personal observation). Many of the nekton species observed at the reference site can grow faster and larger than mummichogs, and are potentially superior predators (Werme, 1981; Sardá *et al.*, 1998), which may have influenced the growth potential of mummichogs at this site.

Although there have been several attempts to investigate pollution impacts on fish bioenergetics, food consumption rates in many of these studies are laboratory-based or model-simulated (e.g., Stoner and Livingston, 1978; Muller and Nisbet, 1997; Nisbet *et al.*, 1997; Beyers *et al.*, 1999a; Beyers *et al.*, 1999b). Energetic responses of fish to habitat conditions (e.g., stress-induced energetic costs) may, however, be difficult to detect or occasionally misleading without *in situ* food consumption estimates (i.e., energy

gain) (Sherwood *et al.*, 2002; Morinville and Rasmussen, 2003). Due to logistical difficulties in estimating *in situ* food consumption rates of wild populations of fish (Chipps and Wahl, 2008), except for a few studies (e.g., Sherwood *et al.*, 2000; Trudel *et al.*, 2000), pollution impacts on food consumption and subsequent allocation of consumed energy have often not been fully explored in the field setting (Beyers and Rice, 2002). A traditional approach to estimating *in situ* food consumption rates using the gut evacuation method is highly labor-intensive (Sherwood *et al.*, 2002), and may thus be impractical for field-based comparative studies.

Annual average daily food consumption rates of mummichogs estimated by the mercury mass balance model in the current study (~0.06 to 0.15 $g \cdot g^{-1} \cdot day^{-1}$) were fairly consistent with field estimates using the gut evacuation method (~0.13 $g \cdot g^{-1} \cdot day^{-1}$) by Weisberg *et al.* (1981) as well as laboratory estimates (~0.043 $g \cdot g^{-1} \cdot day^{-1}$) by Weisberg and Lotrich (1982a). The *in situ* daily food consumption rate estimates in the current study also revealed that the northern Arthur Kill (Richmond Creek, Main Creek, and Neck Creek) populations of mummichogs with elevated total metabolism consumed 2 to 3-fold more food than the reference population. This substantial difference in food consumption suggests that mummichogs in the Arthur Kill may be capable of adjusting their energy intake to compensate for elevated metabolic costs incurred by anthropogenic stressors. The compensatory food consumption by mummichogs has also been observed in an experimental study by Weisberg and Lotrich (1982a), in which fish fed with low energy-content prey (*Uca sp.*) consumed more than those fed with high energy-content prey (*Palaemonetes sp.* and *Nereis sp.*). This energy-based adaptive strategy of compensatory food consumption is likely to be used by wild populations of fishes when

interspecific exploitative competition is concurrently reduced, when prey availability is increased, or both. In the Arthur Kill, low nekton species diversity (i.e., lower competition and predation risk) and high abundances of tolerant benthic macroinvertebrate species (i.e., higher prey availability, Chapter 2) may have allowed mummichogs to increase their food consumption as a compensatory strategy.

Despite elevated food consumption, however, the Arthur Kill populations of mummichogs in the present study did not show a proportional increase in growth rate, which resulted in substantially lower (as much as 80%) growth conversion efficiencies than that of the reference population. This substantial decrease in conversion efficiency suggests that growth enhancement observed in some of the Arthur Kill populations of mummichogs may be a by-product of compensatory food consumption induced by elevated metabolism (i.e., overcompensation). A decrease in energy conversion efficiency at the individual level can lead to reduced trophic efficiencies at the community level. Inefficient energy fluxes in stressed ecosystems have been frequently documented (Clements and Newman, 2002), and could ultimately result in trophic bottlenecks (Sherwood *et al.*, 2002) as well as disappearance of large-bodied apex predators (Clements and Newman, 2002).

Conclusions

The present study demonstrated that habitat degradation in urban tidal salt marshes in the Arthur Kill had clearly induced energetic costs (e.g., elevated metabolism) in mummichogs. Although these Arthur Kill populations of mummichogs appeared to be capable of adjusting food consumption to compensate for elevated metabolic costs in

order to maintain growth rates, their growth conversion efficiencies were substantially reduced in these highly stressful habitats. The importance of mummichogs as a conduit of energy and marsh production transport to open coastal environments has been well recognized (Valiela *et al.*, 1977; Weisberg *et al.*, 1981; Kneib and Wagner, 1994; Teo and Able, 2003). Reduced energy conversion efficiencies in mummichogs observed in the present study are, therefore, likely to have significant implications for the overall trophic efficiencies in the Arthur Kill and adjacent coastal ecosystems (i.e., potential disruption in trophic relay processes).

A bioenergetics modeling approach has been frequently used in fisheries research to examine the effects of biological and environmental factors on energetic performances of fishes and shellfishes (e.g., Kamler *et al.*, 1994; Grant, 1996; Feller and Gerday, 1997; Megrey and Hinckley, 2001; Ciannelli, 2002). As effects of anthropogenic stressors on fishes and shellfishes can be expressed by alterations in energy intake (i.e., food consumption) and expenditures (e.g., metabolism), bioenergetics modeling is a valuable tool for understanding their functional responses to habitat degradation (Beyers *et al.*, 1999a; Beyers *et al.*, 1999b; Sherwood *et al.*, 2000; MacRury *et al.*, 2002). Furthermore, individual-level responses in bioenergetics can also be integrated into higher levels of biological organization (e.g., population dynamics) to elucidate the underlying mechanisms associated with habitat degradation from the energetics perspective (Nisbet *et al.*, 1997; Carlisle, 2000; Beyers and Rice, 2002; Moiseenko, 2002; Garvey *et al.*, 2003). Wild populations of fishes chronically exposed to anthropogenic stressors may exhibit altered life history traits such as smaller body size, shorter life span, and fewer spawning occasions (Toppin *et al.*, 1987; Moiseenko, 2002). By incorporating population

and trophic dynamics, the bioenergetics approach can contribute to a mechanistic understanding of habitat degradation impacts on fish populations and communities in urban coastal ecosystems (Nisbet *et al.*, 1997; Beyers and Rice, 2002; Garvey *et al.*, 2003; Klanjscek *et al.*, 2006).

Table 5-1. Summary of parameter values used for the Hg mass balance model.

Symbol	Parameter description	Value	Source†
AE_d	Assimilation efficiency of CH_3Hg from decapods	0.55	This study
AE_p	Assimilation efficiency of CH_3Hg from polychaetes	0.67	This study
AE_a	Assimilation efficiency of CH_3Hg from amphipods	0.68	This study
AE_{il}	Assimilation efficiency of CH_3Hg from insect larvae	0.81	This study
AE_m	Assimilation efficiency of CH_3Hg from mollusks	0.25	1
Φ	Coefficient of Hg elimination	0.0029	2
β	Allometric exponent of Hg elimination	–0.20	2
γ	Temperature coefficient of Hg elimination	0.066	2
GSI_m	Gonadosomatic index of male mummichogs	0.037	3, 4, 5
GSI_f	Gonadosomatic index of female mummichogs	0.161	3, 4, 5, 6, 7, 8

†1, Pentreath (1976); 2, Trudel and Rasmussen (1997); 3, Kneib and Stiven (1978); 4, Leblanc *et al.* (1997); 5, Shimizu (1997); 6, Taylor (1986); 7, Hsiao *et al.* (1994); 8, Hunter *et al.* (2007).

Table 5-2. Results of 2-way analysis of variance (ANOVA) for the effects of site and sex on age 2+ and age 3+ mummichog food consumption rate, growth rate, growth conversion efficiency, and total metabolic rate. *SS* = sum of squares, *DF* = degrees of freedom, and *MS* = mean square. Statistically significant differences are indicated in **bold** ($p < 0.05$)

		Age 2+					**Age 3+**				
		SS	*DF*	*MS*	*F*-value	*p*-value	*SS*	*DF*	*MS*	*F* -value	*p*-value
Food Consumption Rate	Intercept	71.990	1	71.99	172290	**0.000**	73.31	1	73.31	93140	**0.000**
	Site	1.652	4	0.413	988.2	**0.000**	0.676	4	0.169	214.7	**0.000**
	Sex	0.000	1	0.000	1.000	0.309	0.014	1	0.014	18.13	**0.000**
	Site x Sex	0.073	4	0.018	43.90	**0.000**	0.034	4	0.008	10.74	**0.000**
	Residual	0.029	69	0.000			0.048	61	0.001		
Growth Rate	Intercept	437.3	1	437.3	40685	**0.000**	513.3	1	513.3	15100	**0.000**
	Site	0.320	4	0.080	7.430	**0.000**	0.467	4	0.117	3.440	**0.014**
	Sex	0.140	1	0.140	13.05	**0.000**	0.471	1	0.471	13.84	**0.000**
	Site x Sex	1.093	4	0.273	25.42	**0.001**	0.488	4	0.122	3.590	**0.011**
	Residual	0.742	69	0.011			2.073	61	0.034		
Growth Conversion Efficiency	Intercept	8191	1	8191	8204	**0.000**	12258	1	12258	9608	**0.000**
	Site	112.4	4	28.09	28.14	**0.000**	263.2	4	65.79	51.57	**0.000**
	Sex	2.860	1	2.860	2.864	0.095	10.11	1	10.11	7.924	**0.007**
	Site x Sex	13.07	4	3.267	3.273	**0.016**	10.79	4	2.700	2.114	0.090
	Residual	68.89	69	0.998			77.82	61	1.280		
Total Metabolic Rate	Intercept	37.82	1	37.82	1195	**0.000**	37.45	1	37.45	1806	**0.000**
	Site	2.696	4	0.674	21.31	**0.000**	2.431	4	0.608	29.32	**0.000**
	Sex	0.026	1	0.026	0.828	0.366	0.053	1	0.053	2.568	0.114
	Site x Sex	0.213	4	0.053	1.687	0.163	0.251	4	0.063	3.032	**0.024**
	Residual	2.182	69	0.032			1.264	61	0.021		

Figure 5-1. Mean daily specific food consumption rates ($g \cdot g^{-1} \cdot d^{-1}$) of (a) age 2+ female, (b) age 2+ male, (c) age 3+ female, and (d) age 3+ male mummichogs from Lemon Creek, Mill Creek, Richmond Creek, Neck Creek, and Main Creek. Errors bars indicate ± 1 SE estimated with Monte Carlo simulations (n = 1000). Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test).

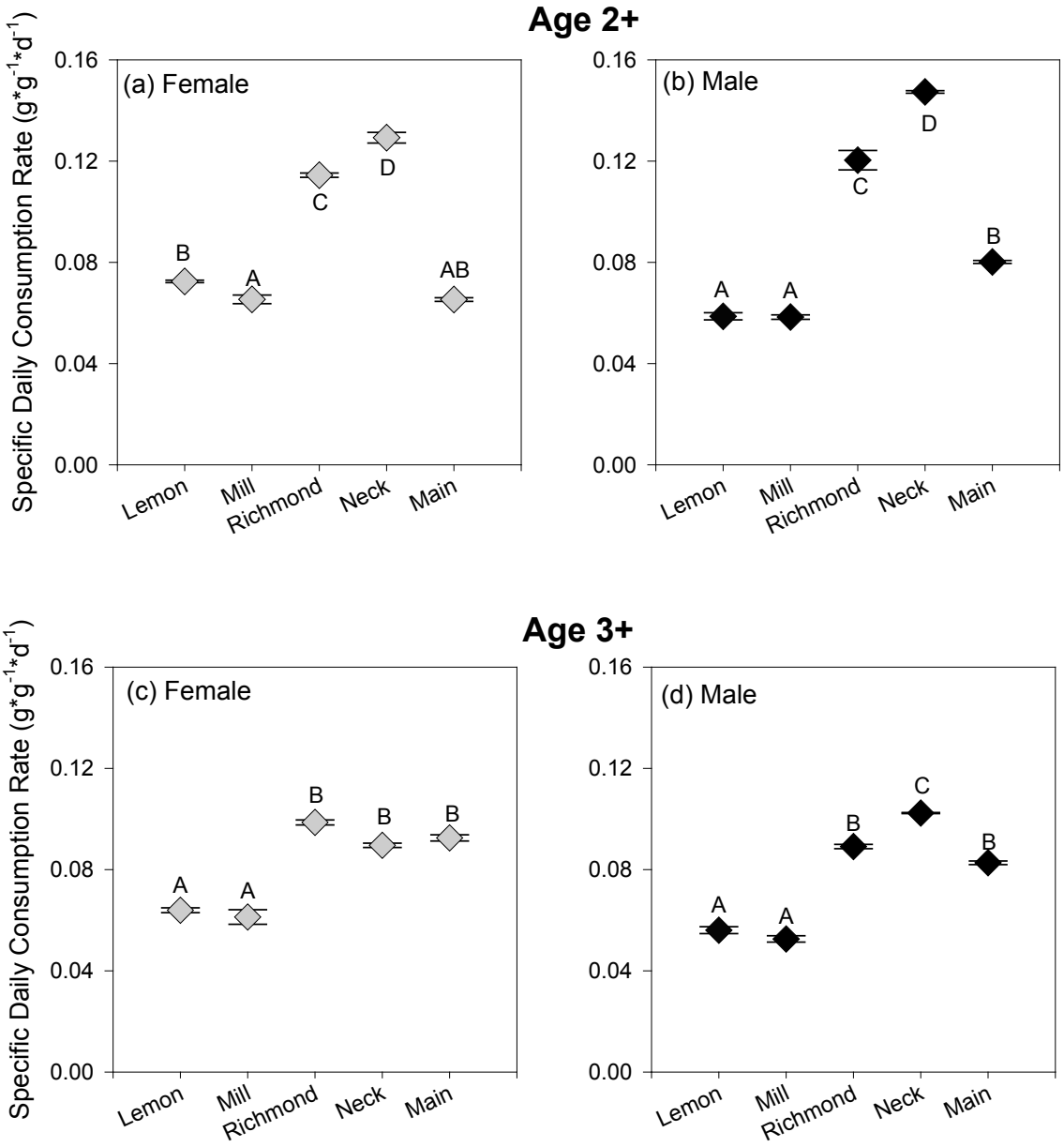


Figure 5-2. Mean daily specific growth rates ($g \cdot g^{-1} \cdot d^{-1}$) of (a) age 2+ female, (b) age 2+ male, (c) age 3+ female, and (d) age 3+ male mummichogs from Lemon Creek, Mill Creek, Richmond Creek, Neck Creek, and Main Creek. Errors bars indicate ± 1 SE estimated with Monte Carlo simulations (n = 1000). Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test).

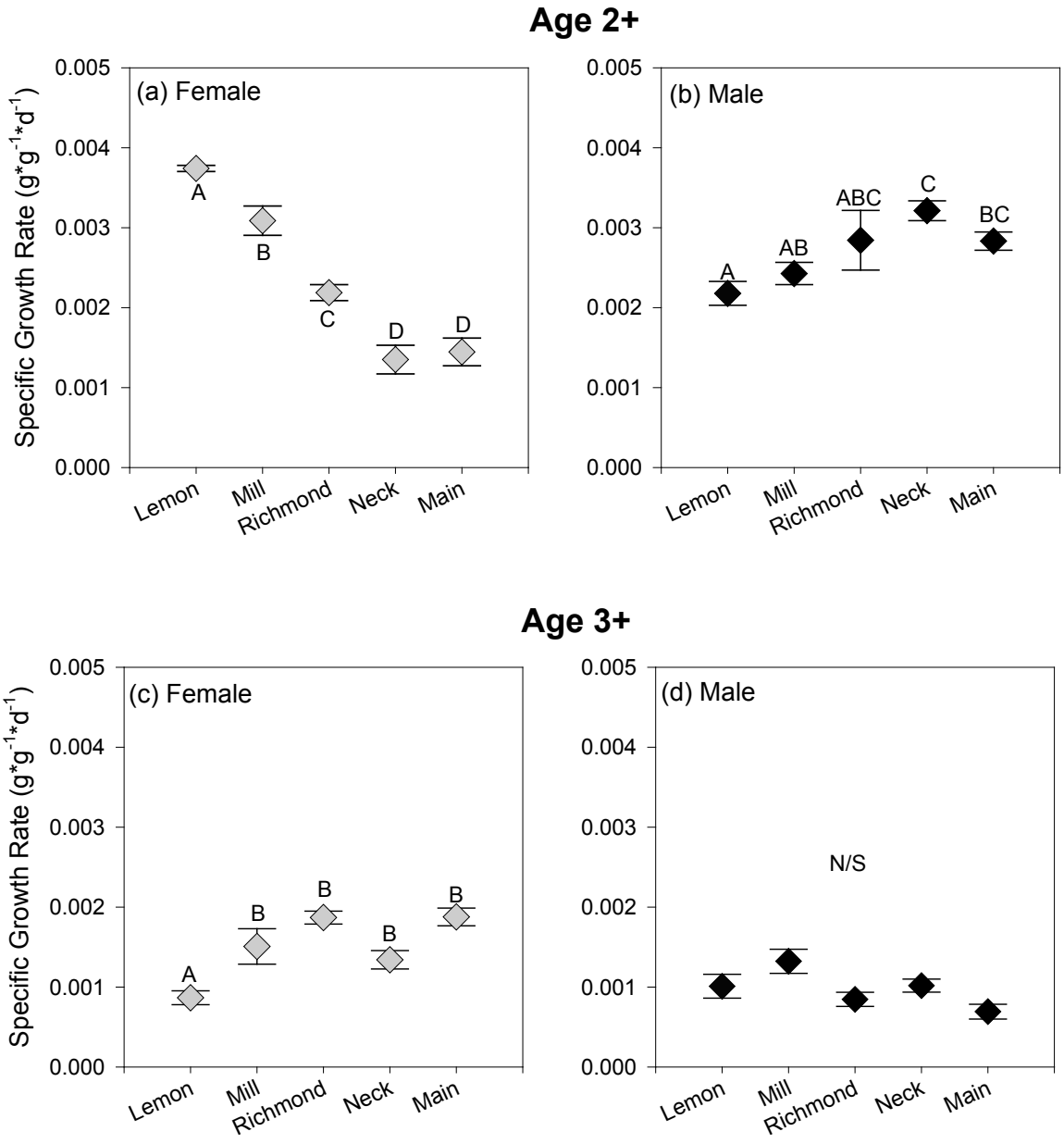


Figure 5-3. Population-specific growth trajectories of mummichogs in (a) total length (cm) and (b) weight (g) derived from the von Bertalanffy growth models fitted with Levenberg-Marquardt least squares method. Solid lines indicate the least squares regression for males. Dashed lines indicate the least squares regression for females.

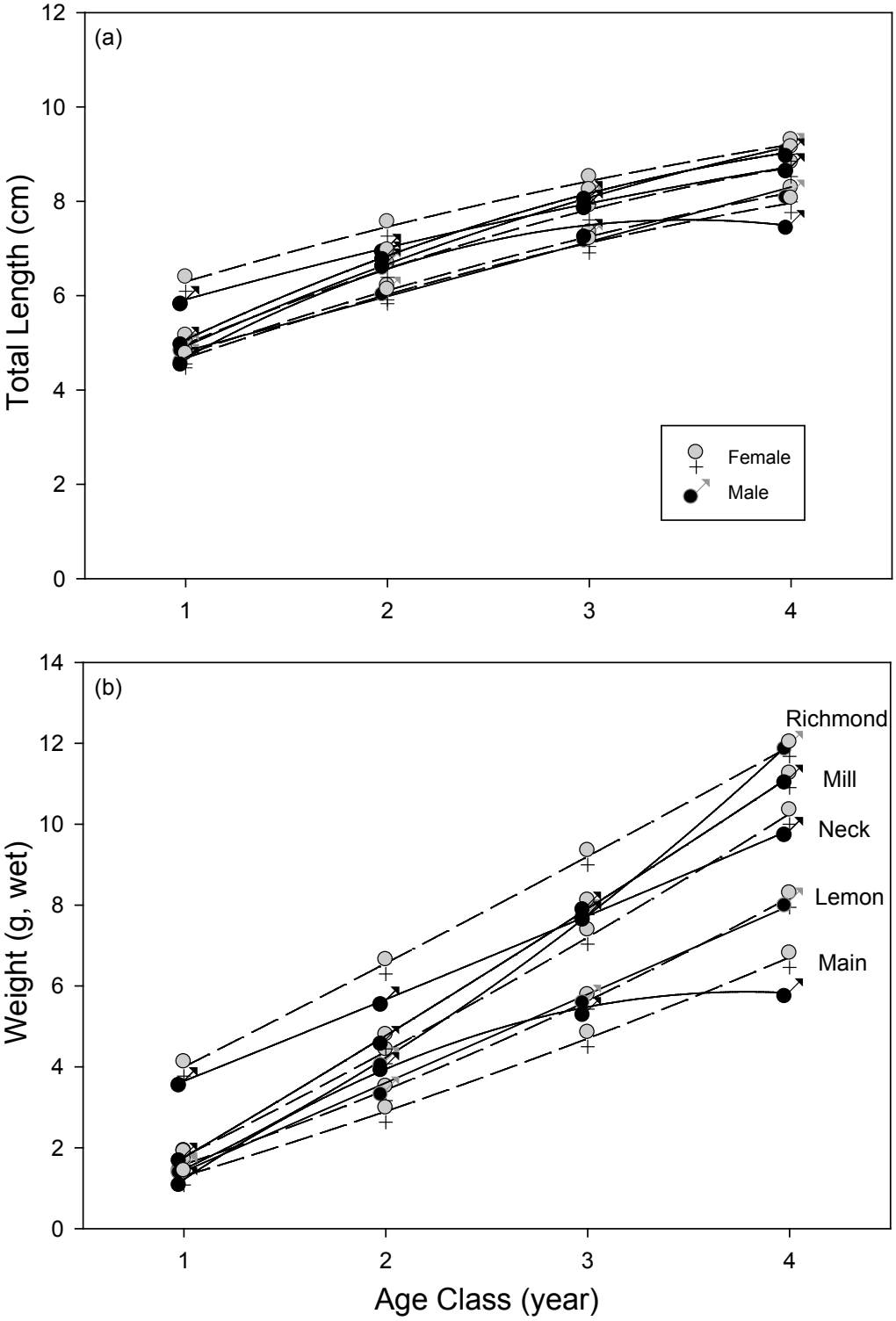


Figure 5-4. Population-specific relationships between food consumption rates ($g \cdot d^{-1}$) and growth rates ($g \cdot d^{-1}$) of female and male mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek.

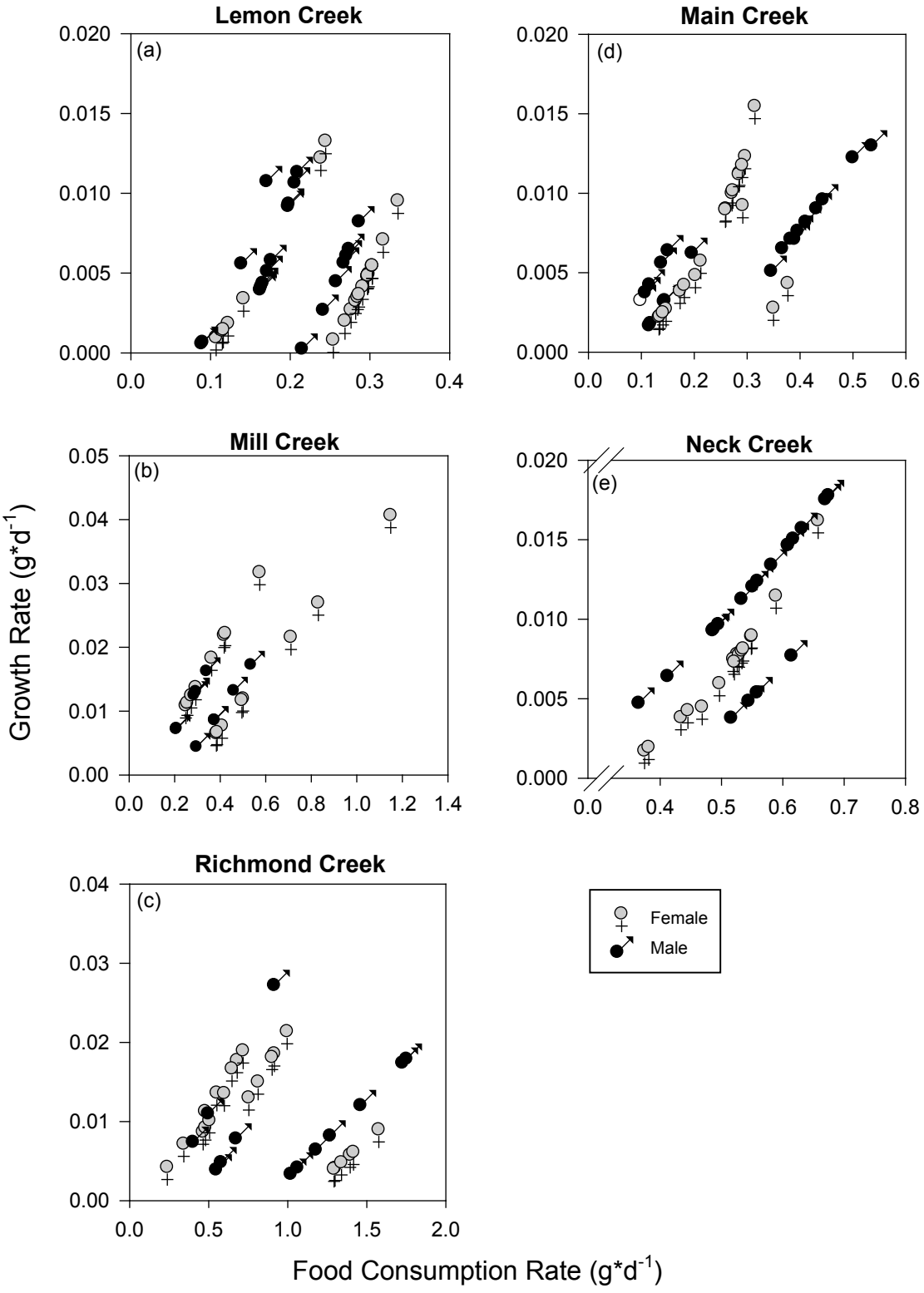


Table 5-3. Results of 2-way analysis of covariance (ANCOVA) for the effects of site and sex on age 2+ and age 3+ mummichog growth rate with food consumption rate as a covariate. *SS* = sum of squares, *DF* = degrees of freedom, and *MS* = mean square. Statistically significant differences are indicated in **bold** ($p < 0.05$)

	Age 2+					**Age 3+**				
	SS	*DF*	*MS*	*F*-value	*p*-value	*SS*	*DF*	*MS*	*F*-value	*p*-value
Intercept	0.361	1	0.361	34.67	**0.000**	0.586	1	0.586	17.26	**0.000**
Site	0.212	4	0.053	5.09	**0.001**	0.472	4	0.118	3.47	**0.012**
Sex	0.155	1	0.155	14.90	**0.000**	0.478	1	0.478	14.07	**0.000**
Site x Sex	0.585	4	0.146	14.04	**0.000**	0.489	4	0.122	3.60	**0.011**
Residual	0.708	68	0.010			2.038	60	0.034		

Figure 5-5. Mean growth conversion efficiency (%) of (a) age 2+ female, (b) age 2+ male, (c) age 3+ female, and (d) age 3+ male mummichogs from Lemon Creek, Mill Creek, Richmond Creek, Neck Creek, and Main Creek. Errors bars indicate ± 1 SE estimated with Monte Carlo simulations (n = 1000). Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test).

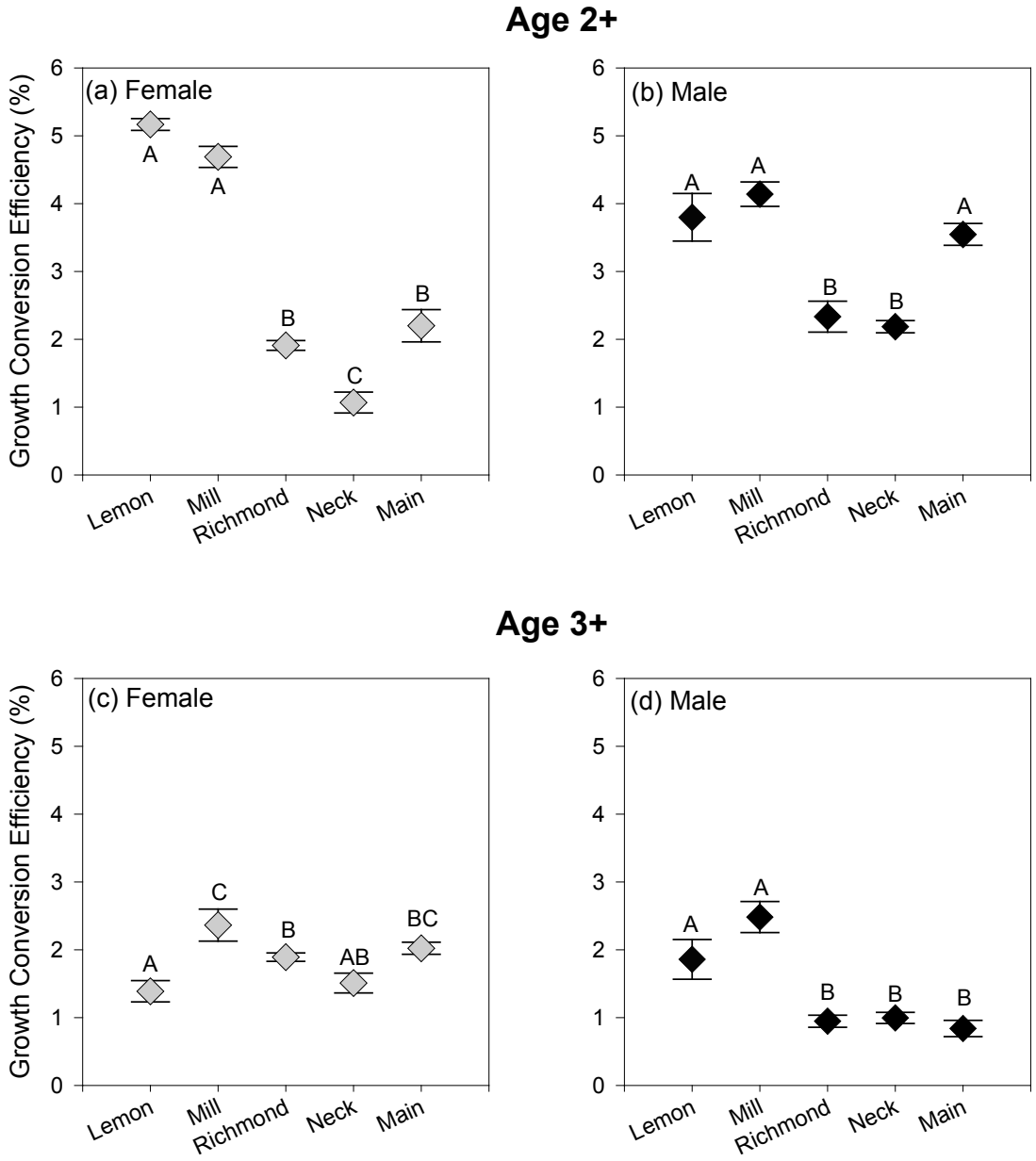


Figure 5-6. Population-specific relationships between total metabolic rates ($kJ \cdot d^{-1}$) and weight (g) of female and male mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate the least squares regression for males. Dashed lines indicate the least squares regression for females.

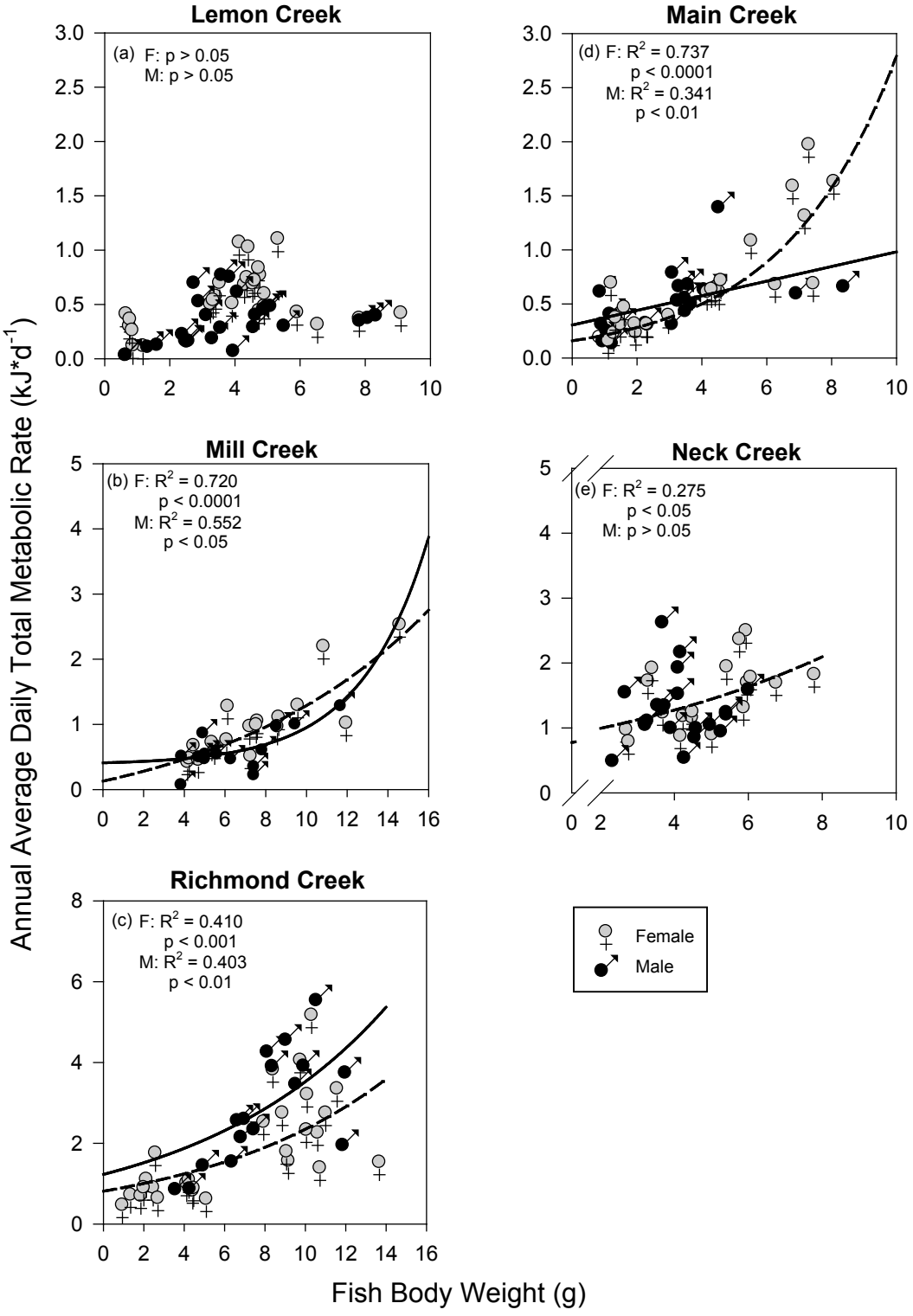
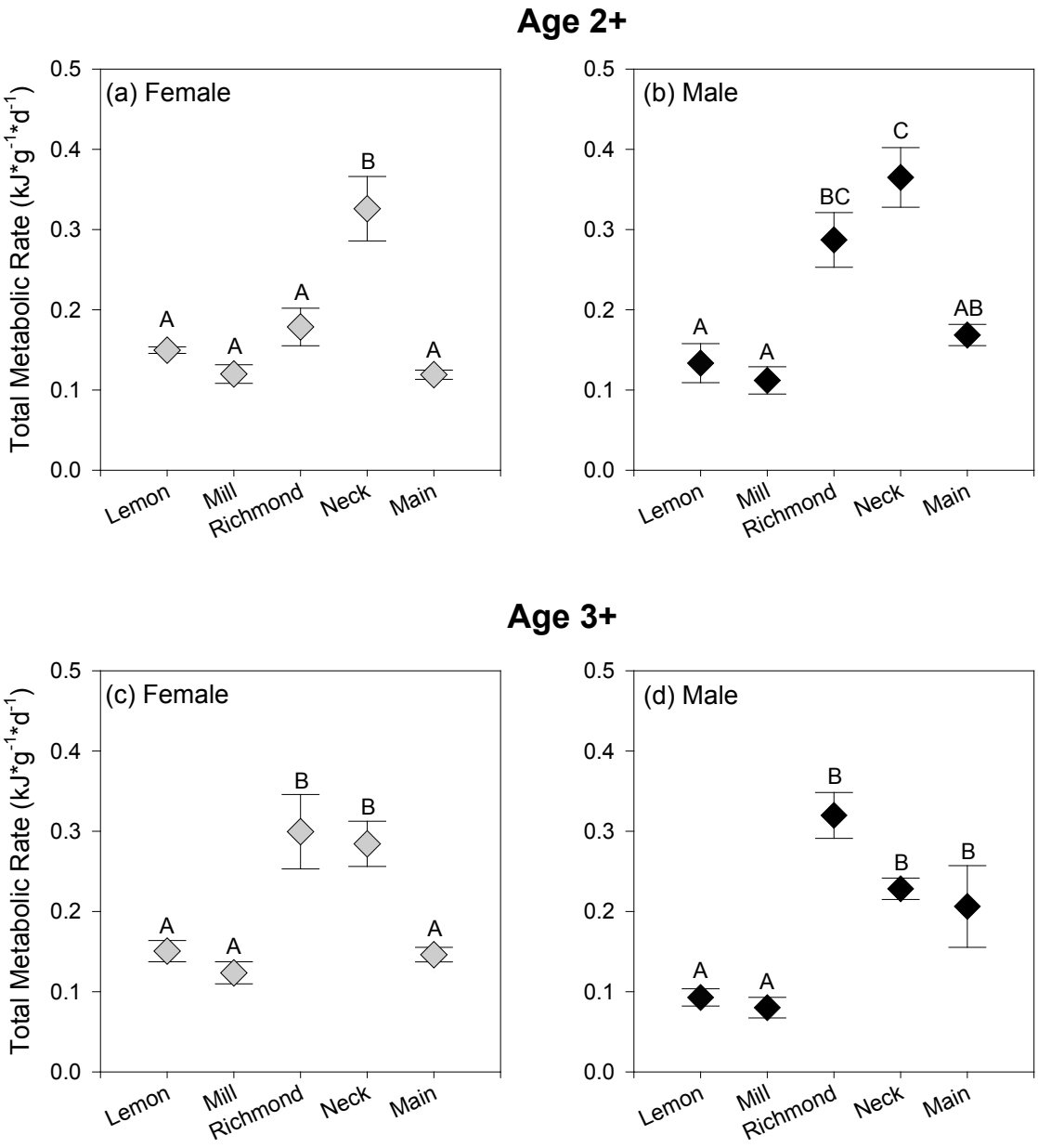
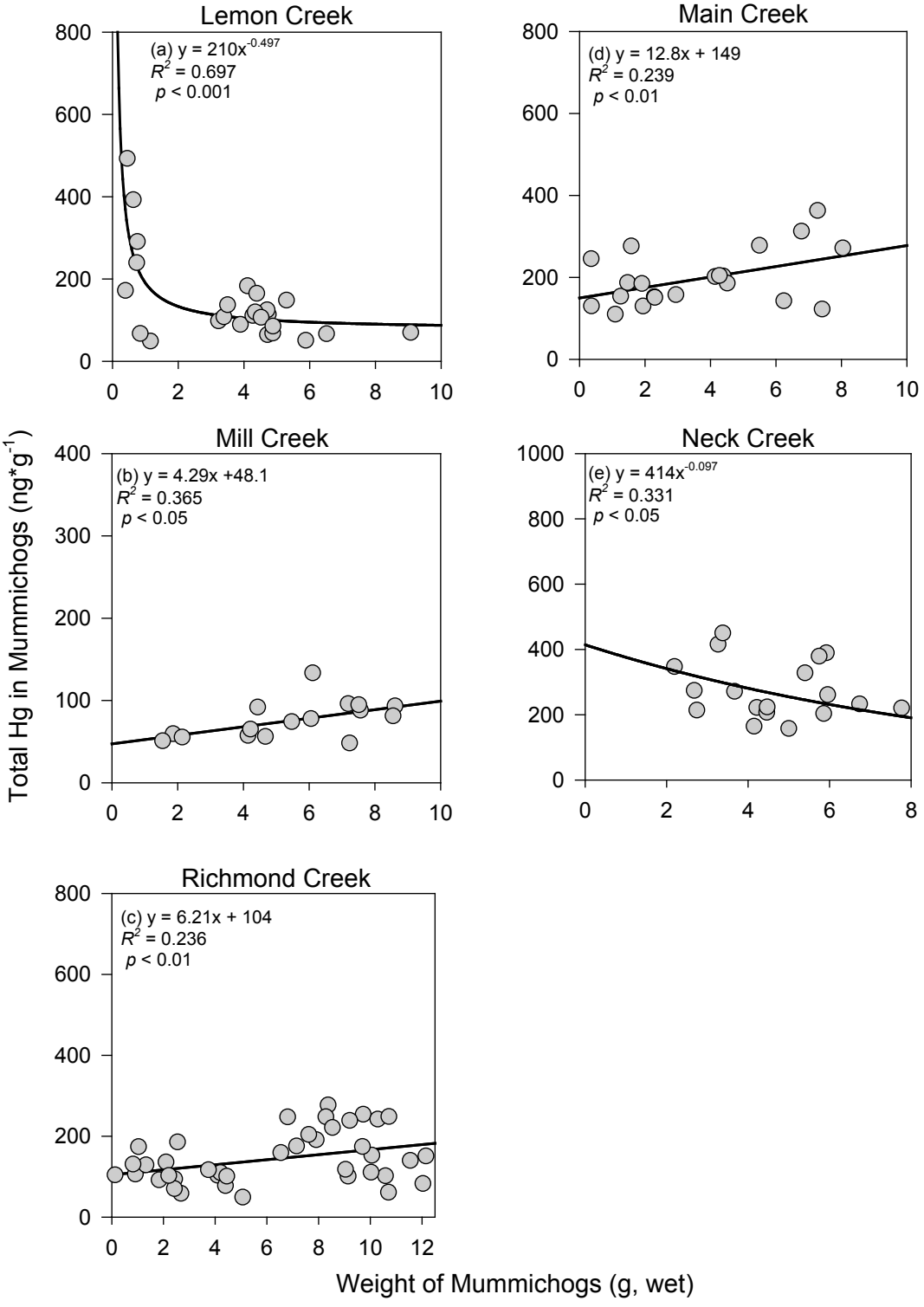


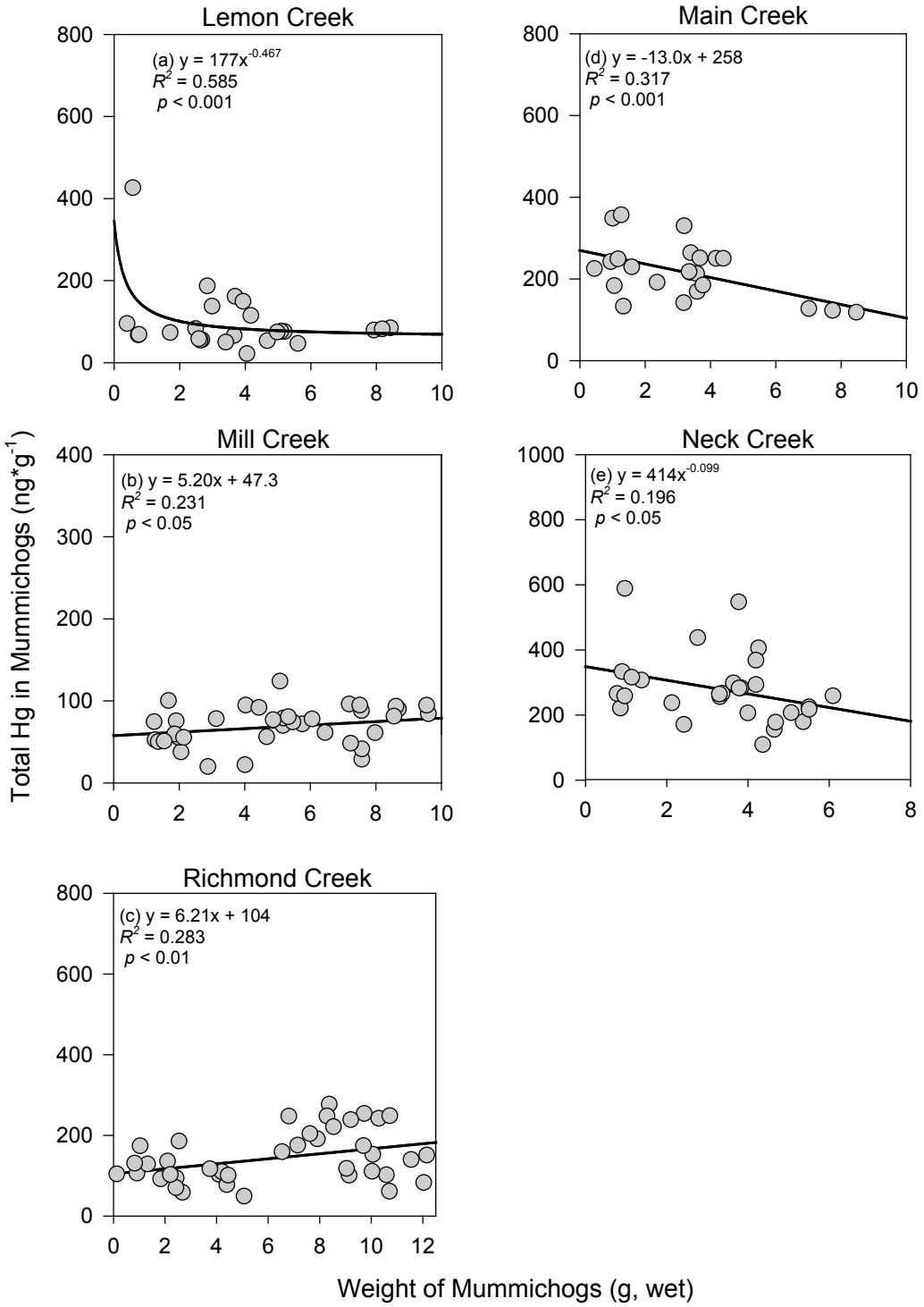
Figure 5-7. Mean total metabolic rates ($kJ \cdot g^{-1} \cdot d^{-1}$) of (a) age 2+ female, (b) age 2+ male, (c) age 3+ female, and (d) age 3+ male mummichogs from Lemon Creek, Mill Creek, Richmond Creek, Neck Creek, and Main Creek. Errors bars indicate ± 1 SE estimated with Monte Carlo simulations (n = 1000). Different letters below/above each symbol indicate statistically significant difference among sites (1-way ANOVA followed by Tukey's HSD test).



Appendix 5-A. Population-specific relationships between total Hg body burden ($ng \cdot g^{-1}$) and weight (g) of female mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate the least squares regression. The equation for the length-weight regression line is in each panel.



Appendix 5-B. Population-specific relationships between total Hg body burden ($ng \cdot g^{-1}$) and weight (g) of male mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate the least squares regression. The equation for the length-weight regression line is provided in each panel.

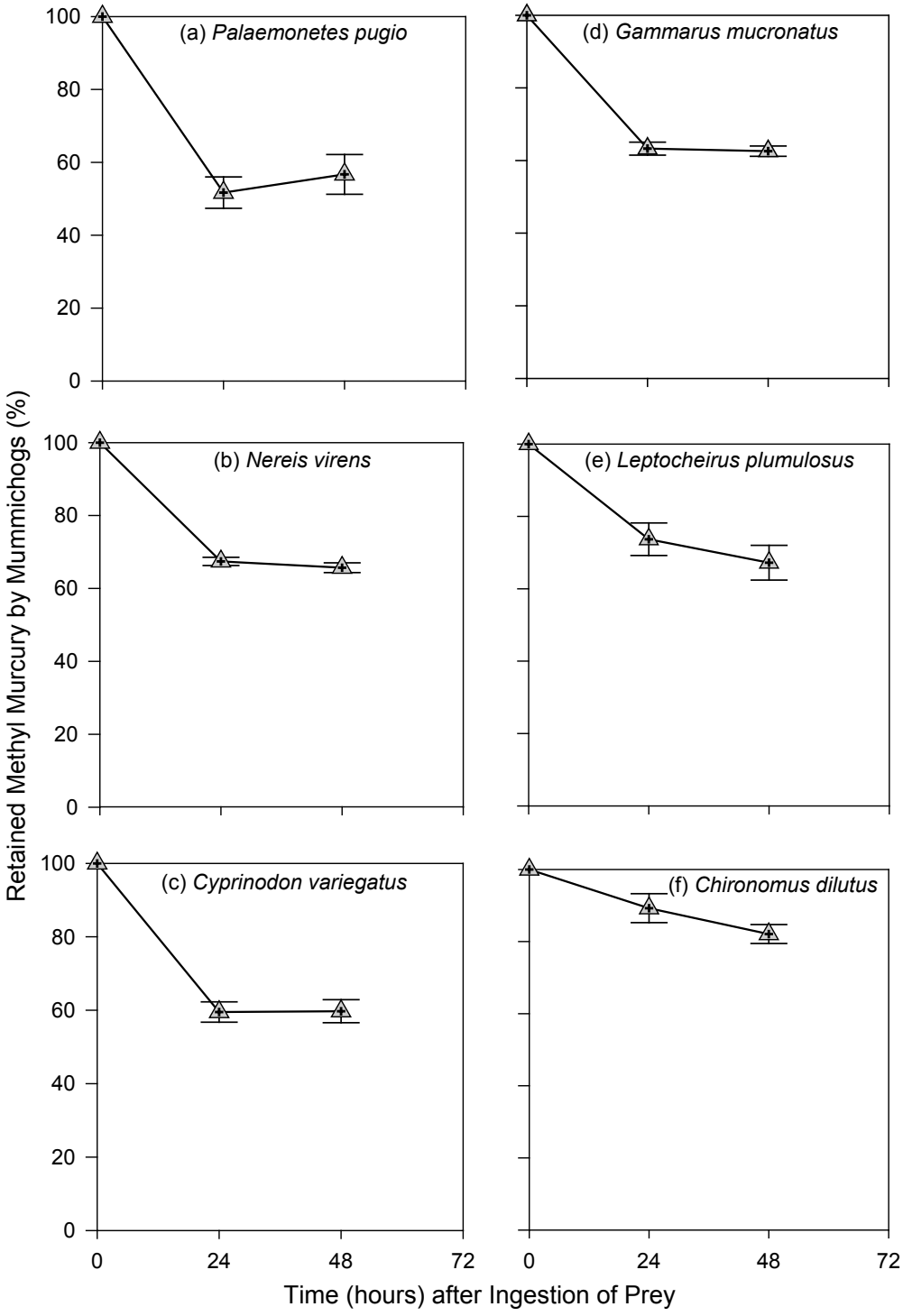


Appendix 5-C. Organic Hg contents ($ng \cdot g^{-1}$) in the major prey taxa found in the gut contents of mummichogs Lemon Creek, Mill Creek, Richmond Creek, Main Creek, and Neck Creek.

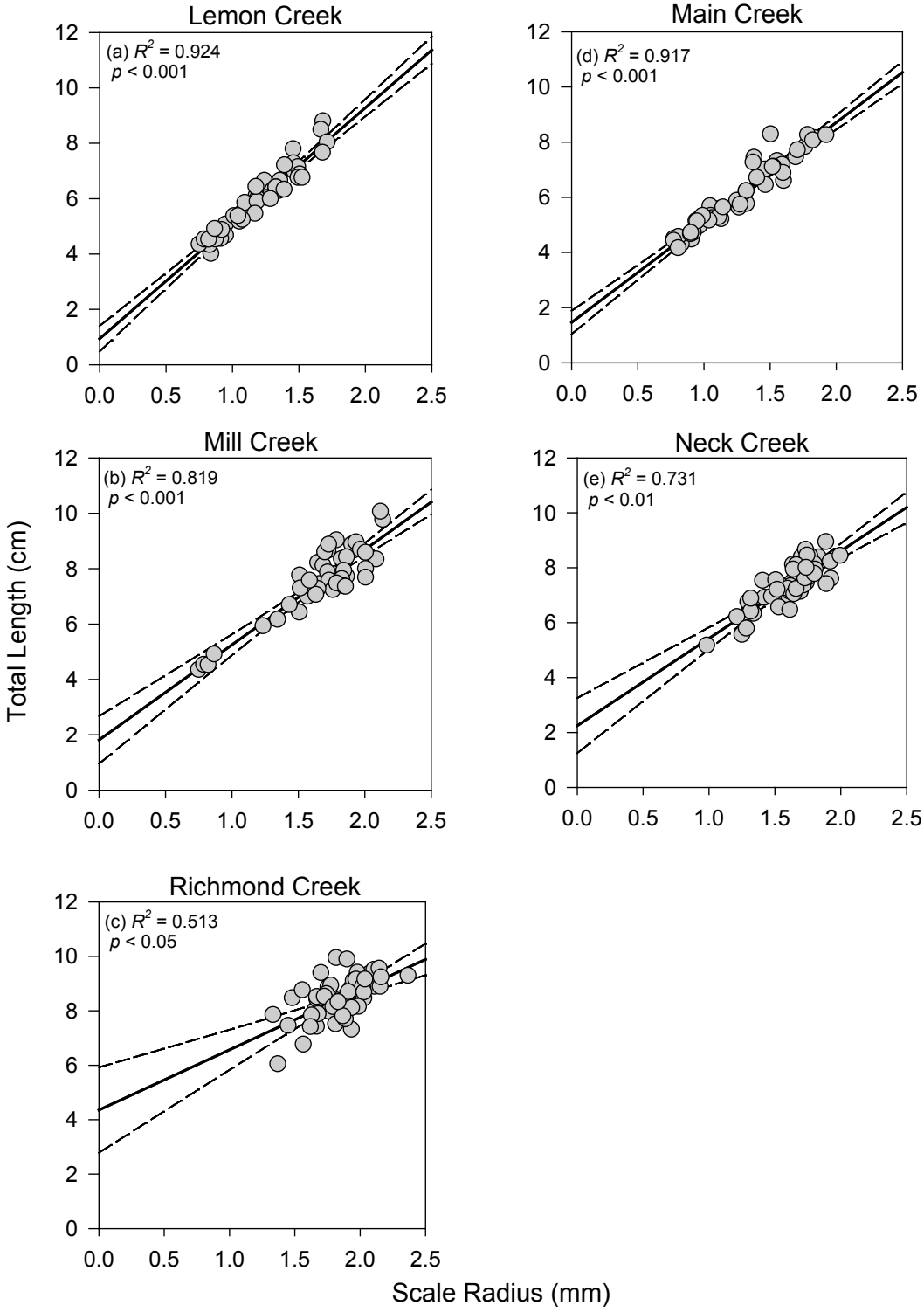
	Organic Hg in Prey ($ng \cdot g^{-1}$)				
	Lemon Creek	Mill Creek	Richmond Creek	Main Creek	Neck Creek
Decapoda	48.42	57.46	38.06	100.92	91.65
Isopoda	97.47	32.83	97.48	153.03	113.09
Amphipoda	–†	–†	–†	–†	113.09
Polychaeta	77.20	40.66	44.87	80.60	96.43
Insecta	289.87	131.30	417.67	294.53	–†
Gastropoda	43.22	32.83	–†	–†	–†
Cirripedia	–†	–†	97.48	153.03	–†

†Samples were not available for these taxonomic groups.

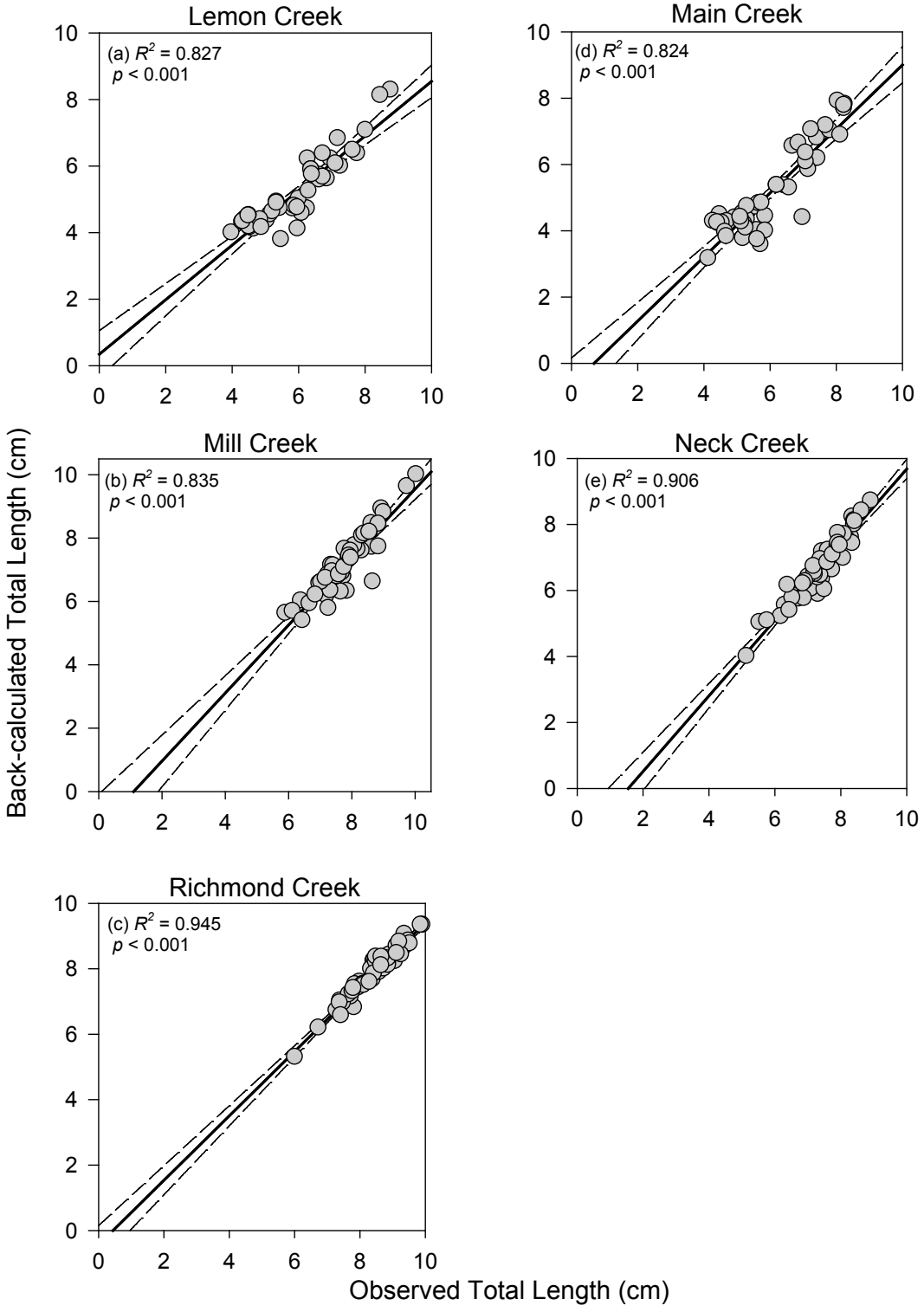
Appendix 5-D. Percentages of $CH_3{}^{203}Hg$ (▲) retained in mummichogs after 24 and 48 hours following pulse-feeding of radiolabeled (a) *Palaemonetes pugio*, (b) *Nereis virens*, (c) *Cyprinodon variegatus*, (d) *Gammarus mucronatus*, (e) *Leptocheirus plumulosus*, and (f) *Chironomus dilutes*. Errors bars indicate ± 1 SE. *n* = 6 for each prey item.



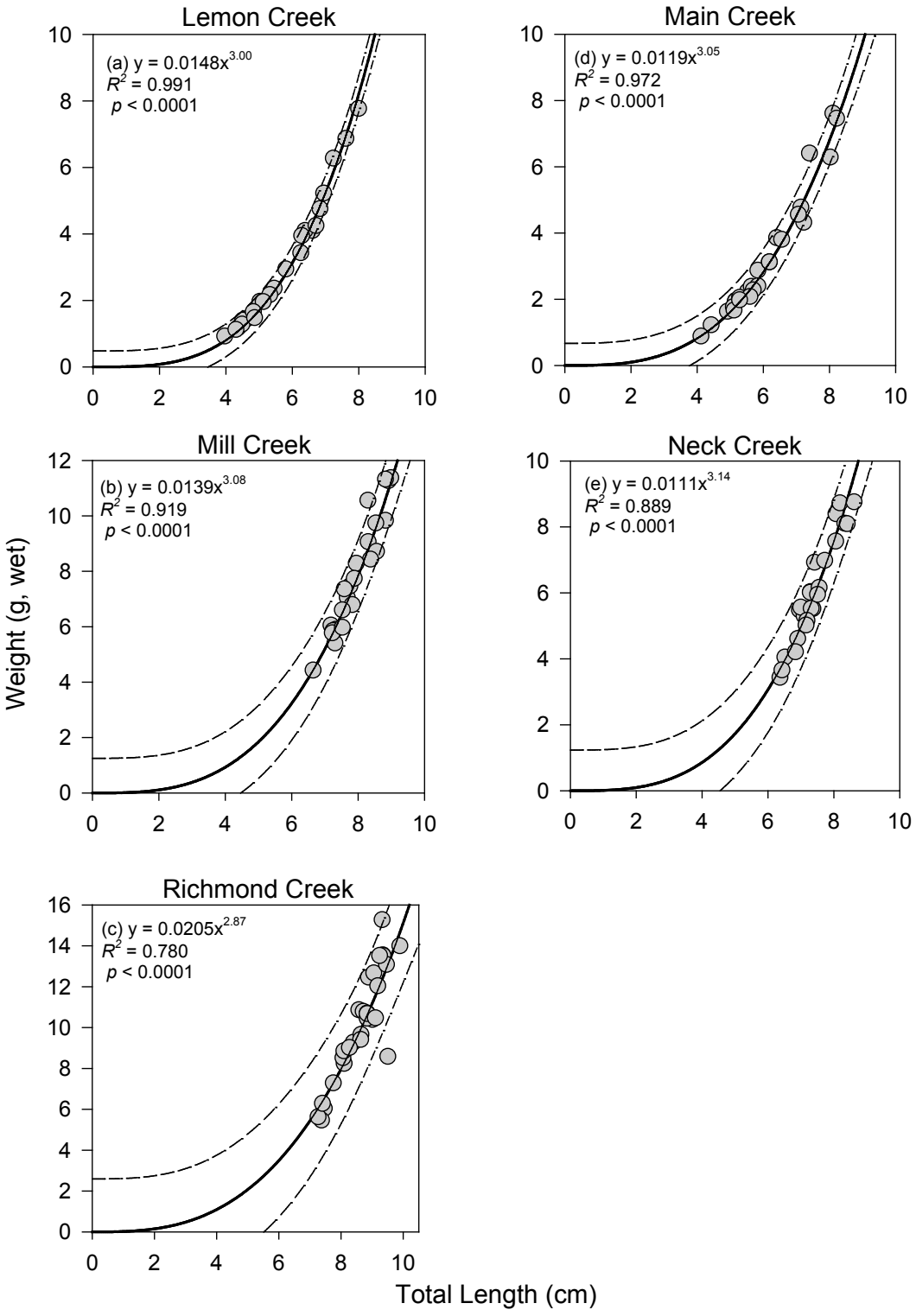
Appendix 5-E. Population-specific relationships between total length (cm) and scale radius (mm) of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.



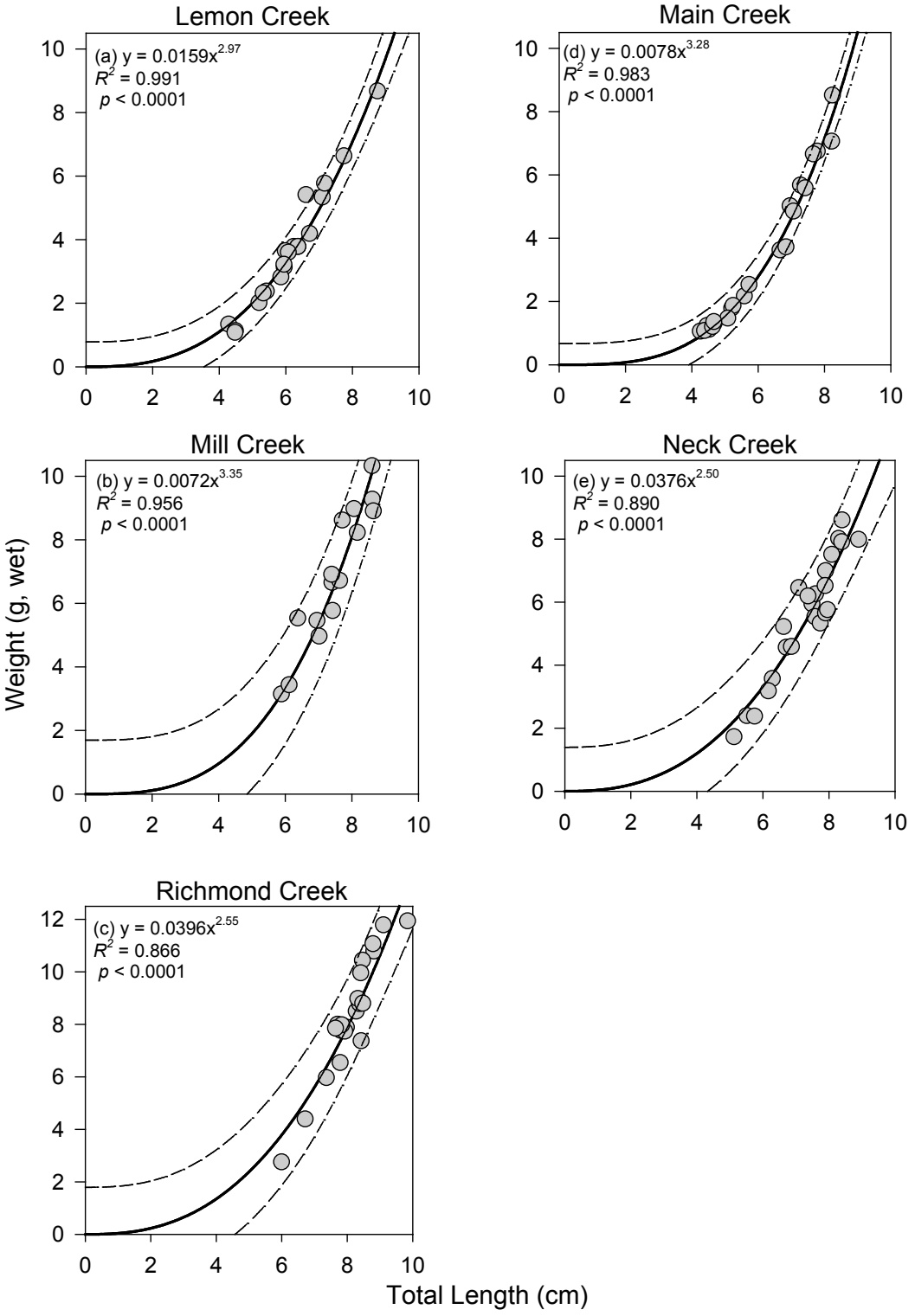
Appendix 5-F. Population-specific relationships between back-calculated total length (cm) based on Fraser-Lee models and observed total length (cm) of mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals.



Appendix 5-G. Population-specific relationships between weight (g) and total length (cm) of female mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals. The equation for the length-weight regression line is provided in each panel.



Appendix 5-H. Population-specific relationships between weight (g) and total length (cm) of male mummichogs from (a) Lemon Creek, (b) Mill Creek, (c) Richmond Creek, (d) Main Creek, and (e) Neck Creek. Solid lines indicate the least squares regression. Dashed lines indicate 95% confidence intervals. The equation for the length-weight regression line is provided in each panel.



CHAPTER 6

Significance of the findings: *Synthesis*

Many areas of the New York/New Jersey (NY/NJ) Harbor Estuary Complex, especially the Arthur Kill, have been exposed to a variety of anthropogenic stressors over the years (Franz and Harris, 1988). Despite considerable improvements in water quality over the last few decades (Bopp *et al.*, 2006), the ecological integrity of benthic habitats in the Arthur Kill largely remains altered (Chapters 2 and 3; Crawford *et al.*, 1994; Adams *et al.*, 1998; Adams and Benyi, 2003; Cerrato, 2006). This dissertation explored how altered ecological status of benthic habitats had directly and indirectly affected a resident forage fish, mummichogs (*Fundulus heteroclitus*), in severely polluted urban tidal salt marshes in the Arthur Kill.

Tidal salt marshes in the Arthur Kill provide an essential habitat for resident estuarine fishes, notably mummichogs, which primarily feed on benthic macroinvertebrates (Chapter 3). The present study showed that soft-sediment benthic macroinfaunal communities (the base of salt marsh food webs) in the Arthur Kill sites stil exhibited typical characteristics of chronically disturbed salt marshes (Chapter 2). These characteristics include low species diversity, numerical dominance by small-bodied opportunistic annelid species, and a few molluskan and crustacean species (Chapter 2). Adverse effects of habitat degradation were particularly evident in the northern part of the Arthur Kill. For example, one of the tributaries of Fresh Kills Complex, Main Creek, consistently exhibited characteristics of high-level degradation (Chapters 2). More than 90% (in both abundance and biomass) of the benthic macroinfaunal community at Main Creek was comprised of oligochaetes and two polychaete species (*Hobsonia florida* and *Nereis acuminata*) throughout the study period (Chapter 2).

Urban coastal marine ecosystems are often simultaneously affected by multiple (natural as well as anthropogenic) stressors, and soft-sediment benthic macroinfaunal communities are particularly susceptible to these stressors (Chapter 2; Rakocinski *et al.*, 1997; Lenihan *et al.*, 2003). Multivariate analyses on benthic macroinfaunal communities consistently indicated that among the anthropogenic stressors measured in the Arthur Kill, sediment-associated total mercury was strongly associated with the among-site variations in abundance and biomass of benthic macroinfaunal assemblages (Chapter 2). This relationship suggests that trace metal pollution is likely to be partially responsible for the current status of benthic macroinfaunal assemblages as well as higher trophic-level organisms (e.g., fish) in the Arthur Kill.

There were, however, also indications of improvements from historical pollution impacts at some of the Arthur Kill sites (Chapter 2). Although opportunistic macroinvertebrate species such as oligochaetes were still abundant at many of the Arthur Kill sites, their abundances substantially decreased over time (Chapter 2). A reduction in oligochaete abundance is frequently considered as an indication of improvement in environmental conditions in tidal salt marshes (Kelaher *et al.*, 2003). Furthermore, species diversity also gradually increased, and a few crustacean and molluskan species appeared at some of the Arthur Kill sites (Chapter 2). Still, the benthic macroinfaunal communities at some of the Arthur Kill sites (especially, the northern sites) remained species-poor (Chapter 2), suggesting that the cumulative effects of historic chemical and physical disturbances may have hampered recovery processes of biological assemblages.

The direct trophic relationship with benthic macroinvertebrates in degraded salt marshes can result in a variety of cascading effects on benthivorous fishes (e.g., energy

flow and pollutant transfer), integrating anthropogenic impacts on benthic habitats (Fig. 6-1, Chapters 3, 4, and 5; Kneib, 1997). The feeding strategy of both the Arthur Kill and Raritan Bay (reference) populations of mummichogs appeared to be highly flexible (i.e., generalists), and their feeding habits generally reflected overall patterns in benthic macroinfaunal assemblages (Chapters 2 and 3). Some taxonomic groups such as aquatic insects and gastropods were frequently ingested only by the reference population of mummichogs (Chapter 3). Reduction or disappearance of sensitive invertebrate groups including many gastropods, bivalves, and crustaceans in benthic macroinfaunal communities has been frequently documented in degraded tidal salt marshes (Weston, 1990; Warwick and Clarke, 1994; Warwick, 2001), including the Arthur Kill (Chapter 2). Furthermore, increased abundance and biomass of polychaetes at degraded benthic habitats in the Arthur Kill sites (Chapter 2) also clearly influenced the diet composition of mummichogs; higher relative proportions (by weight) of polychaetes were ingested by the Arthur Kill populations of mummichogs than the reference population (Chapter 3).

A large amount of decapods, especially *Palaemonetes spp.*, also frequently appeared in the gut of adult mummichogs, which resulted in decapods being the most 'preferred' prey item, revealing a strong trophic link between mummichogs and decapods at both the Arthur Kill and reference sites (Chapter 3). At the northern Arthur Kill sites, however, mummichogs ingested decapods considerably less frequently than at the other sites (Chapter 3). Furthermore, although the body size of grass shrimp (*Palaemonetes spp.*) ingested by mummichogs generally increased with total length of mummichogs at all sites, the majority of the northern Arthur Kill fish populations ingested considerably smaller shrimp than the other populations (Chapter 3). Anthropogenic stressors such as

chemical pollutants can adversely affect feeding behaviors of mummichogs in urban tidal salt marshes, which may have reduced the efficiency of capturing relatively large prey such as decapods (Smith and Weis, 1997; Weis *et al.*, 2001). In addition to altered benthic macroinfaunal assemblages, thus, altered feeding behaviors of mummichogs may have influenced their feeding habits in polluted habitats in the Arthur Kill (Weis *et al.*, 2001). Partial trophic decoupling between mummichogs and grass shrimp observed in the northern Arthur Kill sites may have further implications for energy transfer (Chapters 3 and 5) and biogeochemical cycling of materials (e.g., trace elements) in this severely degraded coastal ecosystem (Chapter 4 and 5).

As fish living in chronically polluted habitats are under severe stress, their energetic expenditures are often elevated, due mostly to increased metabolic activities induced by a combination of direct physiological and indirect food web-mediated effects. Many benthic organisms in tidal salt marshes are inherently resilient to a certain level of environmental stresses (Boesch and Rosenberg, 1981). These aquatic organisms use a variety of physiological and biochemical processes to ameliorate the direct adverse effects of anthropogenic stressors, including an induction of metal-binding proteins and formation of metal-rich granules for trace metals (Chapter 4; Klerks and Bartholomew, 1991; Wallace *et al.*, 1998). The importance of intracellular partitioning of trace metals as detoxification and tolerance mechanisms for aquatic organisms in chronically polluted habitats is well documented (e.g., Klerks and Bartholomew, 1991; Cain and Luoma, 1998; Mouneyrac *et al.*, 2003; Campbell *et al.*, 2005). The majority of Pb accumulated in the Arthur Kill populations of mummichogs, for example, was stored as biologically-detoxified metals (= metal-binding proteins and metal-rich granules) (Chapter 4).

Chemical detoxification processes such as the induction of detoxifying proteins can, however, also increase energetic demands in aquatic organisms (Douben, 1989; Calow, 1991; Moiseenko, 2002). Most of the Arthur Kill populations of mummichogs consistently had 2 to 3-fold higher total metabolic costs (= standard metabolism + active metabolism + specific dynamic action) than the reference population (Chapter 5).

In general, actively foraging fishes such as mummichogs need to balance energy gained from food consumption and energy expended for metabolism including foraging activities in order to maximize energy conversion efficiency (Handy *et al.*, 1999; Campbell *et al.*, 2002). Elevated energy expenditures incurred by anthropogenic stressors may be compensated for by fish through several adaptive strategies including a reduction in activity (Handy *et al.*, 1999), a reallocation of stored energy (Campbell *et al.*, 2002; Levesque *et al.*, 2002), and an increase in food consumption (Beyers and Rice, 2002). Increased energy requirement from pollution-induced metabolic costs (e.g., the detoxification of chemical pollutants, Chapter 4) in the Arthur Kill populations of mummichogs appeared to be partially compensated for by a reallocation of energy that could have been available for growth. The growth rates of age 2+ females of the Arthur Kill populations of mummichogs were, for instance, considerably lower than those of the reference population.

The allocation of energy available to growth of some fishes may, however, also be indirectly maintained by compensatory strategies (Calow, 1991; Health, 1995). Despite substantial alterations in prey availability (Chapter 2) and elevated metabolism (Chapter 5), growth of some of the Arthur Kill populations of mummichogs were maintained (Chapter 5). For instance, growth rates of the Arthur Kill populations of age 3+

mummichogs were similar to or slightly higher than those of the reference population (Chapter 5). In urban habitats, tolerant fishes such as mummichogs may also benefit from reduced exploitative competition as well as increased abundances of pollution-tolerant prey species (Chapters 2 and 3; Ryan and Harvey, 1980; Barlaup *et al.*, 1989). Some of the Arthur Kill populations of mummichogs were apparently able to adjust their energy intake to compensate for elevated metabolic costs (Chapter 5). The annual average daily food consumption rates of the Arthur Kill populations of mummichogs with elevated total metabolism were 2 to 3-fold higher than that of the reference population (Chapter 5). Low nekton species diversity (i.e., lower competition and predation risk) and high abundances of tolerant benthic macroinvertebrate species (i.e., higher prey resources) in the Arthur Kill (Chapters 2, 3, and 5) may have allowed mummichogs to increase their food consumption rates as a compensatory mechanism. The flexible feeding habits may thus be considered as an adaptive strategy to acquire sufficient energy to maintain growth, accommodating to altered prey availability and environmental conditions (Jeffree and Williams, 1980; Gerking, 1994; Elser and Hessen, 2005; Woodward *et al.*, 2005).

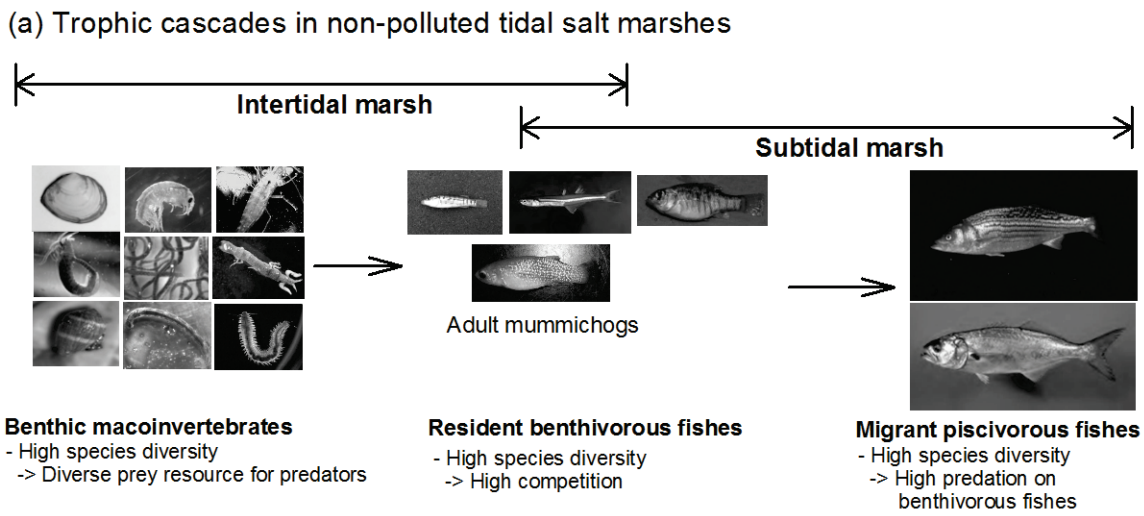
Although altered trophic structures in the Arthur Kill appeared to have benefitted mummichogs to a certain extent, there were also clear indications of adverse effects for living in these severely polluted habitats (Chapters 3 and 5). Despite their higher food consumption, the growth rates of the Arthur Kill populations of mummichogs did not proportionally increase, resulting in a substantial reduction in growth/energy conversion efficiency (Chapter 5). Reduced energy conversion efficiency at the individual level can also lead to a decrease in trophic efficiencies at the community level, which could ultimately lead to “trophic bottlenecks” in ecosystems (Fig. 6-1, Sherwood *et al.*, 2002).

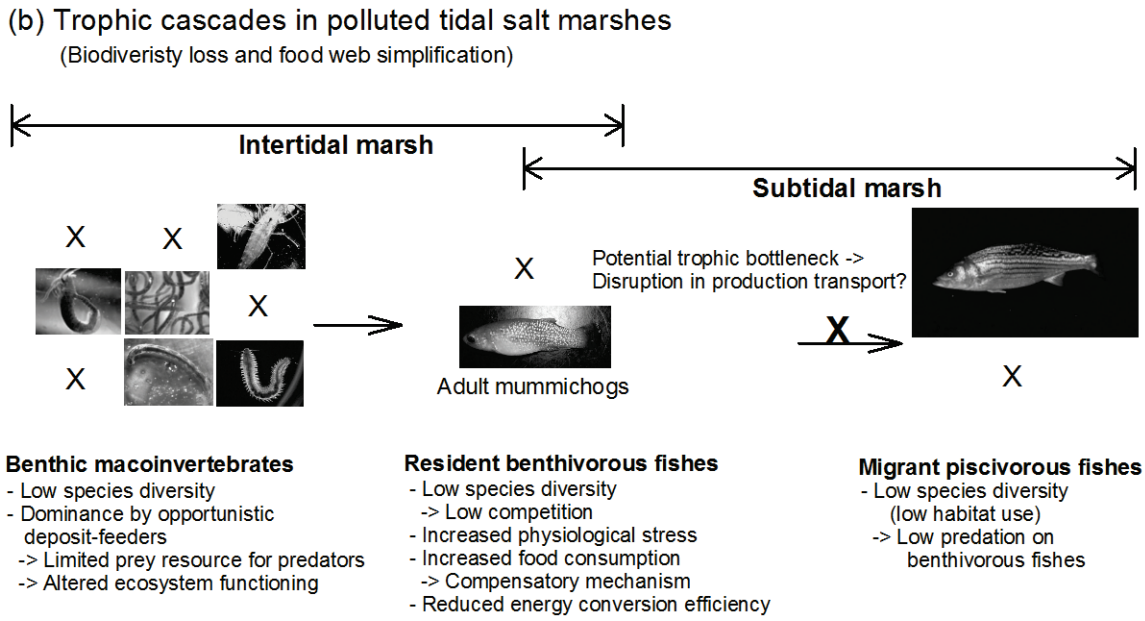
This dissertation demonstrated that trophic ecology and bioenergetics of the Arthur Kill populations of mummichogs are clearly influenced by direct physiological effects including chemically induced stresses (e.g., detoxification of non-essential trace metals) as well as indirect food web-mediated effects (e.g., altered prey resources) (Fig. 6-1, Chapters 2, 3, 4, and 5). At the same time, these fish also appear to be capable of adjusting their diet habit and energy intake to compensate for altered prey resources and elevated energetic costs, and thrive in these severely polluted coastal habitats (Chapter 5). The importance of mummichogs as a conduit of energy flow and marsh production transport to open coastal habitats has been well recognized (Valiela *et al.*, 1977; Weisberg *et al.*, 1981; Kneib and Wagner, 1994; Teo and Able, 2003). Reduced energy conversion efficiencies of mummichogs due to degraded habitat conditions can, therefore, have significant implications for overall trophic efficiencies (e.g., disruption in tidal salt marsh trophic relay processes) in the Arthur Kill and surrounding coastal marine ecosystems (Fig. 6-1).

The results of individual-level bioenergetics of the salt marsh resident fish from this research can also be integrated further into higher levels of biological organization to understand mechanisms associated with habitat degradation in urban coastal ecosystems from the energetics perspective (Nisbet *et al.*, 1997; Carlisle, 2000; Beyers and Rice, 2002; Moiseenko, 2002; Garvey *et al.*, 2003). Low biodiversity ecosystems such as tidal salt marshes are likely to have low buffering capacity (e.g., high potential food chain collapse) toward further anthropogenic disturbances (Loreau and Thébault, 2005; Woodward *et al.*, 2005). Although the importance of integrity of trophic structure to ecosystem functioning is widely recognized (Clements and Newman, 2002),

anthropogenic impacts on trophic interrelationships and energy transfer in coastal marine environments have not been fully explored (Rose, 2000). By incorporating population and trophic dynamics, the bioenergetics approach could also be expanded to elucidate the underlying mechanisms associated with intra-/inter- specific interaction dynamics (e.g., altered prey-predator biomass dynamics) in urban coastal ecosystems (Nisbet *et al.*, 1997; Beyers and Rice, 2002; Garvey *et al.*, 2003; Klanjscek *et al.*, 2006).

Figure 6-1. Comparison of trophic cascades in (a) non-polluted tidal salt marshes and (b) polluted tidal salt marshes.





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CHAPTER 5

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CHAPTER 6

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