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Biodiversity and Zoogeography of the Fishes of the Hudson River Watershed and Estuary

JOHN R. WALDMAN

Queens College, Biology Department
65-30 Kissena Boulevard, Flushing, New York 11367 USA
john.waldman@qc.cuny.edu

THOMAS R. LAKE

New York State Hudson River Estuary Program
21 South Putt Corners Road, New Paltz, New York 12561 USA

ROBERT E. SCHMIDT

Simon's Rock College of Bard
84 Alford Road, Great Barrington, Massachusetts 01230 USA

Abstract.—The Hudson River Estuary (defined here as the Hudson River drainage and New York Harbor) is home to a large and diverse ichthyofauna. Estimates of species richness reflect both their geographic boundaries and time periods. The most complete estimate is for the Hudson River drainage north of the southern tip of Manhattan, where, as of 2005, 212 fish species have been recorded. This includes 11 new forms not reported in the most recently published tally (1990). We categorize the fishes of the Hudson River drainage as derived from 12 zoogeographic or anthropogenic sources (including species for which we make no judgment [n = 26]), the largest contributions from which include temperate marine strays (n = 65), introduced species (n = 28), and freshwater species that survived Pleistocene glaciations in Atlantic coastal refugia (n = 21). Additional species appear to have invaded from the Mississippi refugia, some naturally (n = 11) and some later, via canals (n = 11). Only ten diadromous fishes occur in the estuary, but many of these are, or have been, commercially and recreationally important (e.g., Atlantic sturgeon *Acipenser oxyrinchus*, American shad *Alosa sapidissima*, and striped bass *Morone saxatilis*). Extremely high seasonal temperature changes in the main-channel Hudson River foster a seasonally dynamic ichthyofauna with relatively few species occurring year round. However, the small number of resident estuarine fishes (n = 8) often occur in high abundances. Species richness peaks between June and September and reaches a minimum in winter. Long-term data indicate that although species richness has increased with the additions of new species, diversity is decreasing because of the decrease in population size of certain species, especially native cyprinids. The Hudson estuary hosts a population of one federally endangered species, shortnose sturgeon *Acipenser brevirostrum*, which is flourishing. Only one species, the anadromous rainbow smelt *Osmerus mordax* appears to have become extirpated in the Hudson Estuary.

Introduction

The Hudson River watershed and the Hudson River Estuary have a diverse ichthyofauna derived from many zoogeographic sources. These fishes have been unusually well studied because of their occurrence in a region of high human population density and because of the management issues that arise from such proximity. Records also extend relatively well back in time because of the early European settlement of the region (Daniels et al. 2005). However, much of the data on its fishes is piecemeal; in this paper we attempt to synthesize information and characterize this assemblage across the entire system.

The major features of the Hudson River system include the tributaries that feed the mainstem Hudson River (i.e., its upland watershed), the mainstem Hudson River, and its estuary, which includes New York Harbor. The Hudson River begins in New York's Adirondack Mountains and drains a total of about 35,000 km^2 from portions of five states. It is tidal to the federal dam at Troy, New York, 243 km inland from the southern tip of Manhattan at the Battery (Cooper et al. 1988). Its estuary may be defined as the tidal Hudson River downriver from the federal dam and including tidal waters of its tributaries, in addition to New York Harbor. New York Harbor has been inconsistently defined (Waldman 1999). However, we consider New York Harbor to include those waters landward of the Sandy Hook–Breezy Point transect to the Battery, the East River, Arthur Kill, Newark Bay, lower Hackensack and Passaic rivers, Raritan Bay and the lower Raritan River, and any smaller brackish or marine water bodies within this complex.

This complex geography and associated system. In their review of fishes reported from the salt and brackish waters of New York, Briggs and Waldman (2002) listed 335 species, many of which also have been found in the Hudson Estuary. Beebe and Savidge (1988) tallied 140 species of fishes from the tidal river between the federal dam and the George Washington Bridge, 19 km upriver of the Battery. Smith (1985) reported approximately 150 species occurring between the southern tip of Manhattan Island and the federal dam; of these, about 80 are freshwater or diadromous forms and 50 occur regularly in inshore areas. Smith and Lake (1990) developed an annotated list of fishes documented from the entire Hudson River drainage south to the Battery. They noted 201 species, including many that are found far from saline waters. One of us (TRL) maintains a current list of all fish species found in the Hudson River watershed north of the Battery. As of July 2005, this list stood at 212 species. Our objectives are to provide a synthesis of diverse information of the biodiversity and zoogeography of the fishes of the Hudson River estuary and an update on the new species additions. However, because of better documentation, we place greater focus on the ichthyofauna of the Hudson River watershed and estuarine waters north of the Battery than on its estuarine waters outside of the mainstem Hudson.

Historical Studies

Mitchill (1815) prepared a detailed systematic account of fishes found around Long Island and New York City, followed by a species list for the region (Mitchill 1818). DeKay (1842) published a list of New York's fishes, including many collected from the lower Hudson River, as part of the state's first natural history survey. Smith (1897) [...]

work on New York's fishes, both freshwater and marine, was Bean's (1903) monograph, which includes taxonomic and life history information.

Prior to the compilation by Briggs and Waldman (2002), the most complete list of New York's marine fishes was by Nichols and Breder (1927). The fishes of New York Harbor were described in a short paper by Breder (1938). The first broad surveys of Hudson River fishes were conducted by the New York State Conservation Department in the 1930s; Greeley (1937) presented results for the lower river and Greeley (1939) for Long Island and Staten Island drainages to New York Harbor. Other useful papers about the Hudson's fishes include Breder and Nigrelli (1934); Alevras (1973); Friedman and Hamilton (1980); Young et al. (1982); and Waldman (1985).

Major Components of the Ichthyofauna of the Hudson River Drainage

Classification of species to zoogeographic origin allows for better understanding of the development of a faunal community. We classify the ichthyofauna of the Hudson drainage according to its probable zoogeographic origin (Table 1), using the scheme of Smith and Lake (1990), but including new species records and new zoogeographic information.

(1) **Introduced** (28 species). Species released into the system from elsewhere. Examples of purposeful introductions that have resulted in reproducing populations include brown trout *Salmo trutta* and common carp *Cyprinus carpio*; purposeful introductions that failed include Atlantic salmon *Salmo salar*. Individual specimens may also be il[...] and alligator gar *Atractosteus spatula* (Bragin et al. 2005).

(2) **Freshwater species from an Atlantic coastal refugium** (21 species). Species whose ranges indicate natural postPleistocene colonization from an Atlantic coastal refugium (Schmidt 1986). Chain pickerel *Esox niger* and tessellated darter *Etheostoma olmstedi* are of this category.

(3) **Freshwater species from the Mississippi refugium** (11 species). Species whose ranges indicate natural postPleistocene colonization from the Mississippi refugium (Schmidt 1986). An example is stonecat *Noturus flavus*.

(4) **Freshwater species from the Mississippi refugium that are likely canal immigrants** (11 species). Species whose ranges indicate recent colonization from the Mississippi refugium through humanmade canals. Among these are freshwater drum *Aplodinotus grunniens* and central mudminnow *Umbra limi*.

(5) **Periglacial freshwater species** (14 species). Coldwater species that colonized via movement along the meltwater bodies behind receding Pleistocene glaciers. Examples include brook trout *Salvelinus fontinalis* and brook stickleback *Culaea inconstans*.

(6) **Freshwater species of uncertain origin** (11 species). Zoogeographic information not sufficient to make a confident determination. This group includes white sucker *Catostomus commersonii* and brown bullhead *Ameiurus nebulosus*.

(7) **Diadromous species** (10 species). Diadromous fishes are either anadromous or catadromous. Anadromous fishes are those [...]

Table 1. Modified Smith & Lake (1990) list for the Hudson River watershed (north of southern tip of Manhattan), updated to 212 species (new ones underlined). (1) Introduced; (2) Freshwater species from an Atlantic coastal refugium; (3) Freshwater species from the Mississippi refugium; (4) Freshwater species from the Mississippi refugium that are likely canal immigrants; (5) Periglacial freshwater species; (6) Freshwater species of uncertain origin; (7) Diadromous species; (8) Estuarine species; (9) Permanent or seasonal resident marine species; (10) Temperate marine strays; (11) Tropical marine strays; (12) Boreal marine strays.

Common name	Latin name	Probable origin
Lampreys - Petromyzontidae		
silver lamprey	*Ichthyomyzon unicuspis*	[4]
American brook lamprey	*Lampetra appendix*	[2]
sea lamprey	*Petromyzon marinus*	[7]
Requiem sharks - Carcharhinidae		
shark	*Carcharhinus* sp.	[10]
Houndsharks - Triakidae		
smooth dogfish	*Mustelus canis*	[10]
Dogfish sharks - Squalidae		
spiny dogfish	*Squalus acanthias*	[10]
Skates - Rajidae		
little skate	*Raja erinacea*	[10]
barndoor skate	*Raja laevis*	[10]
Sturgeons - Acipenseridae		
shortnose sturgeon	*Acipenser brevirostrum*	[9]
Atlantic sturgeon	*Acipenser oxyrinchus*	[7]
Gars – Lepisostidae		
longnose gar	*Lepisosteus osseus*	[1]
Bowfins - Amiidae		
bowfin	*Amia calva*	[1]
Tenpounders- Elopidae		
ladyfish	*Elops saurus*	[11]
Bonefishes - Albulidae		
<u>bonefish</u>	*Albula vulpes*	[11]
Conger eels - Congridae		
conger eel	*Conger oceanicus*	[10]
Freshwater eels - Anguillidae		
American eel	*Anguilla rostrata*	[7]
Snake eels - Ophichthidae		
speckled worm eel	*Myrophis punctatus*	[10]
Herrings - Clupeidae		
blueback herring	*Alosa aestivalis*	[7]
hickory shad	*Alosa mediocris*	[7]
alewife	*Alosa pseudoharengus*	[7]
American shad	*Alosa sapidissima*	[7]
Atlantic menhaden	*Brevoortia tyrannus*	[9]
Atlantic herring	*Clupea harengus harengus*	[10]
gizzard shad	*Dorosoma cepedianum*	[4]
round herring	*Etrumeus teres*	[10]

Table 1. continued.

Common name	Latin name	Probable origin
bay anchovy	*Anchoa mitchilli*	[8]
Mudminnows - Umbridae		
central mudminnow	*Umbra limi*	[4]
eastern mudminnow	*Umbra pygmaea*	[2]
Pikes - Esocidae		
redfin pickerel	*Esox americanus americanus*	[2]
northern pike	*Esox lucius*	[1]
chain pickerel	*Esox niger*	[2]
Bullhead Catfishes - Ictaluridae		
white catfish	*Ameiurus catus*	[2]
yellow bullhead	*Ameiurus natalis*	[6]
brown bullhead	*Ameiurus nebulosus*	[6]
channel catfish	*Ictalurus punctatus*	[1]
stonecat	*Noturus flavus*	[3]
tadpole madtom	*Noturus gyrinus*	[2]
margined madtom	*Noturus insignis*	[1]
brindled madtom	*Noturus miurus*	[4]
Suckers - Catostomidae		
longnose sucker	*Catostomus catostomus*	[6]
white sucker	*Catostomus commersonii*	[6]
creek chubsucker	*Erimyzon oblongus*	[2]
northern hog sucker	*Hypentelium nigricans*	[6]
shorthead redhorse	*Moxostoma macrolepidotum*	[3]
Characins - Characidae		
<u>pirapatinga</u>	*Piaractus brachypomus*	[1]
Minnows - Cyprinidae		
central stoneroller	*Campostoma anomalum*	[4]
goldfish	*Carassius auratus*	[1]
redside dace	*Clinostomus elongatus*	[3]
lake chub	*Couesius plumbeus*	[5]
grass carp	*Ctenopharyngodon idella*	[1]
satinfin shiner	*Cyprinella analostana*	[2]
spotfin shiner	*Cyprinella spiloptera*	[3]
common carp	*Cyprinus carpio*	[1]
cutlip minnow	*Exoglossum maxillingua*	[2]
brassy minnow	*Hybognathus hankinsoni*	[5]
eastern silvery minnow	*Hybognathus regius*	[2]
common shiner	*Luxilus cornutus*	[6]
pearl dace	*Margariscus margarita*	[5]
hornyhead chub	*Nocomis biguttatus*	[4]
golden shiner	*Notemigonus crysoleucas*	[6]
comely shiner	*Notropis amoenus*	[2]
emerald shiner	*Notropis atherinoides*	[4]

Table 1. continued.

Common name	Latin name	Probable origin
bridle shiner	*Notropis bifrenatus*	[2]
blackchin shiner	*Notropis heterodon*	[3]
blacknose shiner	*Notropis heterolepis*	[3]
spottail shiner	*Notropis hudsonius*	[6]
rosyface shiner	*Notropis rubellus*	[3]
sand shiner	*Notropis stramineus*	[1]
northern redbelly dace	*Phoxinus eos*	[5]
finescale dace	*Phoxinus neogaeus*	[5]
bluntnose minnow	*Pimephales notatus*	[3]
fathead minnow	*Pimephales promelas*	[3]
eastern blacknose dace	*Rhinichthys atratulus*	[2]
longnose dace	*Rhinichthys cataractae*	[6]
bitterling	*Rhodeus sericeus*	[1]
rudd	*Scardinius erythrophthalmus*	[1]
creek chub	*Semotilus atromaculatus*	[6]
fallfish	*Semotilus corporalis*	[2]
Trouts - Salmonidae		
cisco	*Coregonus artedi*	[5]
lake whitefish	*Coregonus clupeaformis*	[5]
round whitefish	*Prosopium cylindraceum*	[5]
rainbow trout	*Oncorhynchus mykiss*	[1]
sockeye salmon	*Oncorhynchus nerka*	[1]
Chinook salmon	*Oncorhynchus tshawytscha*	[1]
Atlantic salmon	*Salmo salar*	[1]
brown trout	*Salmo trutta*	[1]
brook trout	*Salvelinus fontinalis*	[5]
lake trout	*Salvelinus namaycush*	[5]
Smelts - Osmeridae		
rainbow smelt	*Osmerus mordax*	[7]
Lizardfishes - Synodontidae		
inshore lizardfish	*Synodus foetens*	[10]
Toadfishes - Batrachoididae		
oyster toadfish	*Opsanus tau*	[10]
Trout-perches - Percopsidae		
trout-perch	*Percopsis omiscomaycus*	[5]
Goosefishes - Lophiidae		
goosefish	*Lophius americanus*	[10]
Codfishes - Gadidae		
Atlantic cod	*Gadus morhua*	[10]
Atlantic tomcod	*Microgadus tomcod*	[7]
pollock	[illegible]	[illegible]

Table 1. continued.

Common name	Latin name	Probable origin
Phycid Hakes - Phycidae		
fourbeard rockling	*Enchelyopus cimbrius*	[10]
red hake	*Urophycis chuss*	[10]
spotted hake	*Urophycis regia*	[10]
white hake	*Urophycis tenuis*	[10]
Merlucciid Hakes - Merlucciidae		
silver hake	*Merluccius bilinearis*	[10]
Cusk-eels - Ophidiidae		
striped cusk-eel	*Ophiodon marginatum*	[10]
Needlefishes - Belonidae		
Atlantic needlefish	*Strongylura marina*	[9]
houndfish	*Tylosurus crocodilus*	[11]
Pupfishes - Cyprinodontidae		
sheepshead minnow	*Cyprinodon variegatus*	[1]
Topminnows - Fundulidae		
banded killifish	*Fundulus diaphanus*	[2]
mummichog	*Fundulus heteroclitus*	[8]
spotfin killifish	*Fundulus luciae*	[8]
striped killifish	*Fundulus majalis*	[10]
Livebearers - Poeciliidae		
western mosquitofish	*Gambusia affinis*	[1]
Silversides - Atherinidae		
brook silverside	*Labidesthes sicculus*	[4]
rough silverside	*Membras martinica*	[8]
inland silverside	*Menidia beryllina*	[8]
Atlantic silverside	*Menidia menidia*	[10]
Cornetfishes - Fistularidae		
bluespotted cornetfish	*Fistularia tabacaria*	[10]
Sticklebacks - Gasterosteidae		
fourspine stickleback	*Apeltes quadracus*	[8]
brook stickleback	*Culaea inconstans*	[5]
threespine stickleback	*Gasterosteus aculeatus*	[9]
ninespine stickleback	*Pungitius pungitius*	[5]
Pipefishes - Syngnathidae		
lined seahorse	*Hippocampus erectus*	[9]
northern pipefish	*Syngnathus fuscus*	[9]
Sea Basses - Serranidae		
black sea bass	*Centropristis striata*	[10]
gag	*Mycteroperca microlepis*	[11]
Temperate Basses - Moronidae		

Table 1. continued.

Common name	Latin name	Probable origin
white bass	*Morone chrysops*	[4]
striped bass	*Morone saxatilis*	[7]
Sunfishes - Centrarchidae		
rock bass	*Ambloplites rupestris*	[1]
bluespotted sunfish	*Enneacanthus gloriosus*	[2]
banded sunfish	*Enneacanthus obesus*	[2]
redbreast sunfish	*Lepomis auritus*	[2]
green sunfish	*Lepomis cyanellus*	[1]
pumpkinseed	*Lepomis gibbosus*	[6]
warmouth	*Lepomis gulosus*	[1]
bluegill	*Lepomis macrochirus*	[1]
smallmouth bass	*Micropterus dolomieu*	[1]
largemouth bass	*Micropterus salmoides*	[1]
white crappie	*Pomoxis annularis*	[1]
black crappie	*Pomoxis nigromaculatus*	[1]
Perches - Percidae		
greenside darter	*Etheostoma blennioides pholidotum*	[3]
fantail darter	*Etheostoma flabellare*	[3]
tessellated darter	*Etheostoma olmstedi*	[2]
yellow perch	*Perca flavescens*	[2]
logperch	*Percina caprodes*	[4]
shield darter	*Percina peltata*	[2]
walleye	*Sander vitreus*	[1]
Bigeyes - Priacanthidae		
short bigeye	*Pristigenys alta*	[10]
Bluefishes - Pomatomidae		
bluefish	*Pomatomus saltatrix*	[9]
Cobias - Rachycentridae		
cobia	*Rachycentron canadum*	[10]
Remoras - Echeneidae		
sharksucker	*Echeneis naucrates*	[10]
Jacks - Carangidae		
crevalle jack	*Caranx hippos*	[9]
Atlantic moonfish	*Selene setapinnis*	[10]
lookdown	*Selene vomer*	[10]
permit	*Trachinotus falcatus*	[10]
Snappers - Lutjanidae		
<u>schoolmaster</u>	*Lutjanus apodus*	[11]
gray snapper	*Lutjanus griseus*	[11]
Mojarras - Gerreidae		
spotfin mojarra	*Eucinostomus argenteus*	[10]

Table 1. continued.

Common name	Latin name	Probable origin
Grunts - Haemulidae		
pigfish	*Orthopristis chrysoptera*	[10]
Porgies - Sparidae		
<u>sheepshead</u>	*Archosargus probatocephalus*	[10]
pinfish	*Lagodon rhomboides*	[10]
scup	*Stenotomus chrysops*	[10]
Drums - Sciaenidae		
freshwater drum	*Aplodinotus grunniens*	[4]
silver perch	*Bairdiella chrysoura*	[10]
weakfish	*Cynoscion regalis*	[9]
spot	*Leiostomus xanthurus*	[9]
northern kingfish	*Menticirrhus saxatilis*	[10]
Atlantic croaker	*Micropogonias undulatus*	[10]
Butterflyfishes - Chaetodontidae		
foureye butterflyfish	*Chaetodon capistratus*	[11]
spotfin butterflyfish	*Chaetodon ocellatus*	[11]
Wrasses - Labridae		
tautog	*Tautoga onitis*	[10]
cunner	*Tautogolabrus adspersus*	[10]
Mullets - Mugilidae		
striped mullet	*Mugil cephalus*	[9]
white mullet	*Mugil curema*	[9]
Stargazers - Uranoscopidae		
northern stargazer	*Atroscopus guttatus*	[10]
Combtooth Blennies - Blenniidae		
<u>feather blenny</u>	*Hypsoblennius hentz*	[11]
freckled blenny	*Hypsoblennius ionthas*	[11]
Gunnels - Pholidae		
rock gunnel	*Pholis gunnellus*	[10]
Sand Lances - Ammodytidae		
American sand lance	*Ammodytes americanus*	[9]
Sleepers - Eleotridae		
fat sleeper	*Dormitator maculatus*	[11]
Gobies - Gobiidae		
<u>highfin goby</u>	*Gobionellus oceanicus*	[11]
naked goby	*Gobiosoma bosc*	[9]
seaboard goby	*Gobiosoma ginsburgi*	[10]
Cutlassfishes - Trichiuridae		
Atlantic cutlassfish	*Trichiurus lepturus*	[10]
Mackerels - Scombridae		
Spanish mackerel	*Scomberomorus maculatus*	[10]

Table 1. continued.

Common name	Latin name	Probable origin
Atlantic mackerel	*Scomber scombrus*	[10]
Barracudas - Sphyraenidae		
northern sennet	*Sphyraena borealis*	[10]
guaguanche	*Sphyraena gauchancho*	[10]
Butterfishes - Stromateidae		
butterfish	*Peprilus triacanthus*	[10]
Sculpins - Cottidae		
slimy sculpin	*Cottus cognatus*	[5]
sea raven	*Hemitripterus americanus*	[10]
grubby	*Myoxocephalus aenaeus*	[9]
longhorn sculpin	*Myoxocephalus octodecemspinosus*	[10]
Searobins - Triglidae		
northern searobin	*Prionotus carolinus*	[10]
striped searobin	*Prionotus evolans*	[10]
Snailfishes and Lumpfishes - Cyclopteridae		
seasnail	*Liparis atlanticus*	[10]
lumpfish	*Cyclopterus lumpus*	[12]
Flying Gurnards - Dactylopteridae		
flying gurnard	*Dactylopterus volitans*	[11]
Lefteye Flounders - Bothidae		
Gulf Stream flounder	*Citharichthys arctifrons*	[10]
smallmouth flounder	*Etropus microstomus*	[10]
summer flounder	*Paralichthys dentatus*	[9]
fourspot flounder	*Paralichthys oblongus*	[10]
windowpane	*Scopthalmus aquosus*	[10]
Righteye Flounders - Pleuronectidae		
winter flounder	*Pseudopleuronectes americanus*	[9]
yellowtail flounder	*Limanda ferruginea*	[10]
American Soles - Achiridae		
hogchoker	*Trinectes maculatus*	[8]
Tonguefishes - Cynoglossidae		
blackcheek tonguefish	*Symphurus plagiusa*	[10]
northern tonguefish	*Symphurus pusillus*	[10]
Filefishes - Monacanthidae		
orange filefish	*Aluterus schoepfi*	[10]
planehead filefish	*Stephanolepis hispidus*	[11]
Boxfishes - Ostraciidae		
scrawled cowfish	*Acanthostracion quadricornis*	[10]
Puffers - Tetraodontidae		
smooth puffer	*Lagocephalus laevigatus*	[11]
northern puffer	*Sphoeroides maculatus*	[10]
Porcupinefishes - Diodontidae		
striped burrfish	*Chilomycterus schoepfi*	[illegible]

spawn at sea and reside in freshwater; the American eel *Anguilla rostrata* is the only catadromous species in the Hudson estuary.

(8) **Estuarine species** (8 species). Estuarine species have broad salinity and temperature tolerances. Because of these constraints, there are not many of these species but they may be highly abundant. Examples include mummichog *Fundulus heteroclitus*, white perch *Morone americana*, and hogchoker *Trinectes maculatus*.

(9) **Permanent or seasonal resident marine species** (17 species). Those that remain within local or immediately-offshore waters all year, such as lined seahorse *Hippocampus erectus* and tautog *Tautoga onitis*.

(10) **Temperate marine strays** (65 species). Typically pelagic or deepwater species not usually seen in estuaries. Examples include little tunny *Euthynnus alletteratus* and Atlantic cod *Gadus morhua*.

(11) **Tropical marine strays** (15 species). Tropical or semitropical vagrants that almost always occur in the Hudson region as juveniles. These include bonefish *Albula vulpes*, Atlantic flyingfish *Cheilopogon melanurus*, scamp *Mycteroperca phenax*, African pompano *Alectis ciliaris*, and gray angelfish *Pomacanthus arcuatus* among many others.

(12) **Boreal marine strays** (1 species). Coldwater species from northern waters. Only lumpfish *Cyclopterus lumpus* fits this category.

Community Composition

The ichthyofauna of the Hudson estuary has received little analysis of community space and time. Regional structure is evident, as shown by Woodhead et al. (1992) who used multivariate techniques to analyze catches from a trawl survey of the lower Hudson River estuary between 1984 and 1986. The 72 fish species recorded clustered as four primary groups. These groups showed some seasonal variation along the salinity gradient that ranged from the southern limit of lower New York Bay to the Hudson River near Peekskill, New York. Seasonal variation in community structure also was found among juvenile fishes in the lower Hudson River (off Manhattan) by Able et al. (1998). They noted an early summer group dominated by Atlantic tomcod *Microgadus tomcod* and winter flounder *Pseudopleuronectes americanus* and a late summer group dominated by striped bass and black sea bass *Centropristis striata*.

On a coarse level, Hudson River fishes also form communities according to primary habitats within the drainage. Daniels et al. (2005) observed that for 210 species found in the drainage (including the Mohawk River), 129 occur in the main channel of the tidal portion of the river, with the remaining 81 confined to tributaries of the lower Hudson River or the upper Hudson or Mohawk systems. Of the species present in the main channel of the tidal portion, 49 are primarily marine visitors and 80 are either resident or diadromous forms.

Gladden et al. (1988) described seasonal occurrences of resident and migratory fishes in the tidal Hudson River, 1974–1977. Among their findings was higher annual variability among migrant than resident species. They also found that maximum species richness occurred between June and September and lowest species richness in December (but later winter months were not sampled). However, only 31 species were collected over this span and that at least 140 were known from that river reach at that time (Beebe and Savidge 1988), Gladden et al. (1988) suggested that many species only use the estuary for short periods. Of the 31 species consistently observed, 22 were considered residents and 9 were considered migrants. Gladden et al. (1988) proposed that temperature and freshwater inflow were the major abiotic factors in determining the abundances of migratory and many resident species.

Hurst et al. (2004) did later find a statistical association between annual variation in river flow from June through August and late-summer and autumn community composition of nearshore fishes in the mesohaline region of the river. In 21 years (1979–1999) of beach seine sampling they encountered 60 species, the most abundant of which were silversides *Menidia* spp., striped bass, white perch, American shad, and blueback herring *Alosa aestivalis*. They also observed unexplained long-term declines in catch rates of freshwater and estuarine species and a dramatic increase in the abundance of silversides.

Community composition also has varied temporally across decades. Daniels (1995) compared late 20th century nearshore fish abundance data from the freshwater reach of the Hudson with information from the 1936 survey by Greeley (1937). Daniels found that, although species richness remained relatively constant, species composition and relative abundance has changed considerably. The two dominant resident species in 1936, spottail shiner *Notropis hudsonius* and white perch, made up 34% of the individuals in the assemblage, whereas their relative abundance in a 1990 survey had nearly doubled (64%). The relative abundance of an additional five persistent species declined species made up 26% of the catch, whereas in 1990 the remaining species accounted for only 7%. Daniels concluded that although richness had increased with the addition of new species, diversity had decreased because of the decrease in population size of certain species, including native cyprinids, such as bridle shiner *Notropis bifrenatus*, common shiner *Luxilus cornutus*, spotfin shiner *Cyprinella spiloptera*, and creek chub *Semotilus atromaculatus*.

Influence of Geography, Oceanography, and Climate on Marine Species

The substantial diversity of fishes that occur in the Hudson River Estuary is due, in part, to its wide variety of habitats. New York Harbor is a mixing zone of waters from rivers, tidal straits, and the New York Bight. Long Island Sound mixes with ocean waters through its eastern outlet and with estuarine waters of New York Harbor via the East River at its western terminus.

Within the Hudson River, detectable salinity (i.e., the "salt front"; as defined as a salinity of 0.1 psu; salinities often are higher in bottom waters of the Hudson River) has ranged from the Bronx to the Kingston area, about 160 km upriver from the mouth of the river (Limburg et al. 1986).

New York lies mid-latitudinally along the North American coast and within the northern portion of the Virginian zoogeographic province, which is bounded on the south by Cape Hatteras and on the north by Cape Cod. A warm oceanic surface current, the Gulf Stream, flows northeasterly along the eastern margin of the New York Bight. The glacial channel of the Hudson River—the Hudson Canyon—cuts diagonally through

the New York coast.

Temperatures of New York marine waters undergo pronounced seasonal changes that are among the greatest worldwide. During winter, coastal surface waters descend to levels not far above freezing (~1°C) and during summer they may reach 26°C; inshore bottom temperatures range between less than 1°C to about 21°C (Parr 1933). In the Hudson River, summer temperatures may be as high as 30°C in shallow areas (Limburg et al. 1986).

Interaction of the Biological and Physical Realms

The combination of geographic, oceanographic, and climatological influences fosters a largely mobile and migratory, rather than resident, ichthyofauna. Many species move north and south annually in conjunction with rising and falling water temperatures. These include anadromous fishes that spawn in the Hudson River or other rivers (e.g., American shad, alewife *Alosa pseudoharengus*, striped bass, and Atlantic sturgeon). Euryhaline fishes such as white perch and shortnose sturgeon *Acipenser brevirostrum* make seasonal movements across a salinity spectrum. Some species, such as bluefish *Pomatomus saltatrix* and Atlantic mackerel *Scombrus scombrus* may cross zoogeographic provinces. Others, such as summer flounder *Paralichthys dentatus*, black sea bass, and scup *Stenotomus chrysops* make less pronounced movements seasonally, retreating somewhat southward and outward to continental shelf waters in winter, but remaining within the Virginian Province.

Oceanic pelagic forms such as little tunny and Atlantic bonito *Sarda sarda* tend to autumn. Ocean currents help disperse young-of-the-year of bluefish, which use coastal bays and rivers as nursery grounds. Warm-core rings from the Gulf Stream are believed to be largely responsible for the appearance each summer of juveniles of a great variety of fishes considered to be tropical or semitropical. The presence and proportions of each species vary each year, but regularly appearing "exotics" include bluespotted cornetfish *Fistularia tabacaria*, snowy grouper *Epinephelus niveatus*, lookdown *Selene vomer*, permit *Trachinotus falcatus*, and gray snapper *Lutjanus griseus*. Anecdotal observations indicate that the less-mobile tropical juveniles neither migrate south nor survive the autumn decline in water temperatures (McBride 1996). The only tropical or semitropical fishes occasionally seen in New York waters as adults, but not juveniles, are tarpon *Megalops atlanticus* and cubera snapper *Lutjanus cyanopterus* (Briggs and Waldman 2002); however, neither has yet been found in the Hudson estuary.

Zoogeography of Freshwater Fishes

The present day Hudson River watershed was covered by glaciers several times during the Pleistocene. The Wisconsinan epoch began approximately 50,000–70,000 years before present (BP) (Strahler 1966) and persisted until about 14,700–12,000 BP (Borns 1973; Strahler 1966). This most recent glacial advance eliminated fishes from the present day drainage. Thus, the focus of the zoogeography of native freshwater fishes in the Hudson watershed is on the processes of postglacial dispersal.

We have divided the fishes into primary division species (Myers 1938) that have little nals to disperse from Lake Champlain into the Hudson include central mudminnow *Umbra limi* (Schmidt and Daniels 2006), silver lamprey *Ichthyomyzon unicuspis*, logperch *Percina caprodes*, and freshwater drum *Aplodinotus grunniens*, although the latter two also could have arrived via the Mohawk Barge Canal. It also is likely that the brindled madtom *Noturus miurus* and white bass *Morone chrysops* invaded the Hudson drainage through the Barge Canal.

Human Introductions of Exotic Species

Most of the nonnative fishes in the Hudson River have appeared via the direct release of individuals by humans. Of the 80 species known from the freshwater sections of the main channel of the Hudson River, 30 are nonnative (Daniels et al. 2005). Some of these introductions occurred before anyone surveyed the fish fauna of the Hudson. For instance, DeKay (1842) discussed carp and rock bass *Ambloplites rupestris* from the Hudson River and Gill (1855) listed largemouth bass *Huro nigricans* = *Micropterus salmoides* in the Fulton Fish Market and smallmouth bass *Centrachus fasciatus* = *Micropterus dolomieu* from the Hudson River.

Later introductions to the Hudson watershed have been overseen by New York State agencies to enhance sport fishing (brown trout *Salmo trutta*, walleye *Sander vitreus*, and tiger muskellunge [northern pike *Esox lucius* × muskellunge *E. masquinongy*]), mosquito control in some locations (western mosquitofish *Gambusia affinis*), or as part of pond management activities (fathead minnow *Pimephales promelas*, green sunfish *Lepomis cyanellus*, and grass carp *Ctenopharyngodon idella*) (W. Keller, personal communication). Introductions may also have occurred without state agency consent, such as channel catfish *Ictalurus punctatus*, which is now well established in the Hudson. The repeated occurrence of the tropical pirapitinga *Piractus brachypomus* in the Hudson drainage is due to ongoing aquarium releases, as is the alligator gar reported from the Hackensack River (Bragin et al. 2005). Other species have been released for unknown reasons (e.g., warmouth *Lepomis gulosus*).

Recent Species Additions

Given the continuous nature and large extent of marine waters, species not seen before within a given area may suddenly be observed either because of a combination of chance and their actual rarity, because of amenable changes in oceanographic conditions, or because of an expansion in their range coincident with an increase in their abundance. One now prominent species in the brackish waters of the Hudson River estuary is the gizzard shad *Dorosoma cepedianum*. About a century ago, Bean (1903) stated that it was found in brackish waters from New York southward. Greeley (1937) did not mention this euryhaline, but largely estuarine species, among the common fishes found in a major survey of the Hudson River conducted in 1936, although Breder (1938) did report specimens from New York Harbor. George (1983) reviewed published reports and concluded that the first record of gizzard shad in the Hudson River did not occur until 1973, when 674 specimens were impinged on the water-intake screens of four power plants. Since then, gizzard shad have remained numerous in the Hudson River estuary (and have expanded their range to other coastal rivers as far north as the Kennebec River; Daniels et al. 2005) but it is not known whether

Barge Canal, or both (Beebe and Savidge 1988).

The 11 documented additions for the Hudson River watershed north of the Battery since Smith and Lake (1990) are mostly temperate or tropical marine strays, including scrawled cowfish *Acanthostracion quadricornis* (Schmidt and Lake 2001), highfin goby *Gobionellus oceanicus*, feather blenny *Hypsoblennius hentz*, northern tonguefish *Symphurus pusillus*, schoolmaster *Lutjanus apodus*, sheepshead *Archosargus probatocephalus*, and bonefish *Albula vulpes*; but they also include a boreal marine stray, lumpfish *Cyclopterus lumpus*, two freshwater introductions, western mosquitofish and the aforementioned pirapitanga, and an estuarine species, spotfin killifish *Fundulus luciae*. However, spotfin killifish may have been present in the Hudson drainage for some time but went unnoticed because it occurs in rarely sampled high intertidal marsh habitats and because of its resemblance to mummichog (Yozzo and Ottman 2003).

Recent Species Losses

The regional diversity of marine fishes may decrease through regional losses of species, but to date, marine fishes have almost never become extinct in historical times (Casey and Myers 1998). These regional losses typically are felt as large decreases in numbers over extended periods, not as complete absences. Two species that were common in New York Harbor and nearby coastal waters in the 19th century, black drum *Pogonias cromis* and sheepshead (Bean 1903; Zeisel 1988) are almost never encountered there today. Both were at the northern end of their ranges and are closely associated with

of coastal populations. Sharks also were common in inshore waters of the New York Harbor and New York Bight in the 1800s. They were even seen and caught off docks in Manhattan, probably drawn there by dumped refuse (Zeisel 1990).

A few species experience very wide fluctuations in abundance that lead to near-absences in New York waters during some periods and high abundances in others. Spot *Leiostomus xanthurus* may appear in very large numbers for only a year or two and then not be seen for almost a decade; they are often called "Lafayettes" because one of their appearances coincided with the visit of the Marquis de Lafayette to New York City in 1824 (Waldman 1999). Bluefish and weakfish *Cynoscion regalis* have also varied in abundance from near absences to high abundances on a scale of decades (Bigelow and Schroeder 1953). At times, two typically southern fishes, Atlantic croaker *Micropogonias undulatus* and Spanish mackerel *Scomberomerus maculatus* were abundant enough to be important in commercial catches in Raritan Bay, the Atlantic croaker in the 1910s, 1920s, and the late 1930s and early 1940s and the Spanish mackerel in the 1880s and 1890s (McKenzie 1990).

Populations of anadromous species fishes may become extirpated. This appears to have occurred in the Hudson for rainbow smelt *Osmerus mordax*, a coldwater species at the southern edge of its range in the Hudson River estuary. Rainbow smelt once ran up both Hudson tributaries and the mainstem but declined in the late 20th century (Rose 1993), appearing to have disappeared from the system in the late 1990s (Daniels et al. 2005; Waldman 2006), probably due to warming temperatures. Also, whether Atlantic salmon were native to the Hudson ing program provided returns but no apparent reproduction (Waldman 1999). However, there is a fossil evidence for their presence (either anadromous or landlocked) in the more southern Delaware River watershed (Peteet et al. 1993).

Diversity, Nonnative Species, and Comparisons with Other Drainages

Carlson and Daniels (2004) inventoried the freshwater and diadromous fishes of New York State, noting 176 taxa (including subspecies) of 171 species. They treated the Hudson drainage as three watersheds: Upper and Lower Hudson, and the Mohawk. Of the 114 taxa identified in the Hudson drainage, 69 were native throughout, which meant that 39% were exotic in at least one of the three watersheds. They believed that among all New York drainages, the Hudson's ichthyofauna has been most affected by introductions of exotic species. For example, they estimated that 33% of the taxa in the Upper Hudson have been gained since 1940. In contrast, apparent total losses of native taxa in the entire drainage have been minor; only the brassy minnow *Hybognathus hankinsoni* is absent from recent surveys.

Carlson and Daniels (2004) also examined the freshwater fish fauna of the Hackensack and Passaic Rivers in New York. This highly urbanized watershed, which drains to Newark Bay, had 51 species reported, of which 33 are native. However, it also has had five native species extirpated since 1950, the highest percentage in all the watersheds of New York State.

Carlson and Daniels (2004) found that the proportion of freshwater and diadromous taxa gained since 1940 for the Hudson drainage was 18%, versus 11% for the Saint

of fishes now found in the Lower Hudson watershed are exotic. Schmidt (1986) compared the native freshwater ichthyofauna of the Hudson River watershed to more northern Atlantic coastal rivers. Comparisons with nearby systems showed faunal resemblance indices of 69.4% with the Housatonic River and 75.2% with the Connecticut River.

Conservation

The biodiversity of New York State's marine ichthyofauna is most susceptible to stresses that influence abundance and species composition (i.e., species-wide or local extinctions are not likely), but substantial changes in the numbers of fish and their relative proportions can occur. The combined effect of commercial and recreational fishing may be the greatest stress on New York's marine fishes. In the Hudson Estuary, commercial fishing has declined but recreational fishing, particularly for striped bass, has increased greatly despite health advisories on consumption (McKenzie 1990; Limburg et al. 2006). In New York, only shortnose sturgeon are on the U.S. federal endangered species list and this species is now flourishing in the Hudson River (Waldman 2006). However, its congener, Atlantic sturgeon was heavily overfished in the late 1980s and early 1990s (Waldman et al. 1996). Atlantic sturgeon are now protected by a long-term fishing moratorium in U.S. waters.

Habitat alteration and degradation can affect the quality of spawning, nursery, feeding, and wintering grounds, and the Hudson estuary has been subjected to myriad habitat changes (Daniels et al. 2005). However, the importance of habitat has been recognized by the National Marine Fisheries Service as being integral to conserving marine fishes and habitat concerns

undertaken to restore intertidal marsh habitats (Waldman 1999) and New York State maintains an artificial reef construction program to provide new fish habitat.

Although the lethality and sublethal effects of pollution are difficult to quantify, contamination with chemical pollutants has resulted in elevated levels of cancer in Atlantic tomcod of the Hudson River (Dey et al. 1993) and in abnormalities of other fishes in New York waters (Sindermann et al. 1982). One threat that deserves vigilance against is the introduction of exotic species of fish and other taxa that can alter the ecology (e.g., Asian shore crab *Hemigrapsus sanguineus*; Ahl and Moss 1999) or parasitize fishes such as an Asian nematode worm found in American eel *Anguilla rostrata* in the Hudson River (Barse and Secor 1999). Also, the colonization of the freshwater portion of the Hudson River by the Eurasian zebra mussel *Dreissena polymorpha* has been shown to strongly modify the ecology of the system, which has instigated both increases and declines in abundance and growth of fishes and in their centers of distribution in the river (Strayer et al. 2004).

A more nebulous concern is the effects of global warming on fish species composition. Long-term data show increasing water temperatures in the Hudson (Ashizawa and Cole 1994; Abood et al. this volume). Climate change may be responsible both for colonization of the Hudson River by gizzard shad and the apparent loss of its rainbow smelt population.

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Patterns of Habitat Utilization by Resident Nekton in *Phragmites* and *Typha* Marshes of the Hudson River Estuary

DAVID T. OSGOOD

Albright College, Department of Biology, Post Office Box 15234
Reading, Pennsylvania 19612-5234 USA
dosgood@alb.edu

DAVID J. YOZZO

Barry A. Vittor and Associates, Inc., 1973 Ulster Avenue
Lake Katrine, New York 12449 USA

RANDOLPH M. CHAMBERS

College of William and Mary, Department of Biology
Post Office Box 8795, Williamsburg, Virginia 23187 USA

SETH PIANKA AND CHRISTINA LEPAGE

University of New Haven, Department of Biology and Environmental Science
300 Orange Avenue, West Haven, Connecticut 06516 USA

JASON LEWIS

U.S Geological Survey, 810 Bear Tavern Road, Suite 206
West Trenton, New Jersey 08628 USA

Abstract.—We compared nekton density and benthic prey availability over a range of flooding conditions within common reed *Phragmites australis* and narrowleaf cattail *Typha angustifolia* at a mesohaline and an oligohaline marsh on the Hudson River Estuary. Nekton were sampled using lift nets at high and low elevations. Marsh surface nekton sampling occurred on 16 high tide events from May–October 1999 and 2000. Hydrology (depth, duration, and frequency) was simultaneously measured. Benthic macroinvertebrate density and richness were measured from sediment cores in June, August, and October, coincident with lift net collections. A total of 690 individuals representing nine species, mostly mummichog *Fundulus heteroclitus* and daggerblade grass shrimp *Palaemonetes pugio* were captured within both vegetation types. Mean nekton density (individuals 6 m^{-2} ± SE) on the marsh surface was not significantly different among reed at the mesohaline marsh (4.1 ± 1.3) and reed (3.4 ± 0.6) and cattail (4.1 ± 0.9) at the oligohaline marsh. Nekton density did not vary predictably across the measured range of flooding depth and duration. Nekton density was also not predictably