

# Shifts in species traits among North American freshwater fish assemblages: ecological homogenization?

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## Abstract

This study examines whether the processes of species invasion and extirpation have produced distinct shifts in mean species traits of North American freshwater fish assemblages. An analysis of 54 species (29 invaders, 25 extirpated taxa) in 7 drainages revealed significant differences in maximum length, native latitudinal range size, habitat specificity, and migratory behaviour. Results suggest a pattern in which extirpated species are being replaced by larger, more environmentally tolerant species capable of occupying a broader range of habitats. Freshwater fish assemblages containing introduced generalist species may have a selective advantage over pristine communities as human-dominated landscapes continue to replace natural systems.

## Keywords

**Freshwater fish:** *Actinopterygii*; **biological invasion:** *introduction and spread of non-native species*; **extinction:** *functional or absolute loss of a species*; **extirpation:** *extinction of a species from a region*; **species:** *group of genetically similar, reproducing organisms*; **species/ecological traits:** *characteristic or average values of a trait associated with a species*; **biotic homogenization,** *increasing similarity of species assemblages over time.*

## Introduction

Humans have historically exerted novel stresses on ecological communities. One such stress is the introduction of a suite of human commensals and favored species as the human population expands into new geographic regions. Indeed, recent studies have identified human population density and associated development as predictive variables influencing the intensity of invasions in several countries, correcting for the well documented species-area effect whereby greater numbers of species are found at larger spatial scales (Gido and Brown 1999; McKinney 2001; Gido et al. 2004; Olden et al. 2006). One outcome of such anthropogenic influence is biotic homogenization: the increased similarity of assemblages resulting from a combination of the introduction and establishment of non-native species and the loss of native and endemic species (McKinney and Lockwood 1999; Rahel 2000, 2002; McKinney 2001; Olden et al. 2006; Olden and Rooney 2006). Thus far, biotic homogenization has been studied primarily at the species diversity level, without consideration of other ecological factors including life history traits.

Ecological traits of aquatic animals have been examined as predictors of invasion success (Angermeier 1995; Kolar and Lodge 2002; Vila-Gespert et al. 2005; Jeschke and Strayer

2005) and extinction risk (McKinney and Lockwood 1999; Purvis et al. 2000). Certain ecological traits may also influence the impact of introduced species on native communities. For example, larger species physically occupy more space or consume greater amounts of resources than smaller species, while species consuming at different trophic levels depend on different primary food sources. The trophic behaviour of a particular species may cause cascading effects in a community through the magnification of stresses exerted on prey species (Currie et al. 1999).

Changes in the ecological characteristics of communities may be examined through the life history traits of different classes of species, namely those gained (introduced) and lost (extirpated). Threatened species of fishes (Williams et al. 1989) have been compared to taxonomically similar species that are not imperiled in order to determine if threatened species differ from unthreatened species in their life history traits (Angermeier 1995; Reynolds et al. 2005; Vila-Gespert et al. 2005; Alcaraz et al. 2005). The present study seeks to quantify differences in ecological traits between introduced and extirpated fishes within North American drainages. We predict that biases in human preferences and differential susceptibility of aquatic species to extinction are driving a shift in the mean species traits of North American fish assemblages.

## Methods and Materials

### Data Collection

Information on the distribution of species and their class status (introduced or extirpated) was recorded from Hocutt and Wiley (1986); each drainage in North America that was reported as having 3 extirpated and extinct species was selected for analysis. Data on life history traits of the introduced and extirpated species were collected from FishBase (Froese & Pauly 2006). In cases where life history categories are unreported for a particular subspecies, we substituted data for the species assemblage. A single extirpated subspecies from the Tennessee River drainage which required such data substitution remains in the final data set. Species of indeterminate status (e.g. possibly introduced), or which entirely lack life history information in FishBase, were excluded from the data set. We also excluded one species (Atlantic salmon *Salmo salar*) that was reported as introduced in two drainages and extirpated from a third.

The final data set consists of 54 species (25 extirpated, 29 introduced) distributed between seven drainages representing four drainage realms, as defined by the contributing authors in Hocutt & Wiley (1986). In order to account for any pseudoreplicative effects stemming from the separate

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evaluation of four of the Great Lakes, a pooled Great Lakes sample was created containing each species examined in the individual lakes. A master list containing species from all drainages was also generated to test cumulative differences across fish assemblages ranging from southern Canada to the Gulf of Mexico. Analyses focused on the most commonly reported traits: maximum recorded length, range of latitudinal distribution, population doubling time, trophic level, habitat preference, typical vertical position in the water column, migratory behaviour and salinity tolerance.

Qualitatively reported life history variables were coded into discrete integer scores after Angermeier (1995) and Alcaraz and coauthors (2005), as averaging the scores over classes (introduced or extirpated) can yield statistically testable class mean values. The scoring convention applied to coded variables is as follows: Habitat preference: lakes 1; rivers 2; lakes and rivers 3; marine and freshwater 4; Migration: non-migratory 1; potamodromous 2; anadromous 3; Population doubling time: < 15 months 1; 1.4-4.4 years 2; 4.5-14 years 3; > 14 years 4; Salinity tolerance: non-euryhaline 1; euryhaline 2; Vertical preference: demersal 1; benthopelagic 2; pelagic 3. All continuous-trait variables (Maximum reported length, Trophic level, and Latitudinal range) were log-transformed prior to analysis to control for differences of scale.

#### Statistical Analysis

Data were recorded and transformed in Microsoft Excel. The effects of life history traits on class status were examined through comparative analysis using the XLSTAT program for Excel (Addinsoft 2006). Parametric tests (two sample, two-tailed t-test) were applied to continuous traits, and non-parametric (two-tailed Mann-Whitney) tests were applied to coded traits. Different tests were selected for different categories of variables in order to maximize the statistical power of each comparison (Zar 1999). Analyses were conducted at two levels: between the drainages, and between the two classes of species within a single drainage. The level of significance for all comparative analyses was established at  $\alpha=0.05$ . Class means of each variable, from each drainage, were then combined to evaluate overall trends in the dislocation of traits across fish assemblages. To avoid unequal contribution by shared trends in the individual Great Lakes to the overall patterns, the pooled Great Lakes sample was the source of the class means for the between-drainage comparison.

Stepwise discriminant analysis using SAS software (SAS 1996) was used to determine whether the life history traits exerted independent influence on class status within drainages, or if any of the traits were associated in some way with each other. Discriminant analysis is commonly used in analyses of multiple traits (Kolar and Lodge 2002). The probability of falsely rejecting the null hypotheses of no contribution of life history traits to class status was calculated using Wilks' lambda test statistic at a significance level of

$\alpha=0.15$ . This significance level is the default value for the SAS stepdisc function, and is in keeping with Angermeier (1995), who observed that establishing a greater level of significance may be beneficial to the elucidation of trends in large scale comparisons.

#### Results and Discussion

The collaborative nature of the species distribution data (Hocutt and Wiley 1986) leads to ambiguities in the status of certain species in different drainage realms. Some contributing authors in Hocutt and Wiley (1986) list extirpated species and group introduced with natives, while others report introduced species with no extirpations. The selection criteria used to compile the data set for the present analysis excluded several drainages in which introduced or extirpated species were not differentiated from native species, creating a small data set of seven drainages.

#### Relevance of Traits

Each of the eight life history traits examined was found to contribute significantly to class status (introduced or extirpated) in one or more drainages (**Table 1**).

Introduced species generally reach greater maximum lengths (LL) (Lakes Huron, Michigan, Ontario), prefer a wider range of habitats (HS) (Lake Ontario, Tennessee River,

Variable	Drainage	Direction of Change
Salinity tolerance (EU) – CV	Master list ( $p=0.0003$ )	Introduced species are more tolerant
Migratory behaviour (MS) – CV	Lake Erie ( $p=0.0065$ )	Introduced species are more migratory
Vertical habitat (HSV) – CV	Lakes Huron ( $p=0.0013$ ), Michigan ( $p=0.124$ ), Ontario ( $p=0.0001$ ); Great Lakes sample ( $p=0.0005$ )	Introduced species prefer pelagic habitat
Habitat preference (HS) – CV	Lake Ontario ( $p=0.0075$ ), Tennessee River ( $p=0.0383$ ), Galveston Bay ( $p=0.0353$ ), Master list ( $p=0.0003$ )	Introduced species are less specialized in their habitat preferences
Population doubling time (DTS) – CV	Muskingum River ( $p=0.0401$ ), Master list ( $p=0.0003$ )	Introduced species have longer population doubling times
Maximum length (LL)	Lakes Huron ( $p=0.0004$ ), Michigan ( $p=0.0004$ ), Ontario ( $p=0.001$ ); Great Lakes sample ( $p=0.0002$ )	Introduced species reach greater maximum lengths
Trophic level (LT)	Lakes Erie ( $p=0.0164$ ), Ontario ( $p=0.0018$ ); Great Lakes sample ( $p=0.0001$ )	Introduced species consume at a lower trophic level
Latitudinal range (LLR)	Galveston Bay ( $p=0.0169$ )	Introduced species occupy a wider native range

**Table 1.** Results of stepwise discriminant analysis at level of significance  $\alpha=0.15$ . Significant results indicate that variables exert independent influence on class status (introduced or extirpated). Italicized entries denote conflicting directions of change. CV = coded variable.

Galveston Bay, master list), tend to be pelagic or free-swimming as opposed to demersal or bottom-dwelling (HSV) (Lakes Huron, Michigan, Ontario), occupy a wider latitudinal range (LLR) (Galveston Bay), and consume at a lower trophic level (LT) (Lakes Erie and Ontario, Great Lakes). Salinity tolerance (EU) is greater in introduced species in the master list, and greater in extirpated species in Tennessee River. The average population doubling times (DTS) in the master list and Muskingum River are greater for introduced species, and are greater for extirpated species in Lake Ontario.

#### Significant Changes in Traits

Salinity tolerance (EU) was found to be significantly more frequent in introduced species in all drainage samples

( $p < 0.0001$ ) except for the Tennessee River, where the trend was significantly reversed ( $p < 0.0001$ ). Groups of introduced species in all drainage samples tended to be migratory; this difference was significant in five out of nine samples. Given that the scoring convention used for migratory behaviour assigned the highest integer score to anadromy (migration between freshwater and marine environments), it is not surprising that more introduced migratory species also display greater salinity tolerance. Habitat preference scored higher in introduced species in all samples and was significant in six out of eight samples. The highest integer scores in this category were assigned to mixed habitat, i.e. lakes, rivers and oceans. Presence in varied habitats is an indication of broad environmental tolerance and little adaptation to particular conditions. Vertical position in the water column tended to be higher for introduced fish in the Great Lakes, significantly so in Lake Erie ( $p < 0.0001$ ) and the combined Great Lakes sample ( $p < 0.0001$ ). Introduced fish in the Muskingum ( $p < 0.0001$ ) and Tennessee Rivers and Galveston Bay ( $p < 0.0001$ ), as well

Variable				Variable			
Salinity Tolerance (CV)				Doubling Time (CV)			
	E	I	P		E	I	P
Lake Erie	1	1.5	<0.0001	Lake Erie	2	2.4	<0.0001
Lake Huron	1	1.75	<0.0001	Lake Huron	2.17	2.38	<0.0001
Lake Michigan	1	1.83	<0.0001	Lake Michigan	2	2.17	<0.0001
Lake Ontario	1.17	1.71	<0.0001	Lake Ontario	2.33	2.14	<0.0001
Great Lakes	1.07	1.55	<0.0001	Great Lakes	2.07	2.36	<0.0001
Muskingum R.	1	1.19	<0.0001	Muskingum R.	1.75	2.31	<0.0001
Tennessee R.	1.25	1.2	<0.0001	Tennessee R.	2.25	2.2	<0.0001
Galveston Bay	1	1.13	<0.0001	Galveston Bay	1.67	2.13	0.703
Master List	1.08	1.28	<0.0001	Master List	1.96	2.24	0.021
Habitat Preference (CV)				Vertical Preference (CV)			
	E	I	P		E	I	P
Lake Erie	-	-	-	Lake Erie	1.43	1.5	<0.0001
Lake Huron	1.17	3.75	0.001	Lake Huron	1.33	1.88	0.839
Lake Michigan	1.333	3.83	0.015	Lake Michigan	1.29	1.83	0.841
Lake Ontario	2	3.71	0.015	Lake Ontario	1.67	1.86	0.58
Great Lakes	1.86	3.55	0	Great Lakes	1.47	1.64	<0.0001
Muskingum R.	2.5	3.06	<0.0001	Muskingum R.	1.5	1.25	<0.0001
Tennessee R.	2	3	0.909	Tennessee R.	2	1.6	0.458
Galveston Bay	2	3	0.485	Galveston Bay	1.67	1.378	<0.0001
Master List	2	3.1	0	Master List	1.6	1.41	<0.0001
Migratory Score (CV)				Maximum Length			
	E	I	P		E	I	P
Lake Erie	1.29	2.3	0.557	Lake Erie	1.35	1.99	0.007
Lake Huron	1.17	2.63	0.019	Lake Huron	1.69	2.05	0.013
Lake Michigan	1	2.83	0.001	Lake Michigan	1.5	2.07	<0.0001
Lake Ontario	1.5	2.71	0.155	Lake Ontario	1.62	1.99	0.016
Great Lakes	1.27	2.36	0.626	Great Lakes	1.49	1.98	0.001
Muskingum R.	1.25	1.81	<0.0001	Muskingum R.	1.27	1.78	0.113
Tennessee R.	1.5	1.8	0.627	Tennessee R.	1.35	1.79	0.024
Galveston Bay	1.33	2	<0.0001	Galveston Bay	1.46	1.78	0.384
Master List	1.28	1.93	0.042	Master List	1.39	1.78	0.002
Trophic Level				Latitudinal Range			
	E	I	P		E	I	P
Lake Erie	0.55	0.53	0.488	Lake Erie	1.19	1.42	0.061
Lake Huron	-	-	-	Lake Huron	1.13	1.47	0.001
Lake Michigan	-	-	-	Lake Michigan	1.16	1.52	0.017
Lake Ontario	0.56	0.52	0.177	Lake Ontario	1.25	1.51	0.048
Great Lakes	0.55	0.53	0.449	Great Lakes	1.18	1.43	0.016
Muskingum R.	-	-	-	Muskingum R.	1.36	1.43	0.532
Tennessee R.	-	-	-	Tennessee R.	0.83	1.2	0.288
Galveston Bay	0.49	0.48	0.923	Galveston Bay	1.35	1.43	0.667
Master List	0.52	0.53	0.811	Master List	1.18	1.35	0.096

**Table 2.** Results of comparative analyses. Parametric tests were applied to continuous variable traits and non-parametric tests to coded variable traits at a level of significance  $\alpha = 0.05$ . CV = coded variable.

Between-Drainage Comparison			
Variable	Extirpated	Introduced	P
Salinity Tolerance (CV)	1.06	1.47	0.125
Doubling Time (CV)	2.02	2.25	0.453
Habitat Preference (CV)	1.83	3.39	0.031
Vertical Preference (CV)	1.55	1.61	1.000
Migration (CV)	1.29	2.29	0.016
Maximum Length	1.46	1.92	<0.0001
Trophic Level	0.53	0.51	0.151
Latitudinal Range	1.18	1.43	0.002

**Table 3.** Comparative analyses of grouped means from all drainages, excluding the master list. The Great Lakes sample is used in place of the individual lakes. CV = coded variable.

as the master list ( $p < 0.0001$ ), tended to prefer lower positions. The enormous Great Lakes basin likely provides an environment more suited to pelagic fish than the rivers and estuarine bay. Population doubling time varied significantly in seven out of nine samples, although the direction of change varied. The combined Great Lakes sample ( $p < 0.0001$ ), Muskingum River ( $p < 0.0001$ ), Galveston Bay ( $p < 0.0001$ ) and the master list ( $p < 0.0001$ ) contain introduced species with longer population doubling times, while in Lake Ontario and Tennessee River the trend is weakly reversed (**Table 2**).

There is a distinct trend towards introduced species of greater maximum length, significant in seven out of nine samples. Trophic level is the most underreported life history trait examined, and was only available for three drainages and the two combined (Great Lakes and master) samples. The trophic level of introduced species did not differ significantly from extirpated species, although mean values of trophic level for introduced groups are lower in four out of five samples. Introduced species occupy a wider latitudinal range in all drainages, with the difference being significant in four samples (**Table 2**).

#### Overall Trends

Comparisons of class means between drainages (**Table 3**) reveal overall significant trends towards introduced species which can occupy a wide variety of habitats ( $p = 0.031$ ), display migratory behaviour ( $p = 0.016$ ), reach greater sizes ( $p < 0.0001$ ), and naturally occur across a broader latitudinal range ( $p = 0.002$ ). A weak trend towards introduced species of lower trophic level ( $p = 0.151$ ) and greater salinity tolerance ( $p = 0.125$ ) is also present. Significant differences between classes at both the group and drainage levels are summarized in **Table 4**.

Most North American freshwater fish introductions and extirpations occurred decades ago (Gido et al. 2004). Almost all introductions were intentional, and the success of the introduced species is most likely the effect of human intervention in the form of stocking, thereby providing suprathreshold propagule pressure (Ruesink 2005). In the southern United States, 44% of introductions were conducted by state agencies specifically for sport and recreation (McKinney 2001).

The interest in introduced species, for aquaculture, sport and nuisance factors, has produced an abundance of ecological and life history data on these species. Extirpated species have not received equal attention, perhaps because most extinctions and extirpations occurred historically; consequently, their life history traits are under-represented in our analysis. Several drainages reported in Hocutt and Wiley (1986) met the selection criteria, but had to be removed from analysis as a result of data deficiency on FishBase. Inferring trait values from related species is unsuitable for comparative analysis because phylogenetic relationships are labile for persistent species (Alcaraz et al. 2005), let alone under-reported species which became extinct prior to the development of genetic analysis.

Drainage	Variables							
	Salinity Tolerance (CV)	Population Doubling Time (CV)	Habitat Preference (CV)	Vertical Preference (CV)	Migration (CV)	Maximum Length	Trophic Level	Latitudinal Range
Lake Erie	+	+		+		+		
Lake Huron	+	+	-		+	+		+
Lake Michigan	+	+	-		+	+		+
Lake Ontario	+	-	-			+		
Great Lakes	+	+	-	+		+		+
Muskingum River	+	+	-	-	+			
Tennessee River	-	-				+		
Galveston Bay	+			-	+			
Master List	+	+	-	-	+	+		
Between Drainages			-		+	+		+

**Table 4.** Summary of significant results of parametric and non-parametric comparative analyses. Directions of change are from mean values of extirpated to introduced species. CV = coded variable.

## Conclusions

Our results suggest that fish assemblages are undergoing an ecological homogenization characterized by a shift toward species sharing similar traits. The compositions of modern fish assemblages largely reflect human preferences resulting in the stocking of large fishes, particularly migratory species such as salmonids. It may also reflect a selective advantage for generalist, broadly tolerant species to colonize and thrive in increasingly common human-dominated landscapes.

We have expanded upon previous studies of homogenization which have neglected to consider shifts in the ecological traits of species assemblages. In the present data set, diversity increased even as the biotic communities were homogenized. Under climate change scenarios projected for the next century, widely-introduced generalist species will likely become increasingly significant components of species assemblages. Therefore, ecological traits may provide a more informative measure of biotic homogenization than simple measures of diversity.

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