FishTraits: A Database of Ecological and Life-history Traits of Freshwater Fishes of the United States

Emmanuel A. Frimpong and

Frimpong is assistant professor of fisheries science in the Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University (VPI), Blacksburg. He may be contacted at frimp@vt.edu.

Paul L. Angermeier

Angermeier is professor at VPI and assistant leader of the U.S. Geological Survey (USGS) Cooperative Fish and Wildlife Research Unit (which is jointly sponsored by USGS, VPI, Virginia Department of Game and Inland Fisheries, and the Wildlife Management Institute) in Blacksburg.

ABSTRACT: The need for integrated and widely accessible sources of species traits data to facilitate studies of ecology, conservation, and management has motivated development of traits databases for various taxa. In spite of the increasing number of traits-based analyses of freshwater fishes in the United States, no consolidated database of traits of this group exists publicly, and much useful information on these species is documented only in obscure sources. The largely inaccessible and unconsolidated traits information makes large-scale analysis involving many fishes and/or traits particularly challenging. We have compiled a database of > 100 traits for 809 (731 native and 78 nonnative) fish species found in freshwaters of the conterminous United States, including 37 native families and 145 native genera. The database, named FishTraits, contains information on four major categories of traits: (1) trophic ecology; (2) body size, reproductive ecology, and life history; (3) habitat preferences; and (4) salinity and temperature tolerances. Information on geographic distribution and conservation status was also compiled. The database enhances many opportunities for conducting research on fish species traits and constitutes the first step toward establishing a central repository for a continually expanding set of traits of North American fishes.

FishTraits: base de datos de características ecológicas y de historia de vida de peces dulceacuícolas en los Estados Unidos de Norteamérica

RESUMEN: La necesidad de contar con fuentes de información integradas y accesibles, acerca de las características básicas de las especies para facilitar la realización de estudios ecológicos, de conservación y manejo ha motivado el desarrollo de bases de datos de los atributos esenciales de varios taxa. A pesar del incremento en la cantidad de análisis basados en características básicas de las especies de peces de agua dulce en los Estados Unidos de Norteamérica, no existe una base de datos pública y consolidada sobre este grupo, y mucha de la información útil sobre las especies sólo se documenta en fuentes oscuras de información. La información dispersa e inaccesible convierte a los análisis de gran escala, que involucran datos sobre atributos básicos de las especies de peces, en un reto particularmente difícil. Se logró compilar una base de datos de >100 atributos para 809 especies de peces dulceacuícolas (731 nativas y 78 no nativas) de los Estados Unidos de Norteamérica, incluyendo 37 familias y 145 géneros autóctonos. La base de datos, llamada FishTraits, contiene información que se divide en cuatro grandes categorías: (1) ecología trófica; (2) tamaño corporal, ecología reproductiva e historia de vida; (3) preferencias de hábitat; y (4) tolerancia a temperatura y salinidad. También se incluye información concerniente a la distribución geográfica y estado de conservación de las especies. La base de datos mejora las oportunidades para realizar investigación sobre las características básicas de estos peces y constituye el primer paso hacia el establecimiento de un depósito central para un conjunto de datos, en constante expansión, sobre las características básicas de los peces dulceacuícolas de los Estados Unidos de Norteamérica.

INTRODUCTION

Species traits offer instructive lenses through which to view spatial and temporal variation in the distribution and abundance of species. In particular, the ecological and evolutionary processes that regulate populations and assemblages differentially favor certain traits depending on the environmental context. Ecologists have a long history of using traits to study patterns of species distribution, abundance, and responses to anthropogenic impacts (Balon 1975; Southwood 1977; Gatz 1979; Vannote et al. 1980; Karr 1981; Schlosser 1982; Southwood 1988; Schlosser 1990; Winemiller and Rose 1992; Austen et al. 1994; Townsend and Hildrew 1994; Poff 1997; Lamouroux et al. 2002; Goldstein and Meador 2004; Growns 2004; Winemiller 2005; Blanck et al. 2007). Understanding biotic responses to environmental variation can often be enhanced by focusing on species traits rather than on species taxonomy. For example, more complete knowledge of the traits associated with imperilment may help forestall further imperilment and facilitate biotic recovery.

Many studies have used species traits to address contemporary questions in management and conservation of freshwater fishes. For example, traits have been linked to changes in assemblage composition due to habitat alteration (Berkman and Rabeni 1987; Poff and Allan 1995; Goldstein and Meador 2005; Hoeinghaus et al. 2006), nonnative invasions and assemblage homogenization (Scott and Helfman 2001; Olden et al. 2006; Garcia-Berthou 2007), climate change (Poff et al. 2001; Daufresne et al. 2003), and local extirpations and extinctions (Angermeier 1995; Parent and Schriml 1995; Johnston 1999; Olden et al. 2006, 2008). Protocols for biological monitoring and assessment commonly incorporate traits-based metrics (Karr et al. 1986; Angermeier et al. 2000; Pont et al. 2006; Welcomme et al. 2006). Increasing anthropogenic change in the structure and function of aquatic ecosystems, manifest in the loss or imperilment of many fish species and assemblages, elevates the urgency of developing more effective tools for understanding fish responses to environmental change. A recent synthesis suggests that the number of imperiled taxa (extinct, endangered, threatened, or vulnerable/special concern) in North America has doubled since 1989, due in part to taxonomic revisions, and in part to real changes in conservation status of taxa (Jelks et al. 2008). Clearly, species traits will remain instrumental in future studies of fish ecology, management, and conservation.

For this report, we expand the definition of species traits offered by Goldstein and Meador (2005) and define traits as measurable ecological, life-history, morphological, physiological, and behavioral expressions of species' adaptations to their environment. Traits included in the database are defined at the individual level of ecological organization with or without reference to the organism's environment, and applied to the species over its entire range of distribution. Our definition encompasses the characteristics commonly used to categorize fishes into guilds and functional groups.

Our database arose out of our need to access traits and zoogeography information for most freshwater fishes of the conterminous United States while developing metrics for large scale bioassessment. We initially used data from the U.S. Geological Survey's (USGS) National Water Quality and Assessment program (NAWQA) from across the United States. We reviewed species accounts from nearly all states where accounts existed. Numerous problems and opportunities became apparent, including: (1) accounts are organized by political boundaries whereas species traits transcend political and biogeographic boundaries, (2) knowledge of species traits is expanding faster than can be documented by any single source because accounts typically take decades to compile and additional decades to revise, (3) the precision in the reporting of species traits varies considerably among sources and data formats among sources are often incompatible, (4) significant amounts of species' information are documented only in state or regional accounts or in non-refereed sources such as agency web sites or technical reports, and (5) state and regional accounts of species cite one another liberally without always acknowledging their sources, which often makes the original accounts difficult to identify.

Although frustrating gaps still remain in the knowledge of many species, we accumulated considerable traits information by painstakingly reviewing accessible literature and databases. We compiled this information into a database named FishTraits. Several reasons motivated us to publish FishTraits: (1) we believe that our experience should be documented to guide the planning of future large-scale projects involving traits-based analysis, (2) similar projects can avoid duplicating our efforts, (3) there is a need for a central database on traits of freshwater fishes of the United States, and (4) such a database would catalyze more integrative thinking about traits and expose knowledge gaps in traits. We hope that with the publishing of this database, limited conservation resources will be used more cost-effectively to study (and publish on) the ecology of lesser-studied and imperiled species. We ultimately hope to develop a dynamic database that is suited to the widening scale and scope of current environmental issues and that facilitates reliable, instructive analyses of fish traits.

Our database is primarily intended for researchers engaged in large-scale (generally beyond state boundaries) analyses of freshwater fishes of the conterminous United States. In this report we (1) present the database (FishTraits) and explain the process of selecting traits for inclusion; (2) interpret the traits and associated data; (3) define the trait states; (4) explain data formats, storage, retrieval, and limitations; and (5) propose future research directions and applications of FishTraits. Additional topics such as summary statistics on traits, statistical issues in traits-based analyses, and analyses of traits-based problems in the literature will be presented elsewhere.

METHODS

Traits are reported for 809, including 731 native (37 families, 145 genera) and 78 exotic (24 families, 5 genera) freshwater fish species found in the conterminous United States. Freshwater fishes are defined here as those with a landlocked distribution or documented reproduction in freshwater. Our database includes the approximately 480 species in NAWQA fish assemblage samples and additional species catalogued in Page and Burr (1991). No effort was made to include all exotic species because that list is growing quickly (Nico and Fuller 1999; USGS nonindigenous aquatic species http://nas.er.usgs.gov). We included exotic species listed by Page and Burr (1991) as established, along with exotics present in NAWQA fish samples, which is another indicator of establishment. Additionally, exotic species known to occur in mid-Atlantic drainages were of interest to the authors and therefore selectively included.

Traits in the database

Many traits are reported in the database but many potentially useful traits are still not represented. The traits in FishTraits partly reflect the bioassessment origin of the database. However, we expanded the final list of traits to include many ecologically relevant traits frequently reported in or inferred from species accounts. The categories of traits included are (1) trophic ecology; (2) body size, reproductive ecology, and life history; (3) habitat preferences; and (4) salinity and temperature tolerances. Additionally, aspects of geographic distribution and conservation status are included. Other researchers may sort traits into different categories. For example, Vieira et al. (2006) distinguished biological and ecological traits; biological traits comprised morphological, physiological, and life history traits whereas ecological traits comprised environmental preferences and associated behaviors. Poff et al. (2006) observed that biological traits provide mechanistic explanations for species' responses to environment but may be phylogenetically constrained, whereas ecological traits are more phylogenetically plastic and sensitive to current environmental conditions. Many additional traits suited to user objectives can be defined from combinations or some transformation of those in FishTraits.

Tactics, trait states, and species trait profiles

FishTraits is organized hierarchically. Each trait category may have sub-categories and each sub-category comprises specific traits. An individual fish exhibits a single tactic of a given trait (from a range of possible tactics) at a given time but may exhibit other tactics at other times. Thus, a tactic is the observed expression of a trait. The tactic expressed is a product of phylogenetic history and current environment (Wootton 1998); environmental effects on trait expression are the basis for traits-based biological assessments. When tactics of individuals in a species are aggregated, they typically form a mode in the range of possible expressions of the specific trait. Therefore, trait state may be defined for each trait as the modal tactic for a species. Other researchers have called trait states "modalities" (Poff et al. 2006; Vieira et al. 2006). Although "tactic" has been used primarily in descriptions of reproductive strategies (Diana 1995; Wootton 1998), this term seems applicable to any trait, and our use of tactic allows a consistent relationship between tactics and trait states across all trait categories.

We report traits with different levels of precision, as determined by the nature of each trait and how it is usually reported. The database includes traits that are categorical (e.g., serial versus non-serial spawning), ordinal (e.g., preference for slow, medium, or fast current), binary within each ordered category, or continuous (e.g., maximum total length). Individuals of a species, even within a population, may express different tactics of a trait. The observed variation among individuals is a good indicator of the plasticity of a particular trait. Good trait reporting indicates the variance or range of trait expression in addition to the typical tactic observed (e.g., age at maturation ranged from 2 to 4 years, with most fish maturing at age 3). For FishTraits, we used the typical tactic for a species as the trait state; for continuous traits we averaged tactics across well-supported reports. Categorical and ordinal traits often were not treated as mutually exclusive for a given sub-category. For example, although individuals of a species may occur in only one of the sub-categories "creek," "small river," or "large river" at a particular time, the species (the unit for coding traits) can occur in all sub-categories at the same time. Notably, this implies that association with each sub-category is binary (present versus absent), hence mutually exclusive. It would be more informative to use fuzzy coding (Chevenet et al. 1994) to represent such traits (e.g., 20%, 30%, and 50% for affinities for creek, small river, and large river, respectively). However, the available information was frequently not quantitative enough to allow fuzzy coding. Other traits, for example those associated with mode of reproduction (Balon 1975), were more appropriately treated as mutually exclusive. Where ambiguities may arise in interpretation, the specific rules that we followed for accepting multiple sub-categories are discussed under the trait descriptions.

With species as the unit of trait reporting, the basic structure of the database is a matrix in which each row represents the trait profile of one species and each column represents an identifier for the species, a trait state, or other supplementary information. A species' trait profile describes its functional niche (Poff et al. 2006). The profile for each species in FishTraits currently comprises up to 105 trait states and ancillary information, resulting in a 809 X 105 autecolgy matrix (Suen and Herriks 2006) for the complete dataset. Users can define subsets of the matrix (species and traits) of interest to them when obtaining data, which would greatly facilitate simultaneous analyses of multiple species in communities across spatial and temporal gradients and comparative studies of species.

Sources of traits information

The primary sources of information for most species are state and regional fish accounts typically titled "The Fishes of …." Because species distributions cross state and regional boundaries, numerous species are listed in multiple accounts. This was useful for validating information, although citations of other summarized accounts rather than citations of original sources were very common. The most current or comprehensive accounts were used more heavily for species appearing in numerous sources. However, some older accounts were considerably more informative than some recent accounts. In addition to the regional accounts, three general texts (Lee et al. 1980; Hocutt and Wiley 1986; Page and Burr 1991) were vital sources of habitat and zoogeographic information. Numerous specialized texts, peer-reviewed articles, technical reports such as species recovery plans, online catalogs (e.g., FishBase www.fishbase.org, NatureServe www.natureserve.org), and state and federal agency websites were also consulted, usually to supplement information when state and regional accounts were incomplete for our purpose. All species accounts and other sources that were consulted are listed in the supplementary traits references available through the database website. In all, a still growing list of > 200 texts, articles, reports, and web pages were used as traits references. Sources that were consulted for information on a single species are annotated with the species identification number.

Convention for missing and non-applicable data

Throughout the database, there are the inevitable unknowns and situations where a particular trait or data type is not applicable to some species (e.g., diet of species with non-feeding adults). We distinguish missing data from non-applicable data. For species identifiers, missing information is represented by a dot or blank, depending on the software used to view the database. For all other data fields, we used "-999" for missing data and "-1" for non-applicable data. These numbers are formatted to match the data precision of the associated field.

Data imputation

For our own applications, we found it necessary to use professional judgment to guess unknown traits for some species, a practice we refer to as imputation. This is often done implicitly in published species accounts. We coded data as unknown whenever the only source of information we could find was clearly imputed, so that the database is as unbiased as possible. These unknown data underscore research needs. Many statistical methods cannot accommodate missing data, which leads to imputations performed by software without any biological intelligence or to outright exclusion of all records with missing data. We encourage users to consider and document professional imputation (e.g., by following taxonomic trait patterns) for species that have few missing data rather than allowing automatic imputation by software or exclusion of records.

Species profile interpretation and details of methods

Fields of species profiles are explained under the appropriate category of identifiers, traits, or other information with details in Appendix 1. For each field we provide the code as would be viewed or downloaded from the online database, describe its type of scale (binary, categorical, count, or continuous), and additional details methods and references where necessary.

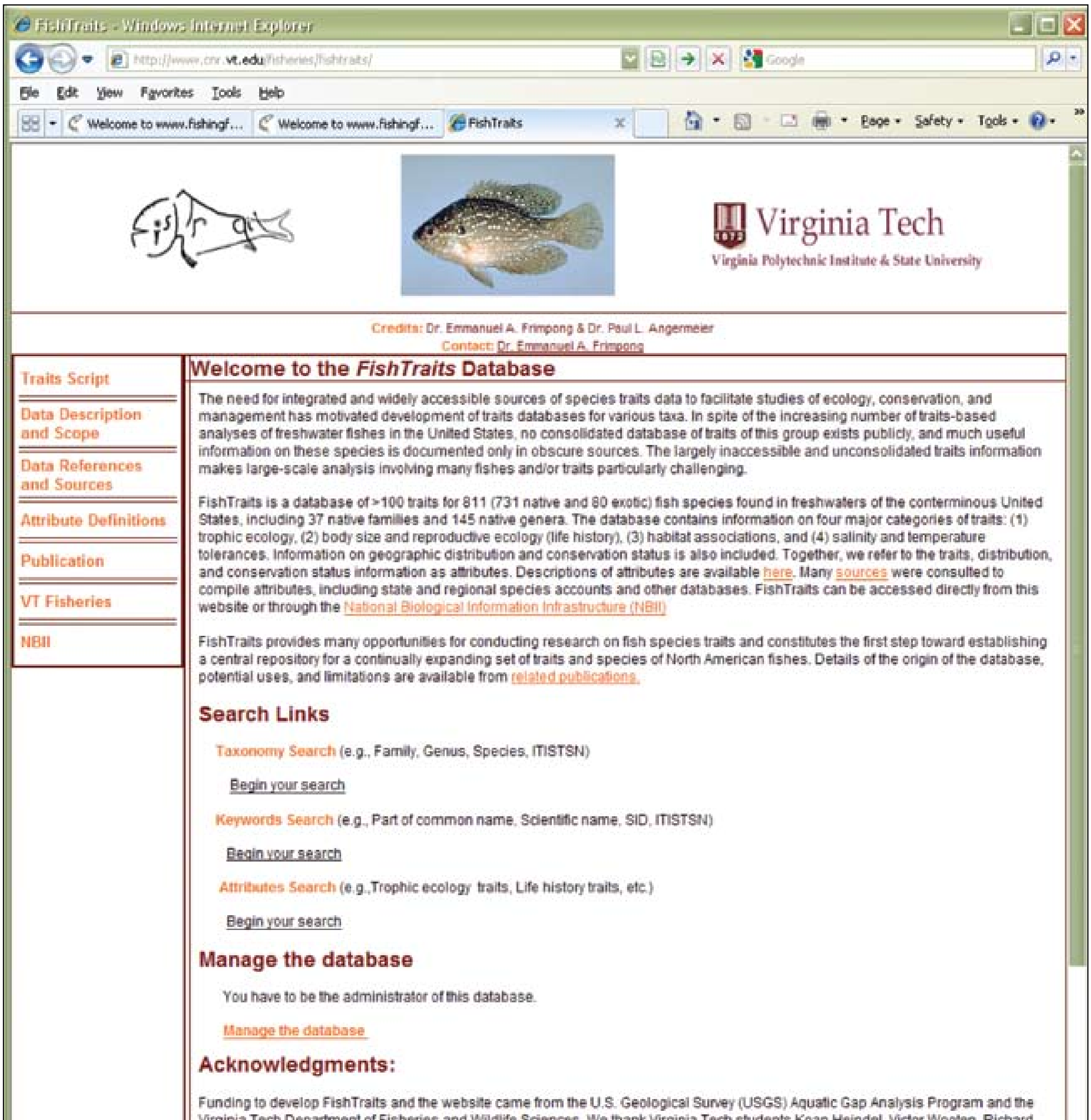
TROPHIC ECOLOGY TRAITS

Feeding ecology traits include whether adults feed at all, the typical feeding location(s) in the water column, and diet components as reported for any time over the species' entire range. Adult feeding was the primary consideration. However, the distinction between adult and juvenile is not always clear-cut in accounts. In addition, food selection is a function of availability, which is a function of time, location, and of the presence of predators and competitors. Consequently, there is disparity among accounts from different seasons and locations that do not control for or report these many co-varying factors. Any item reported in any account as a significant component (> 5%) of the adult diet of a species studied at any time of the year was included in the species' list of diet items. Where numerical values were not given, all reported diet components were considered significant. Therefore, the information provided here may reflect the combined feeding habits across seasons, juveniles, and adults of most species.

BODY SIZE, REPRODUCTIVE ECOLOGY, AND LIFE HISTORY TRAITS

The alphanumerical codes reflect Balon's (1975, 1981, 1984) ethological and ecological classifications of reproductive mode. Assignments are mutually exclusive and each trait is binary. Additional sub-categories (indicated by letters following the original Balon code) in some classes represent an ordinal grouping of species based on reported typical choice of substrate sizes during spawning. If desired, these groups can be aggregated by ignoring the last letters. Balon's guilds were determined from detailed (and sometimes multiple) accounts of a species' mode of reproduction, including choice of substrates and degree of parental care. Reproductive mode assignments provided by Simon (1999) and Coker et al. (2001) were also consulted. When there was a contradiction in assignments, we used (a) the source that cites more independent sources, (b) the most current reference, or (c) the reproductive mode that is more generalized, in that order. Because reproductive mode assignments are based on multiple traits, some of which are inferred from accounts rather than clearly stated, additional knowledge could change assignments for some species. Our default was to assume a species is more of a generalist unless specialization was indicated by a preponderance of evidence. Definitions of the recorded reproductive modes follow and more details can be found in Balon (1975, 1981, 1984). Other traits in this section are maximum total length, age at maturity, lon-

Figure 1. The FishTraits homepage (see www.cnr.vt.edu/fisheries/fishtraits).



gevity, fecundity, frequency of spawning, and timing and length of spawning.

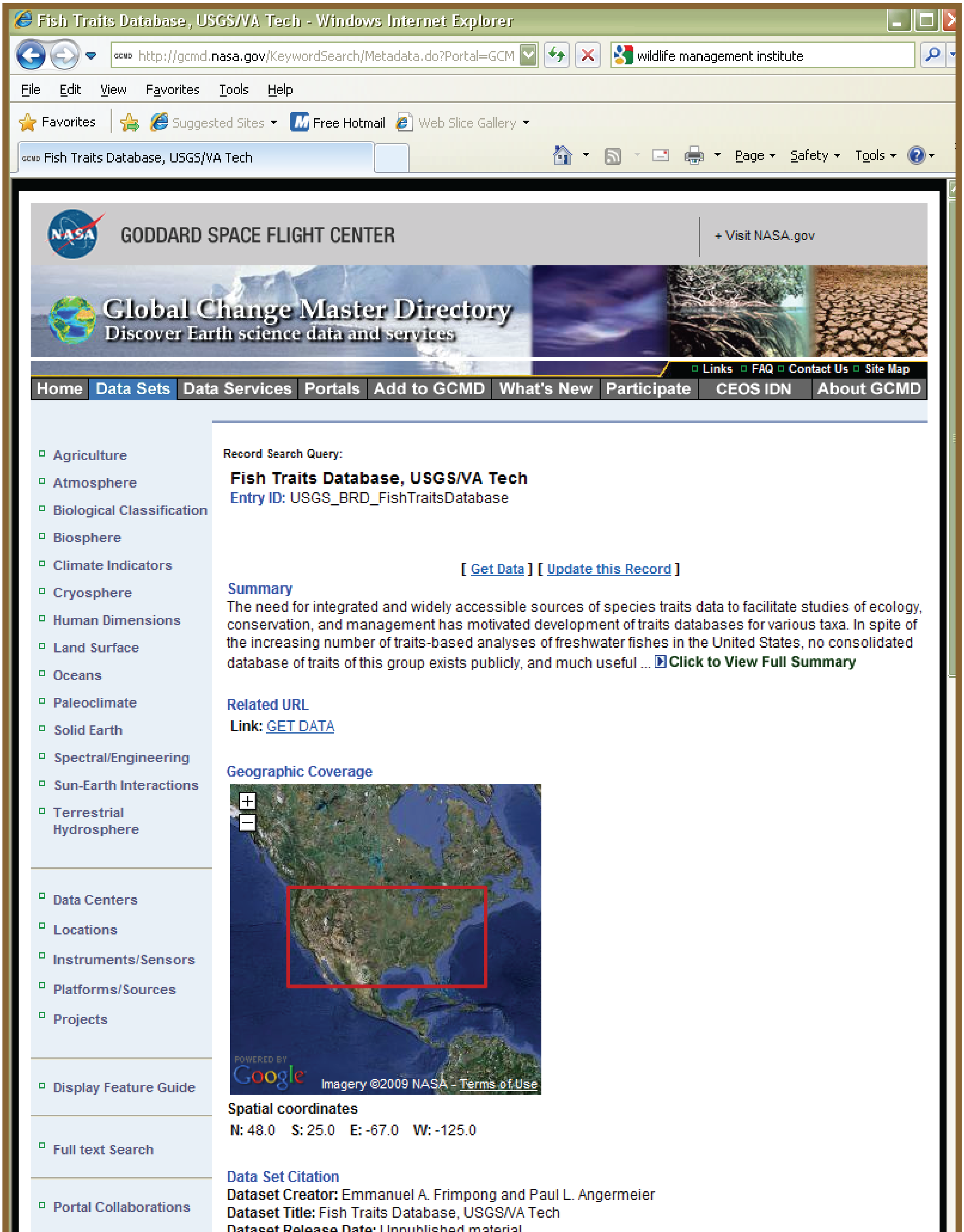
HABITAT PREFERENCE TRAITS

This section consists of trait sub-categories describing species associations with substrate type, lentic versus lotic system, stream size (for lotic species), current speed, and elevation. Twenty-five habitat associations are included in this section, including 11 substrate classes. Three landscape location preferences (upland, lowland, and montane) and species migration behavior, especially as relates to reproduction are included.

SALINITY AND TEMPERATURE TOLERANCES

Salinity tolerance represents the binary trait euryhaline versus stenohaline. Most of the salinity tolerances were obtained from Hocutt and Wiley (1986) or inferred from species distribution maps.

Figure 2. Initial image seen when accessing FishTraits through the NASA Global Change Master Directory (see gcmd.nasa.gov/getdif.htm?USGS_BRD_FishTraitsDatabase).



Temperature tolerances are represented by the 30-year average maximum and minimum temperature at the centroid of the species' range map. The temperature information is not available for species whose ranges are centered outside the conterminous United States.

GEOGRAPHIC DISTRIBUTION

Metrics of native geographic distribution of species were primarily obtained from maps in Page and Burr (1991). For species lacking maps in Page and Burr (1991), which was ~5%, maps were drawn from Lee et al. (1980) or obtained from regional accounts. The principal method for generating distribution metrics was to first scan the map, then georeference the scan to a standard United States map in Albers Equal Area projection in ArcGIS 9.2. Georeferenced distribution maps were then digitized, including native ranges outside the United States, and the resulting shape files were used to calculate the distribution metrics. The main source maps had a minimum mapping unit of about 20 X 20 km (approximately 400 km^2). This has the effect of biasing upwards the estimated area and other metrics for the species with the smallest ranges. Metrics included are range area, perimeter, number of patches, latitudinal range, longitudinal range, and coordinates of the centroid of the species' range. These metrics are suited only for coarse-resolution analyses.

CONSERVATION STATUS

Conservation status of native species (i.e., endangered, threatened, or vulnerable), as reported by AFS (Jelks et al. 2008), and the accompanying threat(s) to the species are included in this section. Also included are extinction status for species classified as extinct according to Harrison and Stiassny (1999). This classification system recognizes degrees of certainty in the extinction process.

DATA ACCURACY AND FUTURE UPDATES

Most data in FishTraits were entered by the first author (EAF). For some tabulated sources of information, undergraduate fisheries technicians entered the data and then entries were double-checked completely or spot-checked with a random sub-sample by EAF. Over 99% of such double-checked entries were correct. However, not all data entries were verified by a second person. Thus, some low level of data entry errors remains. Technical reviews of data for subsets of species in the database were conducted by regional experts in Virginia, Colorado, Missouri, and Minnesota. Reviewers were unable to comment on all traits for all species either because of acknowledged limitation in their expertise or lack of sufficient local information for some traits. Where comments were provided, reviewers were in nearly 100% agreement, taking into account the caveats provided in this article. We will continue to use feedback from peer reviewers and users of the database, as well as our continuing review of literature, to update and correct the database. After making it available to the public, we expect the first full revision of FishTraits to be released no sooner than two years from its first publishing, contingent on significant user feedback and the availability of resources to document new information and revise the current format of the data.

DATA DISTRIBUTION

The database will be available to the public upon publication of this article. Data may be accessed through the host website (www.cnr.vt.edu/fisheries/fishtraits) where a simple user interface is provided (Figure 1) or through the data websites of our partner in this effort, the USGS Aquatic Gap Analysis Program. The USGS provides access to FishTraits through the National Biological Information Infrastructure (NBII; www.nbii.gov) or through data portals of the National Aeronautical and Space Administration's Global Change Master Directory (GCMD; http://gcmd.nasa.gov/getdif.htm?USGS_BRD_FishTraitsDatabase, Figure 2). Once at the data web site, users can use common name, Integrated Taxonomic Information System Taxonomic Serial Number (ITISTSN), or taxonomic identifications to query species and trait information. The subset of data obtained by queries can be viewed and sorted in HTML or exported as a Microsoft Excel table for analyses. All documentation for the database, including related publications and metadata in the format of the Federal Geographic Data Committee are available through associated links.

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Appendix 1. Field codes, data scale, and description of species identifiers, traits, and other information compiled in the FishTraits database.

FIELD CODE	DATA SCALE	DESCRIPTION AND NOTES
Species Identifiers		
SID	N/A	A unique identification for the species. We concatenated the first letter of the generic name and the first seven letters of the specific name or the first two letters of the generic name and the first six letters of the specific name. A blank SID means the species was not found in the current American Fisheries Society (AFS) list of species (Nelson et al. 2004).
ALTSID	N/A	Alternate species identification. This is essentially the same as SID. However, some species identifications were created from scientific names or other names used in the literature prior to our final checking of species names with the AFS list (Nelson et al. 2004). This identification is also unique and available for all species.
FID	N/A	Family identification formed from the first eight letters of the family name (Nelson et al. 2004).
GENUS	N/A	Genus name recognized by AFS (Nelson et al. 2004).
SPECIES	N/A	Species name recognized by AFS (Nelson et al. 2004).
GID	N/A	Genus identification formed from the first eight letters of the genus name.
COMMONNAME	N/A	Common name recognized by AFS (Nelson et al. 2004).
OTHERNAMES	N/A	Other common names encountered in accounts of the species.
NATIVE	Binary	Native status, as determined from the online database of nonindigenous species (Nico and Fuller 1999).
NOTES	Categorical	A unique species number for footnotes and annotations.
ITISTSN	Categorical	Unique Taxonomic Serial Number (TSN) based on the Integrated Taxonomic Information System, www.itis.gov .
FAMILYNUMBER	Ordinal	This number is unique to families and serves more than as an identifier. It also indicates phylogenetic position of the family relative to other families (Nelson 2006). Smaller numbers are associated with more evolutionarily primitive fishes. Because of phylogenetic constraints on traits data, it is often necessary to explicitly recognize phylogeny in traits-based analyses. These numbers are useful under such circumstances.
Trophic Ecology Traits		
NONFEED	Binary	Adults do not feed.
BENTHIC	Binary	Benthic feeder.
SURWCOL	Binary	Surface or water column feeder.
ALGPHYTO	Binary	Algae or phytoplankton, including filamentous algae.
MACVASCU	Binary	Any part of macrophytes and vascular plants.
DETRITUS	Binary	Detritus or unidentifiable vegetative matter.
INVLVFSH	Binary	Aquatic and terrestrial invertebrates including zooplankton, insects, microcrustaceans, annelids, mollusks, etc. This group also includes larval fishes.
FSHCRCRB	Binary	Larger fishes, crayfishes, crabs, frogs, etc.
BLOOD	Binary	For parasitic lampreys that feed mainly on blood.
EGGS	Binary	Eggs of fishes, frogs, etc.
OTHER	Binary	Other diet components distinct from the preceding classes.
Body Size, Reproductive Ecology, and Life History Traits		
A_1_1	Binary	Nonguarders; open substratum spawners; Pelagophils.
A_1_2	Binary	Nonguarders; open substratum spawners; Litho-pelagophils.
A_1_3A	Binary	Nonguarders; open substratum spawners; Lithophils (rock-gravel).
A_1_3B	Binary	Nonguarders; open substratum spawners; Lithophils (gravel-sand).
A_1_3C	Binary	Nonguarders; open substratum spawners; Lithophils (silt-mud).
A_1_4	Binary	Nonguarders; open substratum spawners; Phyto-lithophils.
A_1_5	Binary	Nonguarders; open substratum spawners; Phytophils.
A_1_6	Binary	Nonguarders; open substratum spawners; Psammophils.
A_2_3A	Binary	Nonguarders; brood hiders; Lithophils (rock-gravel).
A_2_3B	Binary	Nonguarders; brood hiders; Lithophils (gravel-sand).
A_2_3C	Binary	Nonguarders; brood hiders; Lithophils (mud).
A_2_4A	Binary	Nonguarders; brood hiders; Speleophils (rock cavity).
A_2_4C	Binary	Nonguarders; Brood hiders; Speleophils (cavity eneralist **QUERY: generalist?**) rock crevices, and also under log bark, openings in vegetation, metal cans, etc).
B_1_3A	Binary	Guarders; substratum choosers; Lithophils.
B_1_4	Binary	Guarders; substratum choosers; Phytophils.
B_2_2	Binary	Guarders; nest spawners; Polyphils.
B_2_3A	Binary	Guarders; nest spawners; Lithophils (rock-gravel).
B_2_3B	Binary	Guarders; nest spawners; Lithophils (gravel-sand).
B_2_4	Binary	Guarders; nest spawners; Ariadnophils.
B_2_5	Binary	Guarders; nest spawners; Phytophils.
B_2_6	Binary	Guarders; nest spawners; Psammophils.
B_2_7A	Binary	Guarders; nest spawners; Speleophils (rock cavity/roof).
B_2_7B	Binary	Guarders; nest spawners; Speleophils (bottom burrows or natural holes associated with structure or bank).
B_2_7C	Binary	Guarders; nest spawners; Speleophils (cavity generalist).
C1_3_4_C2_4	Binary	A lumping of all bearers. May also be regarded as substrate-indifferent.
MAXTL	Continuous	Maximum total length in centimeters. Some records may estimate asymptotic length. We assumed that the difference between maximum observed length and asymptotic length is negligible.
MATUAGE	Continuous	Mean, median, or modal age at maturity in years for females. Where different ages at maturity were obtained for distinct populations, the clearly supported records were averaged. Male maturity age was accepted where female data were not available.
LONGEVITY	Continuous	Longevity in years based on life in the wild wherever available. Where not indicated, the record was assumed to be from the wild. If wild records were not known, a record from captivity was accepted.
FECUNDITY	Count	Maximum reported fecundity.
SERIAL	Binary	Serial or batch spawner, as inferred from evidence in any part of the species range. Accepted evidence included observations that multiple clutches of eggs are released over the spawning season by an individual female or that distinct batches of eggs at different stages of maturation are in the ovaries.
JAN–DEC	Continuous	The proportion of the month in the species' spawning season, following the convention of Menhinick (1991). Data were converted from weeks to proportion of the month, yielding precision of 0.25. See also SEASON and REPSTATE.

SEASON	Continuous	The sum of the proportions of each month in which spawning occurs; approximates length of the spawning season.
REPSTATE	Categorical	Representative state (or region) whose account was used to record spawning season. When the account specified the source of the spawning season information, we placed the record as close as possible to its true geographic origin. Like many traits, spawning season length is correlated with temperature, so some reference to geographic location is useful. The codes are the two-letter state abbreviations. Unconventional codes included CAN (Canada), MEX (Mexico), NES (northeastern states), Great Lakes, L. Huron (Lake Huron), and L. Superior (Lake Superior).
Habitat Preference Traits		
MUCK	Binary	Muck substrate.
CLAYSILT	Binary	Clay or silt substrate.
SAND	Binary	Sand substrate.
GRAVEL	Binary	Gravel substrate.
COBBLE	Binary	Cobble or pebble substrate.
BOULDER	Binary	Boulder substrate.
BEDROCK	Binary	Bedrock substrate.
VEGETAT	Binary	Aquatic vegetation.
DEBRDETR	Binary	Organic debris or detrital substrate.
LWD	Binary	Large woody debris.
PELAGIC	Binary	Open water.
PREFLOT	Binary	Lotic and lentic systems but more often in lotic.
PREFLEN	Binary	Lotic and lentic systems but more often in lentic.
LARGERIV	Binary	Medium to large river.
SMALLRIV	Binary	Stream to small river.
CREEK	Binary	Creek.
SPRGSUBT	Binary	Spring or subterranean water.
LACUSTRINE	Binary	Lentic systems.
POTANADR	Binary	Potamodromous or anadromous. Species that exhibit significant movement related to spawning. We concentrated on movements between marine and freshwater or within freshwater from large river, reservoirs, or lakes to tributary streams.
LOWLAND	Binary	Lowland elevation.
UPLAND	Binary	Highland elevation.
MONTANE	Binary	Mountainous physiography.
SLOWCURR	Binary	Slow current.
MODCURR	Binary	Moderate current.
FASTCURR	Binary	Fast current.
Salinity and Temperature Tolerances		
EURYHALINE	Binary	Species with wide salinity tolerance; mostly obtained from species zoogeographic summaries in Hocutt and Wiley (1986).
MINTEMP	Continuous	The 30-year average minimum January temperature at range centroid in degrees Celsius. Range centroids were used to extract values from 400-m resolution temperature grids obtained from Climate Source, Inc., Oregon.
MAXTEMP	Continuous	30-year average maximum July temperature at range centroid in degrees Celsius. Range centroids were used to extract values from 400-m resolution temperature grids obtained from Climate Source, Inc., Oregon.
Geographic Distribution		
AREA	Continuous	Range area in square kilometers.
PERIMETER	Continuous	Range perimeter in kilometers.
PATCHES	Count	Number of separate patches in the distribution map. This metric is sensitive to map resolution. We assumed that the relative patchiness of species ranges is preserved when maps are compared at the same resolution. This assumption has not been rigorously verified.
LATRANGE	Continuous	Latitudinal range of species in kilometers. This metric may have utility in conjunction with temperatures at range centroids in estimating species temperature tolerances.
LONRANGE	Continuous	Longitudinal range of species in kilometers.
LONGCENTROID	Continuous	Longitude at range centroid in decimal degrees.
LATCENTROID	Continuous	Latitude at range centroid in decimal degrees.
Conservation Status		
LISTED	Binary	Listed as endangered, threatened, vulnerable, or a subspecies is listed as any one of these categories.
REASON	Categorical	Endangered (1), Threatened (2), Vulnerable (3), or subspecies listed as any of these categories (4).
LIST1	Binary	Present or threatened destruction, modification, or reduction of habitat or range.
LIST2	Binary	Over-exploitation for commercial, recreational, scientific, or educational purposes, including international eradication via indirect impacts of fishing.
LIST3	Binary	Disease or parasitism.
LIST4	Binary	Other natural or anthropogenic factors that affect a taxon's existence, including impacts of nonindeginous organisms, hybridization, competitionm and/or predation.
LIST5	Binary	Restricted range.
EXTINCT	Categorical	Classified as extinct under one of the extinction categories in Harrison and Stiassny (1999). The following categories are represented: Resolved Extinction—1500-1948 (A), Unresolved Extinction—Extinctions since 1948 but No Other Ambiguity (C), Taxonomy Substantiated but Effective Extinction Date Unsubstantiated by Sampling (D2), Poorly Defined Extinctions with Taxonomy Substantiated but Effective Extinction Date Unsubstantiated by Population Decline or Environmental Threat (D3), and Species Extinction Status Unclassified but there is reason to further investigate possible extinction (U).