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# Environmental correlates of food-chain length, mean trophic level and trophic level variance in invaded riverine fish assemblages

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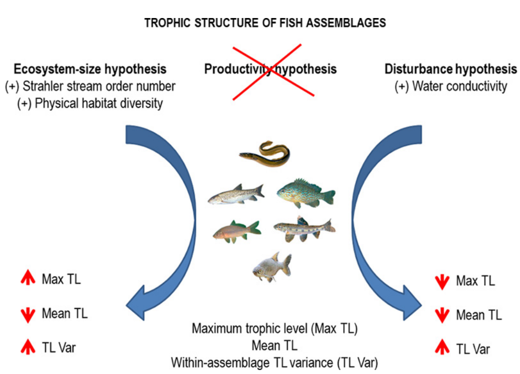
## HIGHLIGHTS

- Among the first studies exploring three food-chain length hypotheses concurrently
- The ecosystem-size and disturbance hypotheses were the best supported.
- The length and diversity of fish food-chains increased with river size but decreased with high conductivity.
- Our outputs were much associated with native fish than with alien species.
- Reducing water conductivity may protect species on the apices of food-chains

## GRAPHICAL ABSTRACT

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## ABSTRACT

Examining how the trophic structure of biotic assemblages is affected by human impacts, such as habitat degradation and the introduction of alien species, is important for understanding the consequences of such impacts on ecosystem functioning. We used general linear mixed models and hierarchical partitioning analyses of variance to examine for the first time the applicability of three hypotheses (ecosystem-size, productivity and disturbance) for explaining food-chain length (FCL) in invaded fish assemblages. We used Fishbase trophic level (TL) estimates for 16 native and 18 alien fish species in an extensive riverine system in north-eastern Spain (99,700 km$^2$, 15 catchments, 530 sites). The FCL of assemblages ranged from 2.7 to 4.42. Ecosystem size-related variables (Strahler stream order, physical habitat diversity) and human-disturbance (conductivity) made the largest contribution to the explained variance in the FCL model after accounting for spatial confounding factors and collinearity among predictors. Within-assemblage TL also was positively associated with Strahler stream order, suggesting that large rivers have the highest trophic diversity. High conductivity was negatively associated with FCL, as did with the mean TL of fish assemblages. However, an inverse association was found between mean TL and Strahler stream order, possibly because the presence of fish species of high TL may be offset by larger numbers of alien species of lower TL in large rivers. Given that there may be trophic replacements among native and alien species, this inference needs to be addressed with detailed trophic studies. However, reducing water conductivity by improved wastewater treatment and better agricultural practices probably would help to conserve the fish species on the apices of aquatic food-webs.



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## 1. Introduction

The structure of biotic assemblages is determined by many factors (Townsend et al., 2003) of which trophic interactions are among the most important (Pimm, 1982; Pauly et al., 2002; Layman et al., 2015). Trophic interactions dictate the number of trophic transfers of energy from basal resources to consumers (i.e. food-chain length, FCL; Thompson et al., 2012). FCL is a central characteristic of food-webs, which affects important ecosystem properties including nutrient cycling, species diversity and atmospheric carbon exchange (Pace et al., 1999; Persson, 1999). Moreover, FCL is associated with the risk of pollutant concentrations increasing from the lowest to the highest trophic level (TL) of food chains (i.e. biomagnification; LeBlanc, 1995).

Identifying the factors that determine FCL long has attracted the attention of ecologists (Lindeman, 1942; Takimoto and Post, 2013; Ward and McCann, 2017), who have erected three main hypotheses to explain FCL. The *ecosystem-size hypothesis* predicts that FCL increases with spatial scale because larger ecosystems have greater habitat availability and diversity, which supports larger populations of more diverse arrays of prey and predators (Post et al., 2000). The *productivity hypothesis* states that nutrient-poor ecosystems should have shorter FCL than nutrient-enriched ecosystems because of the energy loss in each trophic transfer, which limits the population sizes of species at higher trophic levels (TL) (Schoener, 1989). The *disturbance hypothesis* predicts that FCL will be reduced by frequent, intense changes in environmental conditions because the longer the food chain, the more vulnerable the ecosystem is to perturbations (Pimm and Lawton, 1977). Moreover, the most energy-demanding consumers (i.e. those at the highest TLs) are not abundant in ecosystems and, so, their probability of being lost during disturbance events is greatest (Pimm and Kitching, 1987). Although none of these hypotheses has received universal support, ecosystem size has been identified as a crucial determinant of FCL, even though the three hypotheses rarely have been explored concurrently (reviewed by Takimoto and Post, 2013). Moreover, changes in food-web structure are complicated by processes such as species additions or replacements from the introduction of alien species (Eby et al., 2006; Byrnes et al., 2007).

Rivers are important testing grounds for exploring FCL hypotheses because their food-webs are as complex and species-rich in any other ecosystem type (Winemiller, 1990). Rivers have long gradients of variation in size, productivity and disturbance (McHugh et al., 2010; Sabo et al., 2010; Mor et al., 2018). Moreover, alien species often are a major proportion of regional species pools in rivers (Chandra and Gerhardt, 2008; Tockner et al., 2009), which make rivers pertinent study systems to explore the contemporary environmental determinants of FCL. Studies examining the three hypotheses in uninvaded rivers found little support for any hypotheses (Warfe et al., 2013) or a neutral effect of productivity, a positive effect of ecosystem size and a negative effect of disturbance on FCL (Sabo et al., 2010; McHugh et al., 2010). However, these few studies can provide little indication of the generality of the effects of the rival hypothesis.

We used data on riverine fish in an extensive area of north-eastern Spain (99,700 km$^2$, 15 catchments) to explore variation in FCL along environmental gradients and to identify the changes in fish-food chains responsible for such variation. Many studies exploring FCL variation have used a single measure (e.g. maximum or mean TL; Takimoto and Post, 2013), which provides limited ability to distinguish among the rival ideas. A single measure can be the result of very different food-web architectures, but much more discernment might be achieved if one also were to explore within-assemblage TL variation (Fig. 1). Fish assemblages in north-eastern Spain have diverse trophic strategies, ranging from low-order (e.g. *Cyprinus carpio*, *Alburnus alburnus*) to high-order consumers (e.g. *Micropterus salmoides*, *Anguilla anguilla*), which exemplify the trophic guilds of native and alien species in many if not most rivers around the world (e.g. Kottelat and Freyhof, 2007). Variation in fish-species composition in north-eastern Spain mostly has been attributed to river size and to other geographical factors (e.g. elevation and basin name) alongside water quality and habitat degradation (Maceda-Veiga et al., 2017a). A study of functional diversity in the same study system mirrored these findings but ranked habitat degradation before water quality variables, which included nutrient concentrations (Colin et al., 2018). Therefore, studies of the fish assemblages we consider have the potential to explore how the trophic structure of food webs depends on environmental factors, including disturbance, which has been the FCL hypothesis with least support to date (Takimoto and Post, 2013).

By using multimodel inference, we identified the best environmental descriptors of TL variation in fish assemblages along gradients of geographical, hydraulic, physical habitat and water quality variables in north-eastern Spain. We examined the extent to which alien and native species richness affects the TL of fish assemblages given that the percentage of alien fish species in Mediterranean-type rivers, including north-eastern Spain, is high (Leprieur et al., 2008). If FCL and trophic diversity increase with ecosystem size and productivity (Post et al., 2000; Schoener, 1989), then we expected river size and river productivity to be positively associated with the maximum TL and the range of TL of fish assemblages, but negatively related to within-assemblage TL variation. If human disturbances induce opposite effects, then TL measures should be inversely related to measures of poor environmental conditions. Our results have management implications beyond our study system considering the many rivers with Mediterranean-climate around the world (Bonada and Resh, 2013), and the rarity of fish predators in these ecosystems prior to alien fish introductions (Doadrio, 2011).

## 2. Methods

### 2.1. Study area

Fish and environmental data were from several projects conducted in north-eastern Spain from 2002 to 2009 (e.g. Figuerola et al., 2012; Maceda-Veiga et al., 2017a) to assess the ecological status of rivers as required by the Water Framework Directive of Europe (EU Directive 2000/60/EC). The study area was part of the Garonne basin and all catchments drain to the Mediterranean Sea from the Sènia to Muga basins (Fig. 2). The native and alien fish richness in each basin ranges from 1 to 10 and from 1 to 11, respectively (Maceda-Veiga et al., 2010). Sampled sites ($N = 530$) were selected for accessibility and also to include broad gradients of elevation, river size, in-stream hydraulic, physical habitat and water quality (Table 1). The rivers drain relatively well-preserved riparian forests to grasslands, weedy areas and extensive agriculture areas, including regions vulnerable to nutrient pollution (the EU Nitrates Directive). There are many industries in the surroundings of large cities close to the coast that release metals and other biologically recalcitrant compounds into rivers at harmful concentrations for fish and other aquatic taxa (e.g. Maceda-Veiga et al., 2013; Colin et al., 2016). The water quality of rivers is degraded by many urban sewage treatment plants that lack tertiary treatment, which results in eutrophication and in the release of the so-called emerging pollutants (see Muñoz et al., 2009; Munné et al., 2012). The hydrological regime of most of these streams is typically 'Mediterranean', with droughts common in summer and some torrential flooding in autumn. Large rivers peak in flow in spring from snowmelt. We surveyed in low-flow conditions, because this is when fish can be sampled most effectively using electrofishing (see below).

### 2.2. Environmental descriptors of rivers

Each sampling site was characterized using environmental variables related to the three main hypotheses for explaining food-chain length (stream size, productivity and disturbance) (Tables 1 and 2). Disturbance was defined broadly as any reduction in water and physical habitat quality because they may alter the taxonomic composition and