# Déjala correr: efecto de modificaciones hidrológicas sobre las tramas tróficas fluviales

**Anahí López-Rodríguez**

Doctorado en Ciencias Biológicas
PEDECIBA

PEDECIBA
MEC-UDELAR
CURE
Centro Universitario Regional del Este
CENUR
Litoral Norte
cap
COMISIÓN ACADÉMICA DE POSGRADO
ANII
AGENCIA NACIONAL DE INVESTIGACIÓN E INNOVACIÓN
CSIC
COMISIÓN SECTORIAL DE INVESTIGACIÓN CIENTÍFICA
UNIVERSIDAD DE LA REPÚBLICA URUGUAY

Esta tesis fue presentada en el Programa de Desarrollo de las Ciencias Básicas (PEDECIBA), como requisito fundamental para la obtención del título de Doctora en Ciencias Biológicas. Las actividades fueron desarrolladas en el Departamento de Ecología y Gestión Ambiental, Centro Universitario Regional del Este (CURE, Maldonado) y en el Departamento de Ciencias Biológicas, CENUR Litoral Norte, Sede Paysandú, ambas instituciones pertenecientes a la Universidad de la República (UdelaR). Asimismo, parte de las actividades fueron llevadas a cabo en el Departamento de Ecología y Biología Evolutiva (DEBE), Instituto de Investigaciones Biológicas Clemente Estable, Ministerio de Educación y Cultura.

Esta tesis fue realizada bajo la orientación de la Dra. Mariana Meerhoff Scaffo y del Dr. Iván González-Bergonzoni.

Comité Evaluador:

- Dr. Daniel Conde (Sección Limnología, Instituto de Ecología y Ciencias Ambientales-IECA-, Facultad de Ciencias, Universidad de la República, Uruguay)
- Dra. Valentina Franco-Trecu (Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Uruguay)
- Dr. Fernando Pelicice (Universidade Federal do Tocantins, Brasil)

Maldonado, Uruguay - 2024

# Contenido

# Agradecimientos

En primer lugar, quiero agradecerles a mi tutora y a mi tutor, Dra. Mariana Meerhoff y Dr. Iván González Bergonzoni no solo por sus invaluables aportes a nivel académico y científico y por su guía a lo largo de todo el proceso de la tesis, sino también por calidad humana, templanza y por siempre transmitirme seguridad. A Mari, mi "madre académica", por ser un soporte emocional, brindando no solo consejos científicos sino también personales, por las largas charlas de motivación y por su amistad invaluable a lo largo de toda mi incipiente carrera como científica, siempre con la palabra justa para no dejarme caer en los momentos de mayor presión. A Iván por su amistad, por invitarme a participar de sus proyectos, introducirme en el mundo de los isótopos y siempre estar cuando necesité alguna mano. Una combinación de tutores que calzó justo en el momento académico y personal que estaba transitando, y sin los cuales este proceso dudo que hubiera podido ser tan fructífero. ¡Muchas gracias a ambos, por todo!

Un agradecimiento especial a todas las personas que forman y han formado parte del equipo del CURE, con los cuales compartí horas de charlas de oficina y laboratorio desde mis inicios en la vida académica: Franco, Guille, Checho, Mari, Clau, Clemen, JP, Juanpi, Gige, Sami, Maite B, Maite C, Lu C, Marge, Canario, Lu S, Esteban, Fran, Lu G, Pauli, Sole, Miriam, Pache, Cami, Emi, Barbie y toda la "nueva" camada de tomadores de café del laboratorio! Especialmente a las que transitaron todo este camino conmigo y siempre estuvieron para dar su apoyo, ya sea desde acá o a la distancia, y sobre todo por su amistad: a Clemen, por la ayuda en los muestreos, escuchar mis eternos audios de catarsis de la vida científica y personal, y siempre brindar su apoyo y ayudar a bajar la pelota al piso; a Mai astral, por la ayuda fundamental en los muestreos, por sus reportes astrológicos y siempre encontrar una explicación para todos nuestros estados; y a Marge y Lu C por siempre estar.

A las y los integrantes del Polo de Ecología fluvial del CENUR Litoral Norte por dejarme ser parte del grupo y sus proyectos, compartiendo muestreos y charlas: Iván, Ivana, Christine, Joaquín, Noe y Andre. Muy especialmente a Ivana, con la cual transitamos parte de este proceso juntas, haciéndonos el aguante mutuamente, por las horas de laboratorio compartidas y por las largas charlas con mate de por medio.

A todas las personas que integran el Departamento de Ecología y Biología Evolutiva del IIBCE: Anita, Nadia, Maca, Mari, Vero, Pauli, Toscano, Luis, y todas y todos los que de una u otra forma me hicieron sentir parte de ese laboratorio y me brindaron un espacio para trabajar y compartir.

A todos los que participaron de los muestreos, bancándose las inclemencias del tiempo: Iván, Mai B, Clemen, Ivana, Canario, Nico, Joaco, Mati e Inés.

A los co-autores de los trabajos, pero principalmente a Evoy, David y Sunshine por ayudarme cada vez que lo necesité, consiguiendo materiales, información, fotos y por participar de forma tan entusiasta en los trabajos.

A todo el equipo del URI, los nuevos y los viejos!

A la UdelaR, mi segunda casa, que me permitió desarrollarme como estudiante y científica. Por la posibilidad de estudiar de manera gratuita, y a través del PEDECIBA realizar tanto la maestría como el doctorado, que me permitieron estar hoy donde estoy. A la CAP por las becas otorgadas, fundamentales para poder seguir estudiando y trabajando.

A los miembros de la CAS, Dra. Gissell Lacerot, Dr. Danilo Calliari y Dr. Daniel Conde por sus aportes al proyecto y durante toda la etapa del doctorado, que permitieron mejorarlo sustancialmente.

A los integrantes del tribunal: Dr. Daniel Conde, Dra. Valentina Franco-Trecu y Dr. Fernando Pelicice por aceptar ser parte y porque estoy convencida que sus aportes ayudarán a enriquecer este trabajo.

A mis amigas, las de siempre por siempre estar presentes, preguntando, apoyando y por ser un sostén fundamental para mí y para mi familia.

A la red de cuidados que tengo la suerte de que me rodeen y hagan todo un poco más fácil. A los vecinos y vecinas que siempre están para quedarse un rato con los pequeños; a la familia de Mati siempre presente; y principalmente a mi familia, mis hermanos y fundamentalmente a mis padres por siempre confiar y ayudarme a seguir adelante, por ser padres, abuelos, transporte escolar, niñeros y todo lo que necesito! Sin toda esta red de contención, este camino hubiera sido muy difícil de transitar. ¡Muchas gracias a todos, de verdad!

Por último, quiero agradecer a mi “Ohana” (guiño para Ine 😊). A Matías porque realmente se las bancó todas, gracias por hacerme conocer lo más lindo de la vida, por todo lo vivido juntos y por lo que nos queda disfrutar. A mis peques, Ine y Maurito, que llegaron en los momentos justos y me hicieron entender que la vida es mucho más linda y divertida con ellos. ¡Gracias!

# Listado de artículos

## Incluidos en la tesis

| | |
|---|---|
| Artículo 1 | **López-Rodríguez A**., Silva I., de Ávila-Simas S., Stebniki S., Bastian R., Massaro M.V., Pais J., Tesitore G., Teixeirade Mello F., D'Anatro A., Vidal N., Meerhoff M., Reynalte-Tataje D.A., Zaniboni-Filho E. & González-Bergonzoni I., 2019. Diets and trophic structure of fish assemblages in a large and unexplored subtropical river: The Uruguay River. Water, 11, 1374. https://doi.org/10.3390/w11071374 |
| Artículo 2 | **López-Rodríguez A**., Mariana Meerhoff, D'Anatro A., de Ávila-Simas S., Silva I., Pais J., Teixeira de Mello F., Reynalte-Tataje D.A., Zaniboni-Filho E. & González-Bergonzoni I., 2024. Longitudinal changes on ecological diversity of Neotropical fish along a 1700 km river gradient show declines induced by dams. Perspectives in Ecology and Conservation. |

## Manuscrito

| | |
|---|---|
| Artículo 3 | **López-Rodríguez A**., Mariana Meerhoff, D'Anatro A., de Ávila-Simas S., Silva I., Teixeira de Mello F., Reynalte-Tataje D.A., Zaniboni-Filho E. & González-Bergonzoni I., 2024. Dams modify energetic pathways for fish along a large subtropical river. A ser sometido a Ecosystems. |

## Adicionales

| | |
|---|---|
| Artículo 4 | Torremorell, A., Hegoburu, C., Brandimarte, A. L., Rodrigues, E. H. C., Pompeo, M., da Silva, S. C., Moschini-Carlos, V., Caputo, L., Fierro, P., Mojica, J.I., Matta, A.L.P., Donato, J.C., Jiménez-Pardo, P., Molinero, J., Ríos-Touma, B., Goyenola, G., Iglesias, C., **López-Rodríguez, A.,** Merrhoff, M., Pacheco, J.P., Teixeira de Mello, F., Rodríguez-Olarte, D., Barrios Gómez, M., Montoya, J.V., López-Doval, J.C., & Navarro, E., 2021. Current and future threats for ecological quality management of South American freshwater ecosystems. Inland Waters. 11, 125-140. https://doi.org/10.1080/20442041.2019.1608115 |
| Artículo 5 | Vidal, N., Teixeira de Mello, F., González-Bergonzoni, I., **López-Rodríguez, A**., Tesitore, G., Pais, J., Stebniki, S., Silva, I. & D'Anatro, A., 2020. Long-term study of the reproductive timing of the Neotropical catfish *Iheringichthys labrosus* (Lütken, 1874): Influence of temperature and river discharge. Ecology of Freshwater Fish. 29, 334-345.https://doi.org/10.1111/eff.12518 |
| Artículo 6 | Ferreira, V., Boyero, L., Calvo, C., Correa, F., Figueroa, R., Gonçalves, J. F., Goyenola, G., Graca, M.A.S., Hepp, L.U., Kariuki, S., **López-Rodríguez, A.**, Mazzeo, N., MÉrimba, C., Monroy, S., Piel, A., Pozo, J., Rezende, R. & Teixeira-de-Mello, F., 2019. A |

| | |
|---|---|
| | global assessment of the effects of eucalyptus plantations on stream ecosystem functioning. Ecosystems, 22, 629-642. https://doi.org/10.1007/s10021-018-0292-7 |
| Artículo 7 | Figueiredo, B.R., Calvo, C., **López-Rodríguez, A**., Mormul, R.P., Teixeira-de Mello, F., Benedito, E. & Meerhoff, M., 2019. Short-term interactive effects of experimental heat waves and turbidity pulses on the foraging success of a subtropical invertivorous fish. Water, 11, 2109. https://doi.org/10.3390/w11102109 |

## Financiación

- 2018-2021: Beca posgrado CAP
- 2018-2021: Alícuotas PEDECIBA
- 2022-2023: Beca de finalización CAP
- Proyecto CSIC I+D_2016_577-348, Comisión Sectorial de Investigación Científica (CSIC)
- Proyecto FCE_ 2_2016_1_126780, Agencia Nacional de Investigación e Innovación (ANII)
- Proyecto CSIC grupos I+D 2022: “Ecosistemas acuáticos en el Antropoceno: contribución de los ecosistemas artificiales a la biodiversidad y ciclos biogeoquímicos” (CSIC)
- Proyecto CSIC grupos I+D 2022: “Ecología de Ríos y Bosques: la cuenca del Queguay como modelo” (CSIC)

## Artículos de divulgación

- ¿Quiénes andan en el Río Uruguay? Nota de divulgación escrita por Leo Lagos para la sección Ciencia de La Diaria, agosto 2019. Artículo enmarcado en el primer artículo publicado de la tesis. https://ladiaria.com.uy/ciencia/articulo/2019/8/por-primera-vez-se-realiza-investigacion-para-conocer-que-peces-hay-en-los-1800-kilometros-del-rio-uruguay-y-saber-de-que-se-alimentan

- Obstruyendo la diversidad. Nota de divulgación escrita por Leo Lagos para sección Ciencia de La Diaria, abril 2024. Artículo enmarcado en el segundo artículo publicado de la tesis. https://ladiaria.com.uy/ciencia/articulo/2024/4/obstruyendo-la-biodiversidad-la-represa-de-salto-grande-ocasiona-una-perdida-de-diversidad-de-peces-del-51-respecto-de-la-que-tenemos-aguas-arriba/

# Resumen

A escala global se está observando una alteración sin precedentes de los ecosistemas por efecto antrópico.

A pesar de la gran importancia ecológica de la conectividad de los ecosistemas fluviales, a escala global se estima que solo el 37% de los ríos con extensión de más de 1000 km permanece libre de represas construidas para diferentes fines como el abastecimiento de agua potable o la generación de energía hidroeléctrica, entre otros usos. La construcción de represas genera enormes repercusiones en la biodiversidad y el funcionamiento ecosistémico, entre otros. El Neotrópico, particularmente Sudamérica, no es una excepción. Esta región representa un punto crítico para la biodiversidad de agua dulce, particularmente de especies de peces, cuyo conocimiento ecológico es aún escaso. Esto es particularmente cierto para la cuenca del Río Uruguay.

Particularmente para los ecosistemas fluviales, se han propuesto varias teorías que intentan explicar su dinámica ecológica a lo largo del gradiente longitudinal desde las nacientes hasta su desembocadura, incluyendo los patrones de diversidad y la distribución de las especies y el ensamblaje de las comunidades. En sistemas con flujos de agua naturales, se espera que las comunidades de peces aumenten su diversidad taxonómica y funcional, así como la complejidad de la arquitectura de la red trófica, aguas abajo. Asimismo, se esperan cambios en los subsidios energéticos de las redes tróficas (i.e., origen espacial de la biomasa de las comunidades) a lo largo del gradiente longitudinal, con diversos postulados al respecto. Sin embargo, las teorías sobre funcionamiento de ecosistemas fluviales no necesariamente se aplican cuando los flujos hidrológicos se ven interrumpidos por represas. Un marco teórico que se centra en sistemas con interrupciones del flujo hidrológico es el Concepto de discontinuidad seriada (SDC), el cual predice el comportamiento de las comunidades en el gradiente longitudinal, dependiente de las distancias a las represas. Sin embargo, esta teoría no genera predicciones sobre cambios en las redes tróficas y en los sustentos energéticos de las comunidades fluviales.

El objetivo general de esta tesis fue identificar potenciales efectos de las represas sobre la estructura y funcionamiento comunitario, usando como modelo las comunidades de peces del Río Uruguay. Ello implica la generación de conocimiento básico sobre: 1- la riqueza de especies de peces; 2- su nicho ecológico; 3- los cambios en el sustento energético (i.e., biomasa generada por recursos acuáticos y terrestres) de las tramas tróficas; y la puesta a prueba de distintos marcos teóricos y sus predicciones. La hipótesis de trabajo fue que los cambios físicos generados por las represas (e.g., variación del flujo de descarga de agua, cambios en flujos de sedimentos y disminución de turbidez aguas abajo) promueven cambios a escala comunitaria aguas abajo, así como también en el nicho ecológico y en el sustento energético de la biomasa de los peces, debido principalmente a los efectos sobre los niveles basales de las tramas tróficas.

La aproximación de la tesis incluyó el análisis de la estructura trófica de las comunidades y de los roles tróficos de los peces mediante el análisis de dieta y de isótopos estables a lo largo del gradiente longitudinal. Se realizaron muestreos de comunidades de peces en 12 sitios a lo largo del curso principal del Río Uruguay (aproximadamente 1700 km). Se determinó la riqueza de especies, la diversidad trófica (mediante el cálculo de métricas basados en análisis de dieta) y el nicho isotópico (utilizando las proporciones de isótopos de nitrógeno y carbono) como un proxy para el nicho ecológico a nivel de comunidad, con un foco particular en áreas aguas arriba y aguas abajo de las cuatro represas existentes. Asimismo, se realizaron modelos de mezcla isotópica bayesianos para determinar el origen de la biomasa de las comunidades de peces de cada grupo trófico. Para determinar los roles tróficos, se analizó la dieta de cien especies de peces (2309 contenidos estomacales) y se clasificaron en cuatro grupos tróficos, subdivididos en ocho grupos de nivel inferior, y reportamos métricas de diversidad trófica para cada especie.

Encontramos una alta diversidad de especies de peces y un aumento relativo de especies de peces que consumen macroinvertebrados terrestres hacia la sección media del río. Por otra parte, detectamos cambios longitudinales en la riqueza de especies y en la diversidad trófica e isotópica, respaldando -parcialmente- predicciones teóricas generales (por ejemplo, el Concepto de Río Continuo). Sin embargo, la riqueza taxonómica, la diversidad trófica y el nicho isotópico disminuyeron abruptamente inmediatamente aguas abajo de todas las represas, apoyando

predicciones del Concepto de Discontinuidad Seriada. Los modelos de mezcla isotópica bayesianos mostraron mayor sustento energético de origen alóctono para la biomasa de los peces en la sección media del río.

Estos resultados sugieren la acción de mecanismos vinculados a las grandes planicies de inundación en la sección media del río, respaldando teorías globales como el concepto de pulso de inundación. Encontramos también que el acople de las vías energéticas (autóctona y alóctona) parece ser la regla para subsidiar la biomasa de los peces en este río, más que la dominancia por una u otra vía como se ha reportado más habitualmente en la literatura. Sin embargo, el subsidio alóctono parece ser particularmente importante para los depredadores tope, consistentemente a lo largo de todo el gradiente fluvial. Las represas alteraron los patrones longitudinales, llevando a que una u otra vía (i.e., autóctona o alóctona) perdiera relevancia en las áreas cercanas a las represas, con variantes probablemente vinculadas a las características locales. Por otra parte, los tramos libres de represas del Río Uruguay resultan ser fundamentales para la recuperación de la diversidad ecológica.

El conocimiento generado en esta tesis puede contribuir sustancialmente a la gestión y conservación de los ecosistemas fluviales, sirviendo como línea de base en el contexto de futuros cambios ambientales y generando nueva evidencia sobre el funcionamiento de los ecosistemas en esta región climática escasamente estudiada. La evidencia acumulada de los impactos negativos de las represas debe considerarse con urgencia a nivel mundial, y especialmente en el Neotrópico, donde se proyecta la construcción de grandes represas en los próximos años.

# Abstract

At a global scale, an unprecedented alteration of ecosystems due to anthropogenic effects is being observed. Despite the ecological importance of connectivity in river ecosystems, it is estimated that only 37% of rivers longer than 1000 km remain free from dams constructed for various purposes such as water supply or hydroelectric power generation, among others. Dam construction has significant repercussions on biodiversity and ecosystem functioning, among other factors. The Neotropics, particularly South America, are no exception. This region represents a critical point for freshwater biodiversity, particularly fish species, whose ecological knowledge is still scarce. This is particularly true for the Uruguay River basin.

Several theories have been proposed to explain the ecological dynamics of river ecosystems along the longitudinal gradient from the source to the mouth, including patterns of diversity, species distribution, and community assemblages. In systems with natural water flows, it is expected that fish communities will increase in taxonomic and functional diversity, as well as the complexity of trophic network architecture, downstream. Additionally, changes in energy subsidies of trophic food webs (i.e., spatial origin of community biomass) along the longitudinal gradient are expected, with various postulates regarding this. However, theories about the functioning of river ecosystems do not necessarily apply when hydrological flows are interrupted by dams. A theoretical framework that focuses on systems with interruptions in hydrological flow is the Serial Discontinuity Concept (SDC), which predicts community behaviour along the longitudinal gradient, depending on the distances to the dams. However, this theory does not make predictions about changes in trophic networks and energy subsidies in river communities.

The general objective of this thesis was to identify potential effects of dams on community structure and functioning, using fish communities of the Uruguay River as a model. This involves generating basic knowledge about: 1- fish species richness; 2- their ecological niche; 3- changes in energy subsidies (i.e., biomass generated by aquatic and terrestrial resources) of trophic networks; and testing different theoretical frameworks and their predictions. The hypothesis was that physical changes generated by dams (e.g., variation in water discharge flow, changes in sediment flows, and decreased turbidity downstream) promote changes at the community scale downstream, as well as in the ecological niche and energy subsidies of fish biomass, mainly due to effects on basal levels of the food webs.

The thesis approach included the analysis of trophic structure of communities and trophic roles of fish through diet analysis and stable isotopes along the longitudinal gradient. Fish community sampling was conducted at 12 sites along the main course of the Uruguay River (approximately 1700 km). Species richness, trophic diversity (calculated through diet analysis-based metrics), and isotopic niche (using nitrogen and carbon isotope ratios) as a proxy for ecological niche at the community level were determined, with a particular focus on areas upstream and downstream of the four existing dams. Additionally, Bayesian isotopic mixing models were performed to determine the origin of fish community biomass for each trophic group. To determine trophic roles, the diet of one hundred fish species (2309 stomach contents) was analyzed and classified into four trophic groups, subdivided into eight lower-level groups, and trophic diversity metrics were reported for each species.

We found high fish species diversity and a relative increase in species consuming terrestrial macroinvertebrates towards the middle section of the river. Additionally, we detected longitudinal changes in species richness and trophic and isotopic diversity, partially supporting general theoretical predictions (e.g., the River Continuum Concept). However, taxonomic richness, trophic diversity, and isotopic niche abruptly decreased immediately downstream of all dams, supporting predictions of the Serial Discontinuity Concept. Bayesian isotopic mixing

models showed higher allochthonous energy subsidies for fish biomass in the middle section of the river.

These results suggest the action of mechanisms linked to large floodplains in the middle section of the river, supporting global theories such as the Flood Pulse Concept. We also found that the coupling of energy pathways (autochthonous and allochthonous) seems to be the rule for subsidizing fish biomass in this river, rather than the dominance of one pathway as more commonly reported in the literature. However, allochthonous subsidy appears to be particularly important for top predators, consistently along the entire river gradient. Dams altered longitudinal patterns, leading to one or the other pathway (i.e., autochthonous or allochthonous) losing relevance in areas near the dams, with variants likely linked to local characteristics. Furthermore, dam-free stretches of the Uruguay River appear to be fundamental for the recovery of ecological diversity.

The knowledge generated in this thesis can substantially contribute to the management and conservation of river ecosystems, serving as a baseline in the context of future environmental changes and generating new evidence about ecosystem functioning in this poorly studied climatic region. The accumulated evidence of the negative impacts of dams must be urgently considered globally, and especially in the Neotropics, where the construction of large dams is projected in the coming years.

# 1. Introducción general

## 1.1. Ecosistemas fluviales

A escala global se está observando una alteración sin precedentes de los ecosistemas naturales por actividades antrópicas, lo cual promueve cambios en el sistema climático, pérdida de biodiversidad, cambios en los ciclos biogeoquímicos, ciclo hidrológico, entre otras consecuencias (Vitousek et al., 1997; Rockström et al., 2009; Steffen et al., 2015). En el caso de los ríos, una de las alteraciones más frecuentes y de mayor magnitud es la regulación de los regímenes hidrológicos.

Los ecosistemas fluviales se caracterizan por poseer corrientes de agua orientadas a lo largo de un eje longitudinal, desde las nacientes (zona con pendientes pronunciadas) a la desembocadura (pendientes mínimas) (Likens, 2010). Los ríos son sistemas altamente conectados, desarrollándose su conectividad en cuatro dimensiones: longitudinal (aguas arriba-aguas abajo); lateral (conectando el canal principal con las planicies de inundación y áreas riparias); vertical: entre el agua subsuperficial, el río y la atmósfera; y temporal (variación estacional de los flujos de agua) (Ward, 1989). Los ríos conectan el hábitat acuático con el terrestre circundante mediante las planicies de inundación, integrando al ecosistema acuático también recursos provenientes del medio terrestre circundante y viceversa. Estos ecosistemas, además, se encuentran insertos en una red dendrítica conectada por tributarios, que drenan hacia un mismo curso de agua principal, jugando roles clave en los ciclos biogeoquímicos al recibir, transformar y transportar material particulado y disuelto desde las aguas continentales y los ecosistemas terrestres hacia los océanos (Allan & Castillo, 2007; Lehner et al., 2024).

Los ríos y arroyos son naturalmente dinámicos espacial y temporalmente, proporcionando múltiples servicios ecosistémicos, incluyendo la provisión de recursos como agua para consumo o riego, recursos asociados a las pesquerías, servicios de regulación hidrológica (e.g., mitigación de inundaciones), mantenimiento de hábitats y biodiversidad, además de servicios culturales como recreación (Yeakley et al., 2016). Sin embargo, estas funciones ecosistémicas dependen estrechamente de la conectividad de los procesos hidrológicos en las cuencas (Sidle & Gomi, 2024).

## 1.2. Diversidad y funcionamiento de ecosistemas fluviales

Todas estas características hacen a los ríos y arroyos sistemas altamente productivos y con gran heterogeneidad de hábitats a distinta escala espacial, lo que permite que sustenten una gran biodiversidad, tanto sosteniendo especies adaptadas a las características de cada tramo o hábitat

(Allan & Castillo, 2007) como a otras especies que inmigran desde otros sitios de la red hídrica. La alta conectividad de estos sistemas permite también a los organismos moverse en el hábitat fluvial y en los hábitats adyacentes, conectando procesos a escala de cuencas (Pringle, 2003). Las comunidades locales se encuentran entonces estrechamente conectadas mediante el flujo de individuos entre comunidades conectadas a través de la red fluvial, conformando estructuras metacomunitarias clave para el mantenimiento de la biodiversidad (Leibold et al., 2004). Asimismo, estas comunidades locales interactúan con el ambiente circundante, lo que determina en última instancia las dinámicas poblacionales y la estructura de la comunidad (Leibold et al., 2004). Por lo tanto, la conectividad resulta fundamental para el mantenimiento de la biodiversidad en estos ecosistemas (Borthagaray et al., 2020). Asimismo, diversas teorías ecológicas, también relevantes para los ecosistemas fluviales, buscan explicar los patrones de diversidad en las comunidades en función de las características de la matriz ecosistémica en que se encuentran. Por ejemplo, diversas teorías plantean que el tamaño del ecosistema (MacArthur & Wilson, 1967), su productividad (Wright, 1983), o la heterogeneidad tanto espacial como temporal del hábitat (Pringle et al., 1988), son determinantes para la diversidad a través de diversos mecanismos. En ríos, se ha planteado que la mayor probabilidad de que la diversidad aumente hacia aguas abajo a medida que el sistema fluvial se ensancha, se basa en el aumento de la heterogeneidad de hábitats y de la productividad, lo cual permite el sustento de un mayor número de especies (Horwitz, 1978).

En diversos ecosistemas fluviales sin interrupciones en su hidrología ni fragmentación de hábitats por efecto antrópico se han descrito diversos patrones de diversidad y de la arquitectura de las redes tróficas en el gradiente longitudinal. Por ejemplo, se espera un aumento de la riqueza (diversidad alfa) de especies de peces a lo largo del gradiente longitudinal, con acumulación de especies desde las nacientes a la desembocadura (e.g., Pease et al., 2012). Por otra parte, la diversidad beta (i.e., cambios en la diversidad de especies entre comunidades que conforman una metacomunidad) también tiende a aumentar debido a un incremento en el anidamiento. Esto se da ya que las comunidades aguas arriba representan un subset de las especies que se encuentran en las comunidades aguas abajo en el gradiente longitudinal (Peláez & Pavanelli, 2018). La diversidad beta puede estar reflejando dos fenómenos distintos, tanto el anidamiento como el reemplazo de especies (Baselga et al., 2010; Legendre, 2014).

Complementariamente a los estudios de diversidad, los estudios de tramas tróficas son una de las principales y más directas aproximaciones utilizadas para comprender los patrones organizacionales y relaciones (en este caso de consumo) entre las especies en un ecosistema (Elton, 1929; Paine, 1980; Carpenter et al., 1985; Pimm et al., 1991). El estudio de estas relaciones y del rol que ocupa cada especie provee el más complejo y preciso resumen de una comunidad biológica y las interacciones de consumo entre los organismos, permitiendo aproximarnos a entender el funcionamiento a escala ecosistémica (Woodward, 2009). Asimismo, comprender cuál es el sustento energético de las tramas tróficas contribuye a determinar la estabilidad de una comunidad local y a predecir sus respuestas ante perturbaciones externas (Rooney & McCann, 2012).

Evidencias obtenidas de ríos y arroyos sin interrupciones en su hidrología sugieren la existencia de un gradiente longitudinal también en la arquitectura de las redes tróficas, con incrementos en su complejidad (por aumento en la riqueza de especies y el número de conexiones tróficas en la red) e incrementos en el largo de la cadena (aumentos en los niveles tróficos) desde las nacientes a la desembocadura (e.g., Sabo et al., 2010; Winemiller et al., 2010; Pease et al., 2012). Se ha hipotetizado que estos cambios responden a incrementos en el tamaño del ecosistema fluvial, y a una atenuación de los disturbios hidrológicos en las zonas más bajas y con menores pendientes (Sabo et al., 2010).

## 1.3. Marcos teóricos en ecosistemas fluviales

Las características propias de los ecosistemas fluviales han llevado a que se planteen una serie de marcos teóricos que intentan describir las dinámicas y cambios en las comunidades a lo largo de su gradiente longitudinal, enfocándose principalmente en aspectos relacionados a la transformación y asimilación de la materia por parte de los organismos, haciendo especial énfasis en las tramas tróficas y en su sustento energético (Vannote, 1980; Junk et al., 1989; Thorp & Delong, 1994; 2002; Thorp et al., 2006). Todas estas teorías han estado en constante revisión y debate, llegando incluso a plantearse en los últimos años teorías conciliadoras de los diferentes marcos (Humpries et al., 2014). Uno de los marcos teóricos más relevantes de las últimas décadas fue el “Concepto de Río Continuo” (RCC, por su sigla en inglés “River Continuum Concept”), propuesto por Vannote et al. (1980), el cual plantea la existencia de un gradiente en las condiciones físicas desde las nacientes a la desembocadura (gradiente longitudinal de ecosistemas fluviales). Esta teoría sostiene que, en este gradiente, la estructura de las comunidades (principalmente de macroinvertebrados) depende de los recursos disponibles en cada sección del río. Por tanto, en las nacientes se encuentran aquellas comunidades con organismos adaptados a la ingesta de recursos alóctonos, provenientes del bosque ripario característico de las cabeceras de los arroyos templados. A medida que el sistema fluye hacia aguas abajo, el ingreso de material alóctono disminuye, aumentando la materia orgánica particulada fina y la producción de recursos basales de origen autóctono (e.g., algas bentónicas), generando cambios en la estructura de las comunidades (Vannote et al., 1980).

Las principales limitaciones de esta teoría se basan en que sus predicciones son enfocadas en gran medida a comunidades de macroinvertebrados, además de que está basada en evidencia generada en sistemas templados de los Apalaches en EEUU que carecen de planicies de inundación (Junk et al., 1989).

Por otra parte, investigaciones realizadas en ríos tropicales con grandes fluctuaciones hidrológicas resaltaron la necesidad de incorporar la dimensión lateral para la comprensión de las dinámicas y complejidad de los ecosistemas fluviales. Así, se planteó la teoría del "Concepto de Pulsos de Inundación" (FPC, por su sigla en inglés: "Flood Pulse Concept") (Junk et al., 1989). Este marco teórico resalta la importancia de las planicies de inundación, planteando que los ecosistemas fluviales se conectan con las planicies a través de pulsos prolongados y relativamente predecibles que incrementan el intercambio de materia, energía e información genética entre el ecosistema acuático y el terrestre. Por este motivo, se plantea que en aquellos ecosistemas o tramos de los ríos que presentan planicies de inundación, muchas especies se encuentran adaptadas a la utilización de recursos alóctonos provenientes del medio terrestre circundante como principal fuente de energía (Junk et al., 1989).

Como marcos conceptuales opuestos a lo planteado en las dos teorías anteriores, surgen dos teorías: el "Modelo de Río Productivo" ("Riverine Productivity Model", sigla en inglés RPM) (Thorp & Delong, 1994; revisado por Thorp & Delong, 2002) y la "Síntesis del Ecosistema Riverino" ("Riverine Ecosystem Synthesis", RES por su sigla en inglés) (Thorp et al., 2006). Estas dos teorías coinciden en el planteo de que la principal fuente de energía que sustenta a las tramas tróficas en los ecosistemas fluviales tiene origen autóctono. La RPM plantea como principal fuente de energía de las redes tróficas fluviales a los recursos de origen autóctono, independientemente de la disponibilidad de material alóctono. Esto se debería a que el carbono de las algas bentónicas es más fácil de asimilar y más rico energéticamente que el carbono terrestre (Thorp & Delong, 2002). Por otra parte, la RES (Thorp et al., 2006) no describe a los ecosistemas fluviales como un continuo, sino que los entiende como una conjunción de parches hidrogeomorfológicos, fuertemente asociados a la geomorfología y al clima. Esta teoría, al igual que la RPM, postula que la mayor parte de la biomasa de los organismos acuáticos proviene de recursos autóctonos, con la excepción de algunas especies y estaciones en parches con una entrada significativa de material de origen alóctono (Thorp et al., 2006).

En los últimos años se ha postulado una teoría que integra los marcos teóricos anteriores: el "Concepto de Onda de Río" ("River Wave Concept", RWC por su sigla en inglés- Humphries et al., 2014). En ésta se plantea que la hidrología determina la fuente principal de energía que utilizan las comunidades acuáticas. En este sentido, a altos niveles de flujo predominará el ingreso y asimilación de material alóctono desde las planicies de inundación y por tanto la producción secundaria se basará en energía alóctona. Por el contrario, cuando los niveles de flujo sean bajos, la biomasa de las tramas tróficas será sostenida por energía basada de recursos autóctonos, producidos localmente en el sistema (Humphries et al., 2014).

Sin embargo, excepto RCC, la mayoría de las teorías en ecosistemas fluviales se basan casi exclusivamente en el sustento energético, sin plantear predicciones asociadas a los cambios en los patrones de diversidad a lo largo del gradiente fluvial.

Por otra parte, la mayoría de las diversas teorías que explican el comportamiento de los sistemas fluviales no pueden ser aplicadas a sistemas con embalses ya que se basan en la continuidad de la conexión longitudinal y/o lateral del ecosistema (e.g., Vannote et al., 1980; Junk et al., 1989; Thorp et al., 2006; Humphries et al., 2014), aspectos interrumpidos por las represas. Una teoría que surge como modificación al Concepto de Río Continuo intenta explicar la dinámica de los ecosistemas fluviales con presencia de represas: el "Concepto de Discontinuidad Seriada" ("The Serial Discontinuity Concept"-SDC- Ward & Stanford, 1983; 1995). Esta teoría postula que los ecosistemas fluviales presentan un gradiente longitudinal predecible en las condiciones biofísicas, que dependen de las condiciones ambientales y de la distancia a las represas. Sin embargo, esta teoría es bastante limitada en cuanto al alcance de sus predicciones y no permite generar predicciones sobre los efectos que los cambios producidos por las represas generarán sobre varias características de la biota, principalmente en lo que refiere a cambios en las redes tróficas y en los sustentos energéticos (Ward & Stanford, 1995).

A pesar de la gran cantidad de marcos teóricos desarrollados en ecología fluvial, es necesaria la generación de evidencia empírica que identifique y explique los impactos en las comunidades locales, dado que la gran mayoría de los ríos están sometidos a una gran presión antropogénica y a la interrupción de su flujo hidrológico natural. En este sentido, los cambios en los patrones de diversidad por efecto de las represas muy probablemente traen aparejados cambios significativos en el funcionamiento y diversos procesos a escala ecosistémica.

## 1.4. Interrupción de flujos hidrológicos naturales mediante la construcción de represas

A pesar del consenso sobre la importancia de la conectividad en los ríos, éstos están siendo sometidos a uno de los principales impactos antrópicos a escala global: la construcción de represas (Vörösmarty et al., 2010; Poff et al., 2010). El represamiento de ríos se encuentra en expansión a nivel global y se espera que continúe creciendo exponencialmente en las próximas décadas, generando fuertes presiones sobre la biota de los ecosistemas fluviales (Zarfl et al., 2015; 2019; Fig 1), así como sobre procesos ecosistémicos, además de impactos sobre las poblaciones humanas asociadas a los ríos (Flecker et al., 2022). A escala global solo el 37% de los ríos con extensión de más de 1000 km permanece libre de represas, demostrando el estado de alta vulnerabilidad de estos sistemas (Grill et al., 2019).

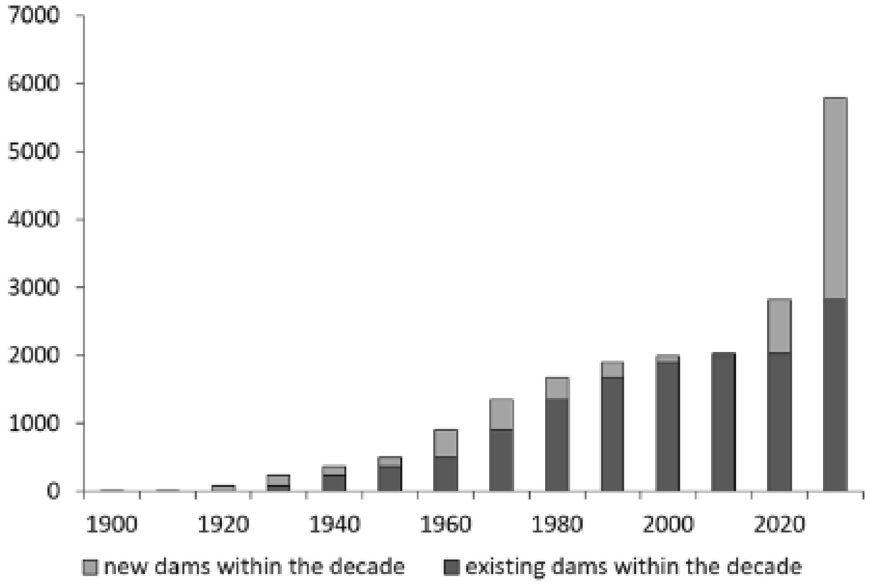


Fig. 1. Número de represas existentes a nivel global y proyección de construcción de nuevas represas al año 2030. Figura extraída de Zarfl et al., 2015.

La construcción de represas para diferentes fines, como el abastecimiento de agua potable o la generación de energía hidroeléctrica, entre otros usos (Baxter, 1977; Dudgeon, 2000; Nilsson et al., 2005; Ormerod et al., 2010; Grill et al., 2019), altera la estructura y el funcionamiento de los ecosistemas lóticos al modificar las condiciones físicas del ambiente, y promover la transformación de ecosistemas lóticos en lénticos, la fragmentación del hábitat, y cambios en la velocidad del flujo de agua y la frecuencia e intensidad de pulsos de descarga aguas abajo (Dudgeon et al., 2005; Allan & Castillo, 2007). Estos cambios afectan también a los ecosistemas terrestres circundantes tanto aguas arriba como aguas abajo. Asimismo, alteran la geomorfología del cuerpo de agua y modifican la temperatura del agua y su concentración de oxígeno disuelto (Allan & Castillo, 2007). Las represas generan también retención de material en suspensión, incluyendo nutrientes, materia orgánica y contaminantes que son secuestrados en los sedimentos del embalse, lo cual altera el flujo de sedimentos aguas abajo de la represa, entre otras perturbaciones (e.g., Baxter, 1997; Nilsson et al., 2005; Barletta et al., 2010; Cross et al., 2011).

Usualmente los grandes ríos presentan varias represas consecutivas en el gradiente longitudinal (i.e., cascada de represas). Esta distribución en cascada afecta fuertemente los patrones observados aguas abajo (e.g., Barbosa et al., 1999; Cheng et al., 2015; Santos et al., 2018; Huang et al., 2018). Se ha observado que el efecto acumulado de los cambios en hidrología, retención de sedimentos, retención de nutrientes y procesos físico-químicos generado por la cascada de las represas suele representar un mayor impacto que la suma de los efectos de represas independientes (Castello & Macedo, 2016; Santos et al., 2018).

Algunos de los principales efectos de la construcción de represas son la modificación de hábitats y pérdida de corredores biológicos (Dudgeon et al., 2005; Pelicice et al., 2015), lo que trae como consecuencia la disminución de la biodiversidad local y facilita la colonización por especies invasoras (Dudgeon et al., 2005; Winemiller et al., 2016). La pérdida de biodiversidad en los tramos aguas abajo de las represas se ha constatado a nivel global para diversos grupos biológicos, por ejemplo, en microorganismos, macroinvertebrados, plancton y peces (Wu et al., 2019). En el caso particular de los peces, se ha observado que la construcción de represas ha generado la pérdida del rango geográfico de distribución de más del 50% de las especies en algunas de las grandes cuencas del mundo (e.g., Brasil, India, Estados Unidos y Sudáfrica) (Keijzer et al., 2024; Fig. 2).

La pérdida de biodiversidad tiene también consecuencias culturales, económicas y sociales, ya que muchas de las especies afectadas son recursos pesqueros de gran significancia económica y/o la principal fuente proteica de muchas localidades, por lo que se puede producir un efecto importante sobre la economía local e incluso a nivel de los países (FAO, 2014).

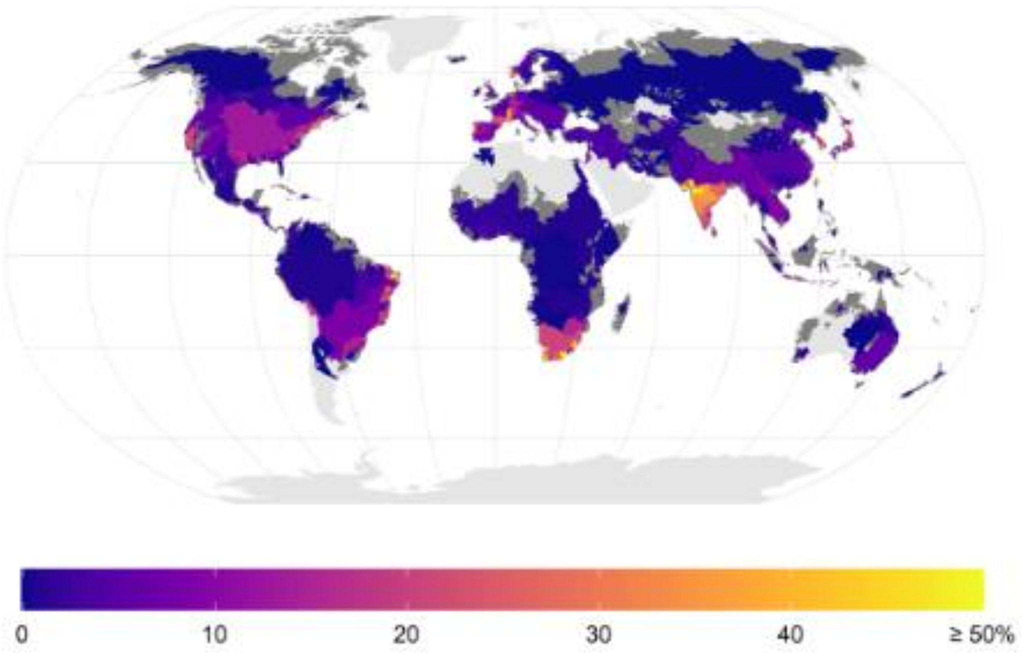


Fig. 2. Pérdida acumulada de rango de distribución de especies de peces (%) debido al aislamiento producido por las represas. Cuencas con ausencia de datos de represas se muestran en gris oscuro. Cuencas con ausencia de datos de especies de peces se muestran en gris claro. Figura extraída de Keijzer et al., 2024.

Los cambios en las condiciones ambientales generadas por las represas tienen efectos sobre las comunidades locales, afectando por ejemplo el ensamble de especies de peces que pueden encontrarse (Junk et al., 1989; Barletta et al., 2010), debido principalmente a que perduran aquellas especies que logran tolerar estas alteraciones en las condiciones físicas del ambiente (Cross et al., 2011). En el caso particular de los peces, se han observado disminuciones en la riqueza de especies, en los tamaños poblacionales y en la diversidad genética en los tramos aguas abajo de cascadas de represas, debido al aislamiento de los ambientes como consecuencia de la fragmentación (Ribolli et al., 2021). Asimismo, las poblaciones de peces se ven afectadas por el bloqueo de las rutas migratorias (Agostinho et al., 2008; Pelicice et al., 2015; Granzotti et al., 2018), y también por impedimentos fisiológicos y comportamentales para alcanzar áreas adecuadas para la reproducción en el nuevo ambiente léntico generado por las represas (Lopes et al., 2024).

Se ha reportado también la existencia de relaciones negativas entre la abundancia y la riqueza de especies con la presencia de cascada de represas, resultando en pérdida de diversidad en las regiones aguas abajo (Ganassin et al., 2021). Sin embargo, también se ha reportado que los sistemas fluviales pueden retornar a las condiciones ecológicas naturales (i.e., sin regulación) a medida que aumenta la distancia a la represa (Ward & Stanford, 1995; Stanford & Ward, 2001).

Por otra parte, la fragmentación de hábitats debido a la construcción de represas puede resultar en la pérdida de especies aguas abajo de las mismas. Sin embargo, también puede generar la incorporación de nuevas especies, alterando por lo tanto los patrones de diversidad beta, cambiando la incidencia de los componentes de reemplazo de especies y anidamiento en el gradiente longitudinal (Ganassin et al., 2021). En el caso del anidamiento, se observa cuando la composición de especies de la comunidad con menor diversidad alfa es un subset de las especies encontradas en la comunidad con mayor diversidad alfa. Por otra parte, el reemplazo de especies refiere a la pérdida de especies de una comunidad a otra, pero también incluye la adición de nuevas especies (Baselga et al., 2010). En este sentido, en ambientes altamente represados, se han observado aumentos en la diversidad beta por aumentos en la diferencia en la composición de especies entre sitios, con pérdida de especies y reemplazo por nuevas especies (i.e, aumento en el componente de reemplazo) (Herrera-Pérez et al., 2019).

Los cambios a nivel comunitario por efecto de las represas pueden generar grandes alteraciones en los procesos a nivel ecosistémico ya que varían, entre otras cosas, las relaciones de consumo (Carpenter et al., 1985; Cross et al., 2011) y por tanto la transferencia de materia y energía. Los cambios en la frecuencia e intensidad de descarga de flujos de agua afectan, no solo la estructura de la comunidad local de peces aguas abajo de la represa, sino que tienen efectos potenciales sobre la estructura y topología de las redes tróficas, generando efectos, por ejemplo, sobre el largo de la trama (Hoeinghaus et al., 2008; Sabo et al., 2010; Ruhí et al., 2016). Se ha observado que los disturbios en la hidrología pueden disminuir el largo de la trama trófica, ya que entre otras cosas se generan alteraciones de los recursos disponibles (e.g., debido al lavado de productores primarios y secundarios locales) (Sabo et al., 2010; Ruhí et al., 2016). Algunos estudios han encontrado disminución o pérdida de grupos funcionales de peces, tanto aguas arriba como aguas abajo de las represas (e.g., de Bem et al., 2021), mostrando declives de grupos como los bentívoros-invertívoros (Granzotti et al., 2018) y detritívoros (Santos et al., 2020), y aumentos en la proporción de especies de peces generalistas luego de la construcción de represas (Turgeon et al., 2019). Por otra parte, la variabilidad en los flujos de agua puede afectar también los patrones de omnivoría y amplitud de nicho, ocurriendo dietas más limitadas por la disponibilidad de alimento luego de una fuerte descarga (e.g., Ruhí et al., 2016). Estos cambios en la proporción de grupos tróficos pueden ser un efecto directo de las alteraciones en la disponibilidad de recursos basales, ocasionando cambios en la diversidad de ítems consumidos y afectando en última instancia el nicho trófico y ecológico ocupado por las especies (Guo et al., 2023).

Asimismo, los disturbios hidrológicos ocasionados por la presencia de represas pueden alterar también el sustento energético de las tramas tróficas. Se ha observado que en ecosistemas fluviales con altas tasas de disturbios hidrológicos tienden a encontrarse redes tróficas basadas en recursos acuáticos (autóctonos) (Guo et al., 2023). Estas redes se asocian con especies de rápido crecimiento y altos recambios poblacionales que puedan responder de forma efectiva ante los disturbios (Townsend et al., 1997). Por otra parte, se ha sugerido que tanto la variación en la descarga de agua, así como los cambios en la penetración de luz, son factores fundamentales que interactúan limitando la producción primaria local en los sectores aguas abajo de los ríos (Roach & Winemiller, 2015). En los sistemas lóticos aguas abajo de las represas suele haber una disminución de la turbidez (relativa a sitios aguas arriba), ya que en la zona lacustre (embalse) tiene lugar una retención de los sedimentos en suspensión. Esto permite una mayor penetración por luz y mayores tasas de producción primaria acuática aguas abajo de la represa (Ward & Stanford, 1983; Johnson et al., 1996). A medida que se aumenta la distancia de la represa, la turbidez aumenta y disminuye la ingesta de material acuático (e.g., algas producidas localmente) (Wellard-Kelly et al., 2013). Igualmente, se ha demostrado que el fitoplancton proveniente de la zona lacustre de los embalses puede contribuir al sustento energético acuático de la trama trófica aguas abajo de la represa, aunque en menor medida que la producción acuática local (Doi et al., 2008).

## 1.5. Antecedentes del caso de estudio: Río Uruguay

A pesar de que se conocen muchos de los impactos del represamiento de ríos, hay evidencia pobre sobre los efectos de las represas sobre las tramas tróficas acuáticas en general y sobre el tipo de recursos que sustenta la biomasa de los consumidores, en particular. Cabe destacar que el tema se encuentra activamente en debate al día de hoy en la literatura especializada (e.g., Guo et al., 2023; Leal et al., 2023). La construcción de represas ha generado alteraciones en la geomorfología y en la hidrología de la mayoría de las grandes cuencas hidrográficas de América del Sur (Agostinho et al., 2007; Winemiller et al., 2016; Torremorell et al., 2021), y Uruguay no escapa a esta problemática, con una gran cantidad de embalses ya construidos para diferentes fines (MVOTMA, 2012; FAO, 2016). Un estudio reciente remarca que Uruguay es el segundo país de América del Sur en número absoluto de represas construidas, superado únicamente por Brasil, con un total de 878 represas, de las cuales solo de cuatro se tiene información precisa de ubicación y datos de su construcción y de la cuenca (Zhang & Gu, 2023).

En particular en Sudamérica, principalmente en Brasil, se ha estudiado en abundancia el efecto de las represas sobre los peces, pero basándose principalmente en patrones de diversidad y en especial en especies migradoras (e.g., Agostinho et al., 2008; Pelicice et al., 2015; Agostinho et al., 2016; Loures & Pompeu, 2018; Pelicice et al., 2018; Ganassin et al., 2021).

El Neotrópico, considerado un *hotspot* de diversidad de peces (Lévêque et al., 2007; Reis et al., 2016) y donde además se están dando la mayor cantidad de alteraciones antrópicas, tiene una gran cantidad de represas proyectadas para las siguientes décadas (Agostinho et al., 2016; Winemiller et al., 2016; Pelicice & Castello, 2021; Flecker et al., 2022). El funcionamiento de los ecosistemas fluviales del neotrópico y la biología de la mayoría de las especies permanece sin conocerse (e.g., Reis et al., 2003; Reynalte-Tataje et al., 2012; Lópes et al., 2019; Vidal et al., 2020). Por su parte, el conocimiento sobre los ensambles de peces presentes en los ríos sudamericanos se enfoca casi exclusivamente en la taxonomía y distribución de especies (Barletta et al., 2010; Reis et al., 2016).

Esto resulta particularmente notable en uno de los mayores ríos de Sudamérica: el Río Uruguay. El Río Uruguay es el segundo tributario más grande de la cuenca del Río de la Plata. Se origina en Brasil en las confluencias de los ríos Canoas y Pelotas, sus tramos medio y bajo separan a Argentina de Uruguay y tiene su desembocadura en el Río de la Plata (Saccol-Pereira, 2008), recorriendo un total de 1800 km. El Río Uruguay se divide en tres secciones basadas en sus características geológicas: alto, medio y bajo Río Uruguay. En las últimas dos décadas, en el alto Río Uruguay se ha dado el desarrollo hidroeléctrico más importante, con la construcción de tres represas. En la actualidad, un total de 4 represas hidroeléctricas operan en este río: tres en el alto Río Uruguay: Machadinho (capacidad: 1140 MW/h; operativa desde 2002), Itá (capacidad: 1450 MW/h; operativa desde 2000), y Foz de Chapecó (capacidad: 855 MW/h; operativa desde 2010), y una en el bajo Río Uruguay: Represa de Salto Grande (capacidad: 1890 MW/h; operativa desde 1979). Las secciones medias y la parte alta del medio Río Uruguay permanecen hasta el momento sin interrupciones en su hidrología, alcanzando una sección de *ca.* 1000 km de aguas corrientes. El Río Uruguay alto se caracteriza por su canal estrecho y la ausencia de planicies de inundación, aunque en la zona más alta se observa gran presencia de bosque ripario (Reynalte-Tataje et al., 2012). La parte media del río, se caracteriza por grandes extensiones de planicies de inundación y presencia de vegetación riparia (principalmente en la parte alta de esta sección). El bajo Río Uruguay, por su parte, tiene presencia de bosque ripario en su sección más hacia el norte, así como también secciones de islas y humedales marginales en su parte media, principalmente en la margen argentina.

A pesar de ser un río muy importante en Sudamérica, la escasa información disponible sobre los peces del Río Uruguay se limita a estudios sobre la biología reproductiva de algunas especies (Zaniboni-Filho et al., 2017; Pachla et al., 2019; Vidal et al., 2020). Por su parte, la mayoría de los estudios de ecología trófica se han limitado a descripciones de dieta de algunas especies clave (e.g., González-Bergonzoni et al., 2010; Masdeu et al., 2011; González-Bergonzoni et al., 2023). En cuanto al sustento energético de las redes tróficas, la información es más escasa aún con un estudio localizado en tres sitios del bajo Río Uruguay (González-Bergonzoni et al., 2019). Sin embargo, en los últimos años se ha incursionado en el estudio de los impactos de las represas localizadas en el alto Río Uruguay sobre la abundancia, biomasa y composición de especies (de Bem et al., 2021) y sobre la diversidad genética (Ribolli et al., 2021). A pesar de este incremento en los estudios en el Río Uruguay, aún desconocemos en gran medida el funcionamiento del río en toda su extensión en el gradiente longitudinal, ya que el conocimiento generado es fragmentado y no abarca la totalidad del gradiente. Asimismo, falta información sobre la ecología trófica, el rol de las especies en las redes tróficas y los principales sustentos energéticos, así como también el potencial impacto de las represas sobre las comunidades de peces y redes tróficas presentes en el río.

Con los mencionados antecedentes, y en el contexto global, y particularmente de Sudamérica de incremento en la construcción de represas, generar evidencia empírica de la variación en el gradiente longitudinal y del potencial efecto de las represas hidroeléctricas sobre múltiples dimensiones de diversidad (i.e., diversidad taxonómica, trófica, de fuentes alimenticias y ecológica) en el Río Uruguay cobra gran relevancia. Cabe destacar que en el Río Uruguay se proyecta la construcción de dos represas hidroeléctricas más, resaltando la urgencia de los estudios en este río. En este contexto, toda la información generada permitirá acercarnos a un mejor entendimiento de los ecosistemas fluviales, particularmente el Río Uruguay, y en consecuencia a un manejo más efectivo e idealmente una disminución de los impactos generados por su fragmentación y modificación (Barletta et al., 2008; Barletta et al., 2010; Ruhí et al., 2016; Flecker et al., 2022).

# 2. Objetivos, hipótesis y predicciones

## 2.1. Objetivo general

El objetivo general de esta tesis fue identificar potenciales efectos de las represas sobre la estructura y funcionamiento comunitario, usando como modelo las comunidades de peces del Río Uruguay. Ello implica la generación de conocimiento básico sobre: 1- la riqueza de especies de peces; 2- su nicho ecológico; y 3- los cambios en el sustento energético (i.e., biomasa generada por recursos acuáticos y terrestres) de las tramas tróficas; y la puesta a prueba de distintos marcos teóricos y sus predicciones.

Este objetivo general se dividió en 3 objetivos específicos, y cada uno de ellos corresponde a un capítulo de la tesis (Fig. 3).

## 2.2. Objetivos específicos

1.1) Identificar taxonómica y funcionalmente a las especies de peces del Río Uruguay, analizando su dieta y generando una clasificación estandarizada en grupos tróficos.

1.2) Describir la variación espacial de la estructura trófica a lo largo del gradiente longitudinal, particularmente entre las tres grandes zonas: Río Uruguay alto, Río Uruguay medio y Río Uruguay bajo (Fig. 4 y 5).

Hipótesis 1. De acuerdo al Concepto de Río Continuo, las características ambientales de los diferentes tramos de los ecosistemas fluviales determinan el ensamble de peces y la estructura trófica que predomina en cada sitio. En particular, el cambio a lo largo del gradiente longitudinal (nacientes-desembocadura) en las condiciones ambientales genera cambios en la disponibilidad de los recursos alimenticios y, por tanto, en los grupos tróficos de peces que dominan tanto en abundancia como en biomasa.

En ese contexto, se predice que, en la región del Río Uruguay alto y medio, debido a la mayor presencia de monte ripario y planicies de inundación (Fig. 5), predominarán aquellos grupos tróficos adaptados al consumo de material de origen terrestre. Por el contrario, en el Río Uruguay bajo, donde el río se ensancha, la velocidad del río disminuye y el flujo turbulento decrece, se espera encontrar grupos tróficos con mayor consumo de productores primarios locales.

2) Evaluar los potenciales efectos generados por las represas sobre la diversidad ecológica de los peces a lo largo del gradiente longitudinal del Río Uruguay. En particular, determinar los cambios sobre: la riqueza de especies, la diversidad beta y sus componentes (anidamiento y recambio de especies), la diversidad trófica (n° de conexiones tróficas) y sobre la diversidad de nicho isotópico, como proxy de nicho ecológico.

Hipótesis 2. Los cambios ambientales a lo largo del gradiente fluvial longitudinal, como el aumento del área del río y la heterogeneidad ambiental, así como también la pendiente menos pronunciada, promueven una mayor diversidad a múltiples niveles. Ésta se expresa en una mayor riqueza taxonómica de especies, mayor diversidad beta (por aumentos en el anidamiento), y mayor diversidad de ítems alimenticios y aumento en el nicho ecológico de los peces. Sin embargo, los cambios físicos generados por las represas (e.g., interrupción del flujo de agua, variación en los flujos de descarga, cambios en flujos de sedimentos y disminución de turbidez aguas abajo), interrumpen el gradiente longitudinal generando disminuciones de la diversidad en sus múltiples dimensiones, debido principalmente a las disminuciones de las fuentes alimenticias.

En particular, se predice que estos cambios promoverán:

1- Menor riqueza de especies de peces de niveles tróficos superiores, ya que son los organismos con mayores requerimientos energéticos.
2- La disminución de la riqueza de especies migradoras aguas abajo, ya que la presencia de barreras impide el flujo de las mismas.
3- Un aumento de la diversidad beta aguas abajo de las represas por aumentos en el componente de reemplazo y una disminución del anidamiento, ya que la fragmentación del hábitat puede resultar en la pérdida de algunas especies y la adición de nuevas especies.
4- Una menor diversidad de ítems consumidos por los peces. Esto se debería a que los cambios en los recursos basales generados por las represas pueden disminuir los recursos disponibles, generando disminuciones en el número de conexiones tróficas.
5- Una disminución del nicho ecológico utilizado por las especies. Esto se debería a que los cambios en las condiciones ambientales pueden resultar en una menor heterogeneidad ambiental y cambios en la disponibilidad de recursos basales, provocando cambios en los hábitats disponibles y disminución de la diversidad de fuentes de alimentación.

3) Evaluar el origen de los recursos (autóctono o alóctono) que subsidian energéticamente la biomasa de los peces a lo largo del gradiente longitudinal del Río Uruguay, evaluando los potenciales efectos generados por las represas ubicadas sobre este río.

Hipótesis 3: En aquellos sitios con alta turbidez y gran ingreso de material del ambiente terrestre circundante los productores primarios experimentan limitaciones para su crecimiento, por lo que se predice que la biomasa de los peces será principalmente subsidiada por carbono de origen alóctono. Por el contrario, las represas incrementan el tiempo de residencia del agua y generan reducciones en su velocidad, además de la retención de sedimentos en las áreas del embalse, reduciendo el transporte de sedimentos aguas abajo y permitiendo una mayor penetración por luz, lo que favorece la acumulación de biomasa de los productores primarios acuáticos.

Como resultado, se predice que, en las regiones aguas debajo de las represas, la contribución a la biomasa de los peces provendrá mayoritariamente de recursos autóctonos.

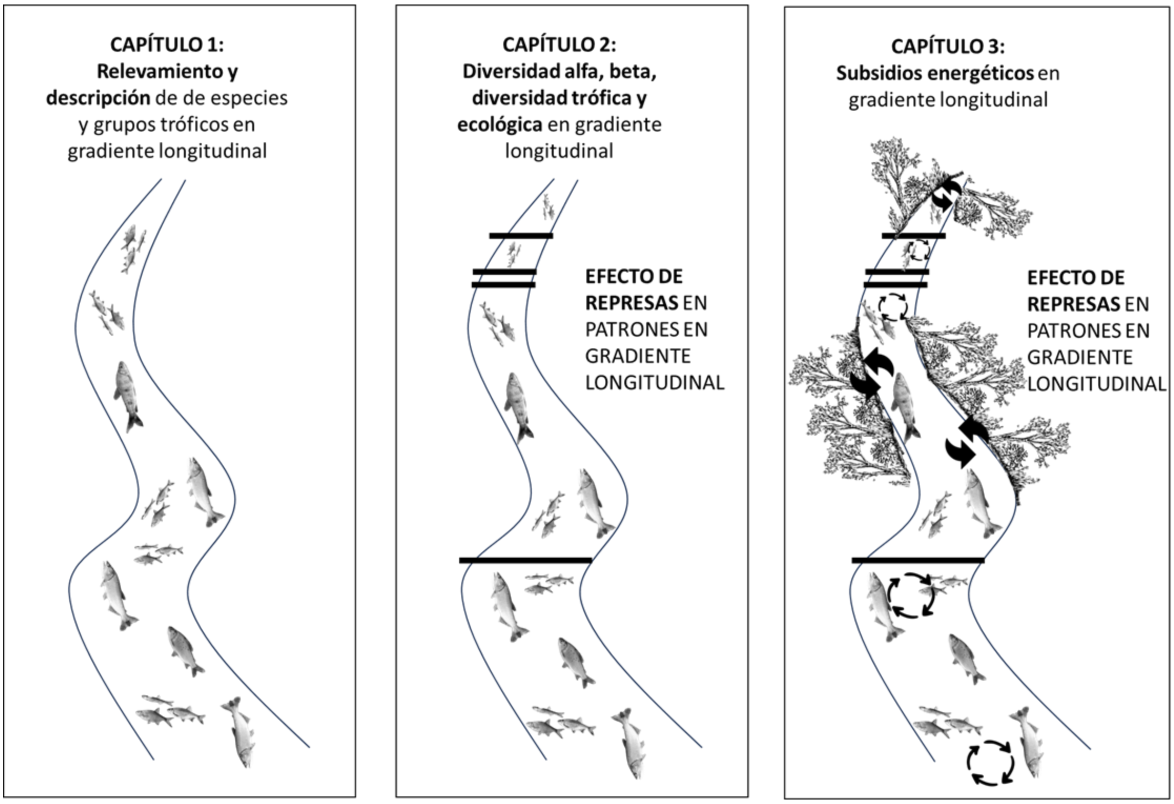


Fig. 3. Resumen gráfico de los objetivos específicos, cada uno de los cuales corresponde a un capítulo de la tesis.

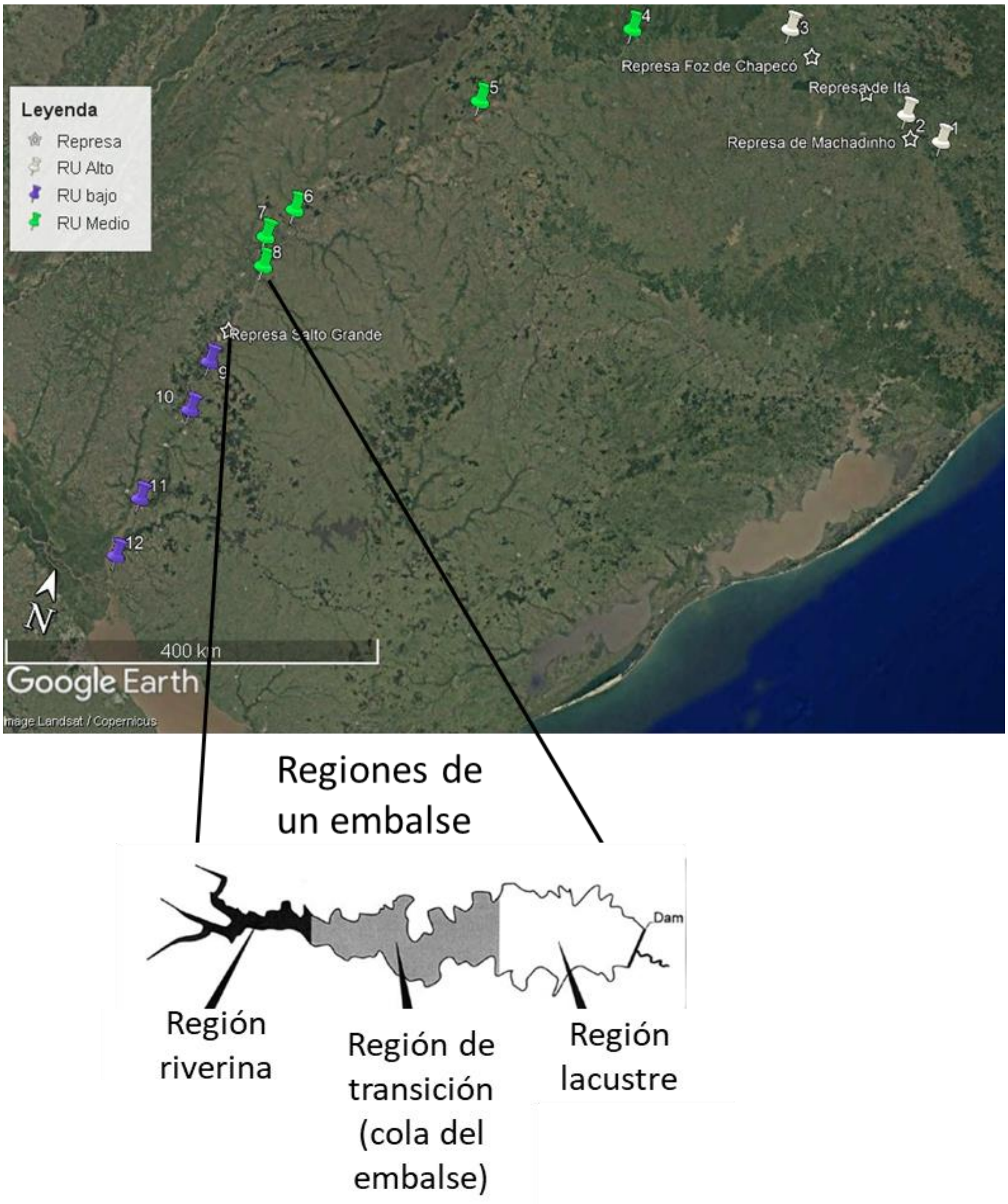


Fig. 4. Ubicación de los 12 sitios de muestreo y de las represas localizadas sobre el Río Uruguay. En blanco: sitios del Río Uruguay Alto; verde: sitios del Río Uruguay Medio; azul: sitios del Río Uruguay bajo. Se muestran las tres zonas en las que se suele dividir de acuerdo a su funcionamiento a los embalses generados por las represas (figura extraída de Thornton et al., 1996), ejemplificadas en el Embalse de Salto Grande.

Fig. 5. Imágenes satelitales de los 12 sitios de muestreo, en las fechas en las que se realizó el muestreo, separados por las tres grandes regiones en las que se divide el Río Uruguay. Los números en el ángulo superior izquierdo de cada figura, corresponden a los números asignados a los sitios de muestreo en el gradiente longitudinal desde las nacientes (sitio 1) a la desembocadura (sitio 12).

## 3. Aproximaciones metodológicas

La tesis se centró en comprender los patrones de diversidad y la distribución de las especies y el ensamblaje de las comunidades, ya que esto resulta fundamental para poder comprender su funcionamiento (Loreau, 2000; Tilman et al., 2014), en condiciones naturales y bajo los efectos de distintas presiones antrópicas y, por tanto, potencialmente para la generación de estrategias de conservación o mitigación de impactos (Baselga et al., 2010; Gutiérrez-Cánova et al., 2013; Socolar et al., 2016).

La tesis se centró en la comunidad de peces como modelo, por su desproporcionada importancia ecológica, social y económica. Para ello, la aproximación seguida fue empírica, mediante la realización de campañas de muestreo para colectar peces y realizar posteriormente análisis de dieta, de nicho ecológico y de sustento energético.

Para el estudio de las redes tróficas acuáticas suelen ser usados los peces ya que ocupan una gran diversidad de nichos tróficos, conectan distintos hábitats en un ecosistema, y son capaces de circular materia y energía desde los recursos basales (autóctonos y alóctonos) hacia niveles superiores de la red (Power, 1990). Los peces poseen la capacidad de desplazarse entre diferentes hábitats y conectar diferentes ecosistemas a través de la búsqueda de refugio, la reproducción, y particularmente la alimentación, por ejemplo, resuspendiendo material del fondo dejándolo disponible en la columna de agua o alimentándose de material terrestre proveniente de las márgenes de los ríos (Power, 1990; Vander Zanden & Vadeboncoeur, 2002).

Existe una amplia variedad de métodos que sirven para estudiar las interacciones tróficas entre los organismos de una comunidad. La combinación de estudios de dieta directa (análisis de contenido estomacal) con análisis de fuentes de asimilación de carbono (C) y nitrógeno (N) (a través de análisis de isótopos estables) permite una buena resolución y por tanto una comprensión más completa de las interacciones tróficas (Post, 2002).

El estudio de dieta permite generar información sobre los hábitos alimenticios de las especies, lo que ayuda a la comprensión más extensa del funcionamiento de los ecosistemas (Woodward et al., 2009). Asimismo, el análisis de la dieta de los peces permite la clasificación en grupos funcionales y tróficos, información que resulta clave para comprender la estructura trófica de las comunidades y sus variaciones espacio-temporales (González-Bergonzoni et al., 2012).

Por otra parte, los análisis de isótopos estables de Carbono y Nitrógeno pueden tener importantes aplicaciones a estudios de flujos energéticos dentro de las redes tróficas (Post, 2002; Layman et al., 2007a) y para comprender el nicho ecológico de las especies, usando como proxy al nicho isotópico (Newsome et al., 2007). Los análisis de isótopos estables se basan en el hecho de que la proporción entre los isótopos estables de C y N en los tejidos de los consumidores refleja la proporción de esos isótopos en los tejidos de las principales presas consumidas (Fry, 2006; Layman et al., 2012).

Por lo tanto, mediante la utilización de herramientas estadísticas robustas como los modelos de mezcla isotópica bayesianos, se puede llegar a estimar la proporción de la biomasa de consumidores subsidiada por los diferentes recursos basales (Parnell et al., 2013) a partir de las señales isotópicas en los tejidos de los consumidores y de todas las potenciales presas, corregida por el fraccionamiento trófico correspondiente (cambio predecible en la señal isotópica que ocurre en cada paso de asimilación, e.g., Post, 2002; Bunn et al., 2013). Además, a partir del nicho isotópico de cada especie y mediante el uso de herramientas estadísticas de modelos bayesianos de nicho isotópico (e.g., métricas de Layman y área de elipses) se pueden estimar métricas de nicho trófico como lo son: diversidad de fuentes de C y N consumidas y diversidad trófica (e.g., Jackson et al., 2011; Layman et al., 2012). En este sentido, la variabilidad en el nicho isotópico de los organismos releja la variabilidad en los recursos asimilados (Newsome et al., 2007).

Para cumplir con todos los objetivos, se realizó un muestreo de peces en 14 sitios a lo largo del gradiente longitudinal del Río Uruguay (3 sitios en el Río Uruguay Alto, 5 en el Río Uruguay Medio y 6 en el Río Uruguay Bajo). Se tomaron muestras de músculo de peces y potenciales fuentes alimenticias para el análisis de isótopos estables de Carbono y Nitrógeno. Lamentablemente, las muestras de isótopos estables de dos de los sitios del Río Uruguay bajo se perdieron al momento del procesamiento, por lo que los análisis de isótopos se realizaron en un total de 12 sitios. Igualmente, es importante resaltar que las muestras que se perdieron correspondían a dos sitios ubicados muy próximos a los sitios 10 y 11, por lo que consideramos que la pérdida de esas muestras no compromete nuestros resultados.

En todos los sitios se realizó la identificación de las especies presentes, evaluando la riqueza de especies (diversidad alfa).

Para cumplir el objetivo 1, la clasificación en grupos tróficos se realizó a través de análisis de contenido estomacal de 15 individuos por especie por sitio (considerando amplio rango de tallas). Para esta clasificación, se agrupó la información de dieta de cada individuo perteneciente a una especie de los diferentes sitios en los que estuvo presente. Finalmente se calculó la abundancia relativa, biomasa y riqueza de especies de cada grupo trófico en cada una de las tres secciones del río (Capítulo 1-Artículo 1: López-Rodríguez et al., 2019).

Para el objetivo 2, basados en la información de diversidad alfa, se calculó la diversidad beta (total, reemplazo de especies y anidamiento) a lo largo del gradiente longitudinal y entre sitios continuos. A partir del análisis de contenido estomacal (Capítulo 1, López-Rodríguez et al., 2019), se realizaron matrices de dieta para reconstruir las tramas tróficas en cada sitio de muestreo, calculando métricas de diversidad trófica (i.e., número de conexiones tróficas).

Se realizó también el cálculo de nicho isotópico a través de modelos Bayesianos y se utilizó el área de elipse corregida por el tamaño de muestra (SEAc) como indicador de nicho ecológico de los peces. Se ajustaron modelos de regresión lineal entre la riqueza de especies, la diversidad beta (y sus componentes) y la diversidad trófica (número de conexiones) con la posición de cada sitio en el gradiente longitudinal.

Finalmente, para el análisis del nicho ecológico testeamos en el marco bayesiano la probabilidad de que el SEAc fuera mayor en un sitio que en otro (comparando sitios de interés; i.e., pre-post represa) (Capítulo 2- López-Rodríguez et al., 2024).

Para el objetivo 3, a partir de la clasificación en grupos tróficos del Capítulo 1 y la información de las señales isotópicas de Carbono y Nitrógeno de las especies de peces y de los recursos basales, se determinó la contribución de los recursos basales a la biomasa de los peces de cada uno de los grupos tróficos en cada uno de los 12 sitios de muestreo. Se calculó la contribución relativa de los recursos basales (autóctonos y alóctonos) a la biomasa de los peces de dos formas: la contribución de los recursos a la biomasa de los peces y la contribución media de cada recurso basal a la biomasa de las especies pesada por la biomasa de cada especie en cada sitio de muestreo. Se realizaron regresiones lineales entre la contribución media de los recursos por sitio y la contribución pesada por la biomasa con las distancias a las nacientes para evaluar patrones en el gradiente longitudinal. Por otra parte, para evaluar potenciales efectos de las represas se realizaron GLM comparando la contribución media de los recursos autóctonos a la biomasa de los peces entre los sitios pre y post represa (Capítulo 3- López-Rodríguez et al. in prep).

# 4. Artículo 1

water

MDPI

Article

## Diets and Trophic Structure of Fish Assemblages in a Large and Unexplored Subtropical River: The Uruguay River

**Anahí López-Rodríguez [1,2,3,*], Ivana Silva [2,3], Sunshine de Ávila-Simas [4], Samanta Stebniki [1], Rodrigo Bastian [5], Marthoni Vinicius Massaro [5], Joaquin Pais [2,3], Giancarlo Tesitore [1], Franco Teixeira de Mello [1], Alejandro D'Anatro [2], Nicolas Vidal [1,2], Mariana Meerhoff [1], David A. Reynalte-Tataje [5], Evoy Zaniboni-Filho [4] and Iván González-Bergonzoni [3,6,*]**

- [1] Departamento de Ecología y Gestión Ambiental, CURE, Universidad de la República, Tacuarembó s/n, 20000 Maldonado, Uruguay
- [2] Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Iguá 4225, Malvín Norte, 11400 Montevideo, Uruguay
- [3] Departamento de Ecología y Biología Evolutiva, Instituto de Investigaciones Biológicas Clemente Estable, 11600 Montevideo, Uruguay
- [4] Laboratório de Biologia e Cultivo de Peixes de Água Doce (LAPAD), Departamento de Aquicultura, Universidade Federal de Santa Catarina (UFSC), 88066-260 Florianópolis, SC, Brazil
- [5] Campus Cerro Largo, Universidade Federal da Fronteira Sul, Av. Jacob Reinaldo Haupenthal, 1580, 97900-000 Cerro Largo, RS, Brazil
- [6] Departamento del Agua, CENUR Litoral Norte Universidad de la República, Ruta 3 Km 363, 60000 Paysandú, Uruguay
- * Correspondence: alopez@fcien.edu.uy (A.L.-R.); ivg@fcien.edu.uy (I.G.-B.)

Received: 11 April 2019; Accepted: 28 June 2019; Published: 4 July 2019

check for updates

**Abstract:** The Neotropics represent a hotspot for freshwater biodiversity with vast number of fish species of scarce ecological knowledge. This holds true for the Uruguay River, where fish assemblages and their diets remain unexplored. Fish assemblages were surveyed in 14 sites along the river main course, from headwaters to mouth (approximately 1800 km), with the aim to identify the trophic roles of fishes and to describe trophic structure of these assemblages, following standardized sampling campaigns and laboratory procedures. One hundred species (2309 gut contents) were analysed and classified into four trophic groups subdivided into eight lower-level groups: Piscivore, piscivore-invertivore, detritivore, omnivore-detritivore, omnivore-invertivore, omnivore-planktivore and omnivore-herbivore. The trophic structure of the assemblages varied along the river, with the relative species richness of fish consuming terrestrial invertebrates increasing towards the middle river section, probably driven by the large floodplains in that areas, supporting global theories such as the flood pulse concept. This study describes the feeding habits of fish along the Uruguay River, being the first dietary description for 29 species. This knowledge is essential for management and conservation, serving as baseline in the context of future environmental changes while generating novel evidence on the functioning of ecosystems in this scarcely studied climatic region.

**Keywords:** trophic groups; Uruguay River fish; feeding habits; trophic guilds; fish feeding ecology

---

### 1. Introduction

The knowledge about trophic structure of communities is essential to understand some of the main relationships among species in ecosystems [1–3]. Information of the feeding habits of species permits a holistic understanding of ecosystem functioning [4]. In aquatic ecosystems, fish are used to describe food webs since they occupy a great diversity of trophic niches and circulate matter and energy from basal resources to the highest levels of the web [5,6]. They are also capable to move between different habitats within the water body and even connect different ecosystems through feeding interactions, for example by feeding on allochthonous material from the riverbanks and riparian zones [5–7] or by migrating between rivers and the sea. The analysis of fish diets is also important to better understand the behaviour of the species [8,9]. Large-scale trophic groups' classification is the basis to understand the trophic structure of assemblages and their natural spatial or temporal variability (e.g., [10,11]). In fluvial ecosystems, longitudinal gradients in fish assemblage trophic structure are often found, where the relative importance of different trophic groups shifts from headwaters to mouth, possibly following changes in energy availability and habitat structure (e.g., [12–17]). Some evidence suggests that the trophic structure of the fish assemblages changes from dominance of small compressed-bodied benthivorous fishes in headwaters towards higher importance of omnivores-herbivores, planktivorous and piscivorous strategists in the lower sections [12–15]. However, most of this evidence comes from streams and low order river ecosystems (e.g., river orders 1–5), but longitudinal patterns in fish trophic structure in large river ecosystems remain largely unexplored.

Moreover, most of the theories that aim to explain river functioning have been generated in temperate regions of the northern hemisphere. Despite that the Neotropical region represents one of the largest hotspots for freshwater fish biodiversity [18,19], the functioning of its riverine ecosystems and the biology of the vast majority of the species remains understudied [20,21]. Besides, while most Neotropical fish assemblage studies focus on tropical and subtropical rivers, with marked flow seasonality (e.g., Amazonas River, Parana River, Orinoco River [22–25]), less research effort has been made in large irregular flow rivers of southern subtropical areas (see [26–28]). Particularly within the La Plata River basin, most studies describing aspects of fish biology focused on the large Parana River (e.g., [29–31]) while its smaller tributary—a 1800 km long and 6000 $m^3/s$ river bearing at least 10 species of long-distance migratory fish of commercial importance—the irregular-flow subtropical Uruguay River remains largely unstudied in its total extension [32]. Research on this region is highly necessary given that, as most freshwaters in South America, it faces a growing biodiversity loss rate [19,29,33].

The knowledge about South America's fish assemblages is based almost exclusively on taxonomical records and species distribution analyses [19,34]. The scarce information available for the Uruguay River is not the exception, consisting mostly on scientific notes reporting length-weight relationships [10,35], or new records of a few rare species [36,37]. Moreover, most fish ecology research made in the Uruguay River has been focused on few commercially important migratory species such as sabalo (*Prochilodus lineatus*), boga (*Megaleporinus obtusidens*) and dorado (*Salminus brasilinsis*) (e.g., [26,38]). Most of these migratory species migrate between Paraná, Río de la Plata and Uruguay Rivers to use different feeding and reproduction grounds along the fluvial gradient; but several local species exist along the river as well [26]. Regarding fish trophic ecology, and to the extent of our knowledge, only few studies describing the diet of limited key species exist (e.g., [39–42]).

The objective of this study was to report the fish species present in the Uruguay River, describing their diets with the aim of reaching a standardized and objective classification in trophic groups. Furthermore, this study was also aimed to describe the spatial variation in the trophic structure of assemblages from upper to lower river sections, facilitating the comprehension of the structure and functioning of the unstudied fish assemblages in this large subtropical river serving as baseline information for management purposes.

## 2. Materials and Methods

### 2.1. Study Area and Fish Sampling

This research was conducted in the Uruguay River, the second largest tributary of the La Plata River drainage basin. This river rises at the confluence of the Pelotas River and the Canoas River in Brazil, and extends for 1800 km to its mouth in the La Plata estuary shared between Uruguay and

Argentina [43]. The drainage basin covers three countries: Brazil, Argentina and Uruguay, with the largest area in the states of Santa Catarina and Rio Grande do Sul, Brazil [44]. According to geological characteristics, the Uruguay River could be divided into three main regions; upper, middle and lower sections. The Yucuma Falls in Brazil represent the division between the upper and middle section, while the Salto Grande Dam (Uruguay) divides the middle from the lower section of the river [45]. The hydrology of the Uruguay River is determined by the precipitation patterns in the upper two-thirds of the catchment (upper and middle sections) and, as opposite to the Parana River, does not show a seasonal pattern in flow, being highly irregular [46]. The hydrological conditions differ between the three sections, with a steeper slope and faster current velocities in the upper than in the middle section. On the other hand, the river flow in the lower section is constrained by the hydroelectric dam of Salto Grande [26]. The dominant substrates in the upper and middle region of the river are typically hard rocks, whereas in the lower section, sandstone substrate prevails [43]. In all the extension of the Uruguay River four hydroelectric dams were built (three in the upper section, and one in the lower section). The middle section remains largely hydrologically undisturbed.

Fish samplings were performed during austral autumn of 2017 (May–early June) in 14 sites of the main course of Uruguay River, from its headwaters (States of Santa Catarina and Rio Grande do Sul, Brazil) to the mouth (Colonia, Uruguay). Three locations were sampled in the upper river section, five in the middle section, and six in the lower section (Figure 1, Tables S1 and S2). Sampling locations were chosen considering available monitoring programs along the river easing logistics for this study. At all sites, littoral habitats of depths from 1–4 m were sampled to cover for a similar range of environmental variability in each area. In large river ecosystems, littoral areas usually host the highest biodiversity. Furthermore, the autumn season was chosen to sample because during that season, a higher diversity of fish size ranges might be expected as the spawning of most species of the region usually occur in spring-summer and then, both juvenile and adults of most species could be collected during autumn.

In the middle and lower sections of the river, fish collections were carried out using multi-mesh Nordic gillnets. In each site, four sets of benthic gillnets were placed in the littoral zone (1.5–2.0 m deep areas at 50–100 m away from the shore) and four in a deeper zone (2–5.0 m deep) about 500 m away from the shoreline. Each Nordic gillnet was 30 m long by 1.5 m high and were composed of 12 mesh sizes (5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0, and 55 mm knot to knot). Gillnets were set from sunset to sunrise (c.a. 12 h). The same sampling effort was performed in each site. Fish sampling and handling procedures were approved by the Honorary Commission of Animal Experimentation (CHEA) in Uruguay (Permit ID 309).

In the upper river section, due to a different standardization of the ongoing monitoring programs subsidizing this study, a set of gill and trammel nets were used, with mesh sizes ranging from 15.0 to 80.0 mm knot to knot, instead of Nordic gillnets. However, time of net set was comparable as net were also set overnight. Gillnets ranged from 20 to 120 m in length and from 1.6 to 8.0 m in height; while trammel nets varied between 30 to 40 m in length with 1.8 m height. Both set of nets were placed in the littoral zone in the evening and removed in the following morning, being set for approximately 12 h. At each site, additional sampling was performed with seine nets and cast nets (both with mesh size of 8.0 mm) in the littoral zone.

In addition to our own sampling campaigns, some commercially important large fish specimens were also obtained from local fishermen in the middle and lower sections of the river, as to complete the sampling wherever these species (known to be present along all the river) were not captured. Furthermore, to complement the diet description of some rare species (i.e., with less than five individuals collected during sampling) gut content data from two previous sampling campaigns arrayed in spring 2014 and autumn 2016 in the lower section of Uruguay River was used (Table S1).

In the field, fishes were identified to the lowest taxonomic level possible (i.e., species level in most cases), measured (total and standard length in cm) and weighed (total fresh biomass in g). For the gut content analysis, the stomach and intestines of 15 individuals per species and site, considering a wide size range (or all individuals obtained, when <15 were caught) were removed and preserved in 10%

formalin for posterior laboratory analysis. A previous study in Uruguayan streams using prey species accumulation curves has established that 15 individuals usually suffice to represent well the richness of diet items [47]. Individuals were selected to cover all length classes obtained at each site (Table S1).

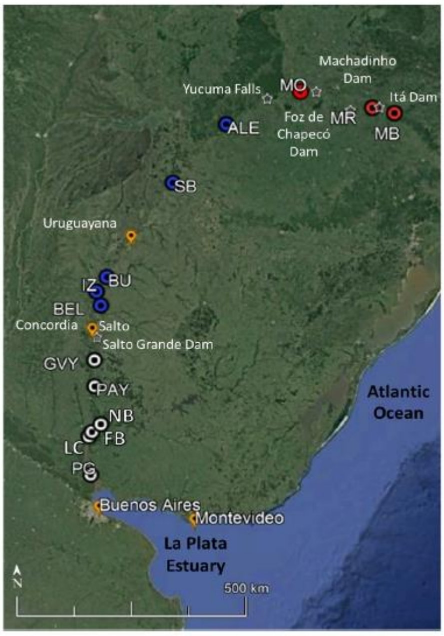


**Figure 1.** Location of the 14 sampling sites of the Uruguay River. The Uruguay River sampling sites are coloured according to the different sections; red: Upper; blue: Middle, and white: Lower. MB: Barracão, at the confluence of Canoas River and Pelotas River; MR: Marcelino Ramos; MO: Mondaí; Ale: Alecrim; SB: São Borja; BU: Bella Unión; IZ: Isla del Zapallo island; Bel: Belén; GVY: Guaviyú; Pays: Paysandú; NB: Nuevo Berlín; FB: Fray Bentos; LC: Las Cañas, and PG: Punta Gorda, at the mouth of the Uruguay River. Major towns (orange) and waterfalls and dams (white star) are represented in the figure.

Gut content analysis (GCA) was performed in the laboratory. The occurring food items were classified broadly into eight item types as follows: Detritus, plankton (zooplankton and phytoplankton), periphyton (diatoms and filamentous algae), aquatic macroinvertebrates (insects, molluscs, and macrocrustaceans), terrestrial macroinvertebrates (terrestrial insects and arachnids), fish remains (entire fish, scales, fins and fish remains) aquatic macrophytes, and terrestrial vegetal matter (seeds, fruits and vegetal tissues). Zooplankton and phytoplankton were pooled because phytoplankton was only present in few individuals along with large amounts of zooplankton. The absolute volume of each food item was measured using standardized Hyslop's indirect volumetric method. With this information, the relative contribution of each food item type to the diet of individuals was calculated [48].

The frequency of occurrence was calculated as the number of occurrences of a food item in the guts of a given species divided by the total number of individuals analysed. Then, the Index of Relative Importance (IRI) of each item for each species was calculated, considering the unit volume of food items weighted by its frequency of occurrence and expressed as percentage [49]:

$$\mathrm{IRI} = (\mathrm{Vi} \times \mathrm{Fi}) / \left(\sum \mathrm{Vi} \times \mathrm{Fi}\right) \times 100$$

where: Vi = volume of the food item i and Fi = frequency of occurrence of the food item i. Data from empty guts and those that only had indeterminate prey items were excluded from the analysis.

For the trophic classification of species, data from each individual belonging to a species from the different river sections was pooled. This procedure was applied in order to obtain a broader view of diet plasticity and to minimize the potential effect of the short time scale and the strong habitat specificity typically considered by GCA [50]. This procedure was followed to use variability in space along the whole river as a proxy of the potential variability across time and different habitat scenarios for a given species. For the classification purpose, the term "omnivores" was used to define species feeding at contrasting trophic levels, such as primary producers and consumers of any kind. This is a pragmatic use of the definition that allows a rather conservative but unequivocal visualization of this feeding strategy [11], but acknowledging that omnivores are strictly those feeding on more than one trophic level [51,52].

### 2.2. Data Analysis

Fish species were grouped and diets were compared using a cluster analysis, following the Bray–Curtis ordination method and Euclidian distance as an index of dissimilitude. This kind of group analysis is commonly used in studies of trophic ecology (e.g., [53]). To complement the cluster analysis, the data was visualized in a principal component analysis (PCA). To test for significant differences in the diet composition between the groups that emerged from the cluster analysis, a non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA; Bray Curtis index; with 999 random permutations) was performed [54]. PCA analysis and the PERMANOVA test without data from detritivore and piscivore fish groups were also run to better visualize and classify the omnivore fish groups. A special focus on this group was made because of the known high relative richness of omnivore species in subtropical and tropical systems [11]. All the statistical analyses were conducted using the free statistical software PAST and the "vegan" package in R (R Development Core Team [55]).

Afterwards, the relative biomass, abundance and species richness of each trophic group was estimated for each sampled site within each river section. In this way, an aim to describe potential changes in trophic structure of assemblages between the upper, middle and lower river sections was made. The relative abundance, biomass and species richness data was used instead of total numbers, to avoid a potential bias given by the slightly different sampling methodologies (different distribution of net mesh sizes) displayed in the upper river section. To analyze potential changes in trophic structure between these sections we performed PERMANOVA tests ($\alpha = 0.05$; Bonferroni-corrected P-values), using metrics for each trophic groups as response variables (i.e., relative biomass, relative abundance, and relative species richness), and the sampling sites within a river section as a replicates. Furthermore, changes in the relative biomass, abundance and species richness of each particular trophic group among river section were tested using Analysis of Variance (One way ANOVA) or Kruskall Wallis, depending on the accomplishments of data homoscedasticity and normality.

To compare the generality of the results, a bibliographic review of dietary descriptions for the same species in other locations was performed using the Google Scholar search engine. For the dietary review of each species, the terms "species name" + "feeding" + "diet" were used as keywords, and we considered the first ten results obtained. This information can help identify the diet plasticity of many species and also the gaps of information for certain species (Table 1).

## 3. Results

One hundred species were recorded in the main course of Uruguay River belonging to nine orders, with the Characiformes and Siluriformes being the most represented (42% and 41% of all the species, respectively) (Table S1). Most were native species, with the record of only one exotic species (*Oreochromis niloticus,* Nile tilapia) collected in the upper river section (Table 1).

From a total of 2309 stomachs analysed, 1890 (82%) were used in the feeding groups classification. The remaining stomachs were empty or with indeterminate dietary content.

**Table 1.** Diet and trophic classification of fish species sampled along a longitudinal gradient in Uruguay River. The values for each dietary item type in each species represent the index of relative importance, which combines the frequency of occurrence and the relative volume of each dietary item to describe the diet of a species. For n and size ranges analysed see Table S2. Previous trophic classification of species for other systems surveyed from literature is shown in the last column and in References Table 1. NA = No data available. The species with * have not been grouped due to unique dietary characteristics.

| Trophic Group | Fish Species | Entire Fish & Fish Remains | Aquatic Invertebrates | Terrestrial Arthropods | Detritus | Aquatic Macrophytes | Terrestrial Plant Remains | Periphyton | Plankton | Trophic Groups in Literature |
|---|---|---|---|---|---|---|---|---|---|---|
| Piscivore | *Ageneiosus militaris* | 0.842 | 0.04 | 0.106 | 0.01 | <0.001 | <0.001 | <0.001 | 0 | Piscivore [42] |
| | *Acestrorhynchus. pantaneiro* | 0.999 | <0.001 | <0.001 | 0 | 0 | <0.001 | 0 | 0 | Carnivore [42]/Piscivore [41,56,57] |
| | *Cynopotamus argenteus* | 0.995 | <0.001 | 0.001 | 0 | <0.001 | 0.003 | 0 | <0.001 | Piscivore [42] |
| | *Catathyridium jenynsi* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | NA |
| | *Cynopotamus kincaidi* | 0.999 | 0.001 | 0 | 0 | 0 | 0 | 0 | 0 | Piscivore [58] |
| | *Crenicichla scotti* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Benthi-piscivore [47] |
| | *Crenicichla vittata* | 0.999 | 0 | 0.002 | 0 | 0 | <0.001 | 0 | 0 | Piscivore [59] |
| | *Galeocharax humeralis* | 0.987 | 0.002 | 0.001 | 0 | 0.003 | 0.006 | 0 | 0 | Piscivore [60] |
| | *Hoplias lacerdae* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | NA |
| | *Hoplias malabaricus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Carnivore-piscivore [61,62]/Piscivore [63–65]/Carcinophagous [66] |
| | *Lycengraulis grossidens* | 0.854 | 0.013 | 0.01 | 0.004 | 0 | 0.094 | 0 | 0.025 | Piscivore [67]/Carnivore-Piscivore [68] |
| | *Luciopimelodus pati* | 0.923 | 0.008 | 0.06 | 0 | 0 | 0.005 | 0 | 0.005 | NA |
| | *Oligosarcus jenynsii* | 0.788 | 0 | 0.209 | 0 | 0 | 0.003 | 0 | <0.001 | Carnivore-Piscivore [69–72]/Piscivore [73] |
| Piscivore | *Oligosarcus oligolepis* | 0.98 | 0 | 0.02 | 0 | 0 | 0 | 0 | 0 | Omnivore-Benthivore [74] |
| | *Pellona flavipinnis* | 0.936 | 0.064 | 0 | 0 | 0 | 0 | 0 | 0 | Piscivore [60]/Carnivore-Piscivore [75]/Carnivore [76] |
| | *Pseudopimelodus mangurus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | NA |
| | *Pygocentrus nattereri* | 0.831 | 0 | 0 | 0 | 0 | 0.169 | 0 | 0 | Piscivore [60,77,78] |
| | *Parastegophilus sp.* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | NA |
| | *Roeboides affinis* | 0.922 | 0.06 | 0.016 | 0 | 0 | 0.003 | 0 | 0 | Lepidophagous-invertivore [60]/Lepidophagous [79] |
| | *Roeboides microlepis* | 0.786 | 0.002 | 0.02 | 0.023 | 0 | 0.17 | 0 | 0 | Piscivore [60,80] |
| | *Raphiodon vulpinnus* | 0.987 | 0.005 | 0.007 | 0 | 0 | 0 | 0 | 0 | Opportunistic piscivore [42]/Piscivore [64,81] |
| | *Salminus brasliensis* | 0.912 | 0.005 | 0 | 0 | 0 | 0.075 | 0.007 | 0 | Piscivore [60,81]/Carnivore-piscivore [82] |
| | *Serrasalmus maculatus* | 0.984 | 0.002 | 0 | <0.001 | 0 | 0.013 | 0 | 0 | Omni-piscivore [77] |

**Table 1.** *Cont.*

| Trophic Group | Fish Species | Entire Fish & Fish Remains | Aquatic Invertebrates | Terrestrial Arthropods | Detritus | Aquatic Macrophytes | Terrestrial Plant Remains | Periphyton | Plankton | Trophic Groups in Literature |
|---|---|---|---|---|---|---|---|---|---|---|
| **Piscivore-invertivore** | *Ageneiosus inermis* | 0.59 | 0.401 | 0 | 0 | 0.009 | 0 | 0 | 0 | Carnivore-insectivore [83] |
| | *Gymnotus sp.* | 0.417 | 0.167 | 0.417 | 0 | 0 | 0 | 0 | 0 | Insectivore [84] |
| | *Megalonema platanum* | 0.562 | 0.009 | 0.397 | 0.032 | 0 | 0 | 0 | 0 | NA |
| | *Potamotrygon brachyura* | 0.6 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | NA |
| | *Pimelodella gracilis* | 0.144 | 0.196 | 0.148 | 0.295 | <0.001 | 0.203 | 0.011 | 0.003 | Omni-pisicvore [81]/Carnivore [85]/Omnivore [86]/Insectivore (Aq) [87] |
| **Piscivore-invertivore** | *Pimelodus maculatus* | 0.293 | 0.352 | 0.076 | 0.065 | 0.011 | 0.203 | 0 | <0.001 | Piscivore [60]/Omni-piscivore [88,89]/Omnivore [90] |
| | *Pseudobuonocephalus sp.* | 0.572 | 0.249 | 0 | 0 | 0 | 0.179 | 0 | <0.001 | NA |
| | *Rhamdia quelen* | 0.294 | 0.323 | 0.007 | 0.304 | 0 | 0.072 | 0 | 0 | Carnivore [66]/Carnivore-piscivore [91] |
| | *Sorubim lima* | 0.405 | 0.595 | 0 | 0 | 0 | 0 | 0 | 0 | Piscivore [92] |
| **Detritivore** | *Cyphocharax platanus* | 0 | <0.001 | 0 | 0.999 | 0.001 | <0.001 | 0 | <0.001 | NA |
| | *Cyphocharax saladensis* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | Detritivore [93]/Iliophagus [94] |
| | *Cyphocharax spilotus* | 0 | 0.012 | 0 | 0.987 | 0 | 0.001 | 0 | 0 | Detritivore [95] |
| | *Cyphocharax voga* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | Detritivore-Algivore [62]/Detritivore [93,96]/Iliophagus [97] |
| | *Hypostomus aspilogaster* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | NA |
| | *Hypostomus commersoni* | 0 | 0.001 | 0 | 0.995 | 0 | 0.004 | 0 | 0 | Detritivore-alguivore [62]/Iliophagous [98]/Periphyton-feeder-detritivore [99] |
| | *Hypostomus isbrueckeri* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | NA |
| | *Hypostomus laplatae* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | NA |
| | *Hypostomus luteomaculatus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | Detritivore [84]/Detritivore-algivore [100,101] |
| | *Hypostomus roseopunctatus* | 0 | 0 | 0 | 0.999 | 0 | <0.001 | 0 | 0 | NA |
| | *Hypostomus uruguayensis* | 0 | 0 | 0 | 0.977 | 0 | 0 | 0.016 | 0.007 | NA |
| | *Loricariichthys melanochelius* | 0 | 0.028 | <0.001 | 0.923 | 0 | 0.042 | <0.001 | 0.008 | Omnivore [102] |

**Table 1.** *Cont.*

| Trophic Group | Fish Species | Entire Fish & Fish Remains | Aquatic Invertebrates | Terrestrial Arthropods | Detritus | Aquatic Macrophytes | Terrestrial Plant Remains | Periphyton | Plankton | Trophic Groups in Literature |
|---|---|---|---|---|---|---|---|---|---|---|
| **Detritivore** | *Loricariichthys platymetopon* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | Detritivore [103,104] |
| | *Oreochromis niloticus* | 0.013 | 0 | 0.014 | 0.908 | 0 | 0.064 | <0.001 | 0 | Omnivore [105] |
| | *Prochilodus lineatus* | <0.001 | <0.001 | <0.001 | 0.971 | 0 | 0.028 | 0 | <0.001 | Detritivore [60]/Iliophagous [103,104] |
| | *Potamorhina squamoralevis* | 0 | 0 | 0 | 0.998 | 0 | 0 | 0 | 0.002 | Detritivore [60,106] |
| | *Rineloricaria parva* | 0 | 0.003 | 0 | 0.997 | 0 | 0 | 0 | 0 | Detritivore [107] |
| | *Steindachnerina brevipinna* | 0 | <0.001 | 0 | 0.999 | 0 | <0.001 | 0 | 0 | Detritivore [108,109] |
| | *Steindachnerina insculpta* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | Iliophagous [103] |
| **Omnivore-detritivore** | *Apareiodon affinis* | <0.001 | 0.013 | <0.001 | 0.78 | <0.001 | 0.057 | 0.149 | <0.001 | Omnivore-detritivore [81]/Algivore [110,111] |
| | *Characidium tenue* | 0 | 0.023 | 0.276 | 0.69 | 0 | 0.011 | 0 | 0 | NA |
| | *Iheringichthys labrosus* | 0.004 | 0.266 | 0.006 | 0.650 | 0.006 | 0.053 | 0.001 | 0.014 | Benthivore [40,103,112,113] /Necto-benthonic-insectivore [114]/Invertivore [115] |
| | *Loricariichthys anus* | 0 | 0.201 | 0 | 0.779 | 0 | 0.019 | 0.001 | 0 | Detritivore [95] |
| | *Pimelodella australis* | 0.05 | 0.112 | 0.025 | 0.705 | 0 | 0.107 | 0 | 0 | Benthi-herbivore [74] |
| | *Rhinodoras dorbygni* | 0.005 | 0.201 | 0.012 | 0.632 | 0.004 | 0.145 | <0.001 | <0.001 | NA |
| **Omnivore-Invertivore (Aq)** | *Brochyloricaria chauliodon* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | Carnivore (mollusk consumer) [116] |
| | *Bryconamericus iheringii* | 0.004 | 0.568 | 0 | 0.011 | 0 | 0.417 | 0 | 0 | Omnivore-herbivore [47]/Omnivore [62]/Benthophagus-omnivore [73]/Benthivore [117] |

**Table 1.** *Cont.*

| Trophic Group | Fish Species | Entire Fish & Fish Remains | Aquatic Invertebrates | Terrestrial Arthropods | Detritus | Aquatic Macrophytes | Terrestrial Plant Remains | Periphyton | Plankton | Trophic Groups in Literature |
|---|---|---|---|---|---|---|---|---|---|---|
| **Omnivore-planktivore** | *Hoplosternum littorale* | 0 | 0.436 | 0.007 | 0 | 0 | 0.028 | 0 | 0.529 | Omnivore-planktivore [144]/Scavengers [145] |
| | *Loricariichthys edentatus* | 0 | 0.214 | <0.001 | 0.024 | 0 | 0.008 | 0 | 0.754 | NA |
| | *Odontostilbe pequira* | 0 | 0.009 | 0.009 | 0 | 0 | 0.074 | 0 | 0.907 | Omnivore [146,147]/Benthivore [148]/Herbivore [149] |
| **Omnivore-Herbivore (Terr)** | *Platanichthys platana* | 0 | 0 | 0 | 0 | 0 | 0.024 | 0 | 0.976 | Microphagus-carnivore [150]/Omnivore [151] |
| | *Parapimelodus valenciennis* | <0.001 | 0.027 | 0.049 | 0.219 | 0.007 | 0.057 | <0.001 | 0.640 | NA |
| | *Astyanax lacustris* | 0.002 | 0.013 | 0.148 | 0.001 | 0.001 | 0.836 | <0.001 | <0.001 | Omnivore (terrestrial vegetation) [73]/Omnivore-herbivore [95]/Omnivore [152] |
| | *Astyanax obscurus* | 0.017 | 0.197 | 0.393 | 0 | 0 | 0.393 | 0 | 0 | Invertivore (Terr.) [73] |
| | *Astyanax spp. aff fasciatus* | 0.002 | 0.078 | 0.337 | 0.005 | 0.072 | 0.501 | 0.006 | <0.001 | Omnivore-herbivore [95]/Omnivore [138,153,154]/Zooplanktivore [155]/Omnivore-zooplanktivore [156] |
| | *Brycon orbignyanus* | 0.001 | <0.001 | 0.095 | 0 | 0 | 0.903 | 0 | 0 | NA |
| | *Geophagus brasiliensis* | 0 | 0 | 0 | 0.225 | 0 | 0.775 | 0 | 0 | Insectivore [66]/Omnivore [95,157–159]/Invertivore [95] |
| | *Pimelodus albicans* | 0.117 | 0.016 | 0.397 | 0.002 | 0 | 0.468 | 0 | 0 | NA |
| | *Pterodoras granulosus* | 0.002 | 0.003 | 0 | 0.190 | 0.176 | 0.628 | 0 | 0 | Herbivore [60]/Omnivore-Invertivore [160]/Omnivore [39,161] |
| | *Schizodon nasutus* | 0 | 0.001 | 0 | <0.001 | 0.024 | 0.975 | 0 | 0 | Herbivore [68,114,162,163] |
| | *Trachyelopterus teaguei* | 0.050 | 0.005 | 0.258 | 0.003 | 0 | 0.685 | 0 | 0 | NA |
| | * *Schizodon platae* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | Herbivore [164] |
| | * *Otocinclus arnoldi* | 0 | 0 | 0 | 0.222 | 0 | 0 | 0.778 | 0 | NA |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Pseudocorynopoma doriae* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | Insectivore [62,140]/Generalist insectivore [141] |
| *Trachyelopterus galeatus* | 0.027 | 0.079 | 0.768 | 0 | 0 | 0.127 | 0 | 0 | Carnivore-insectivore [142]/Insectivore [143] |

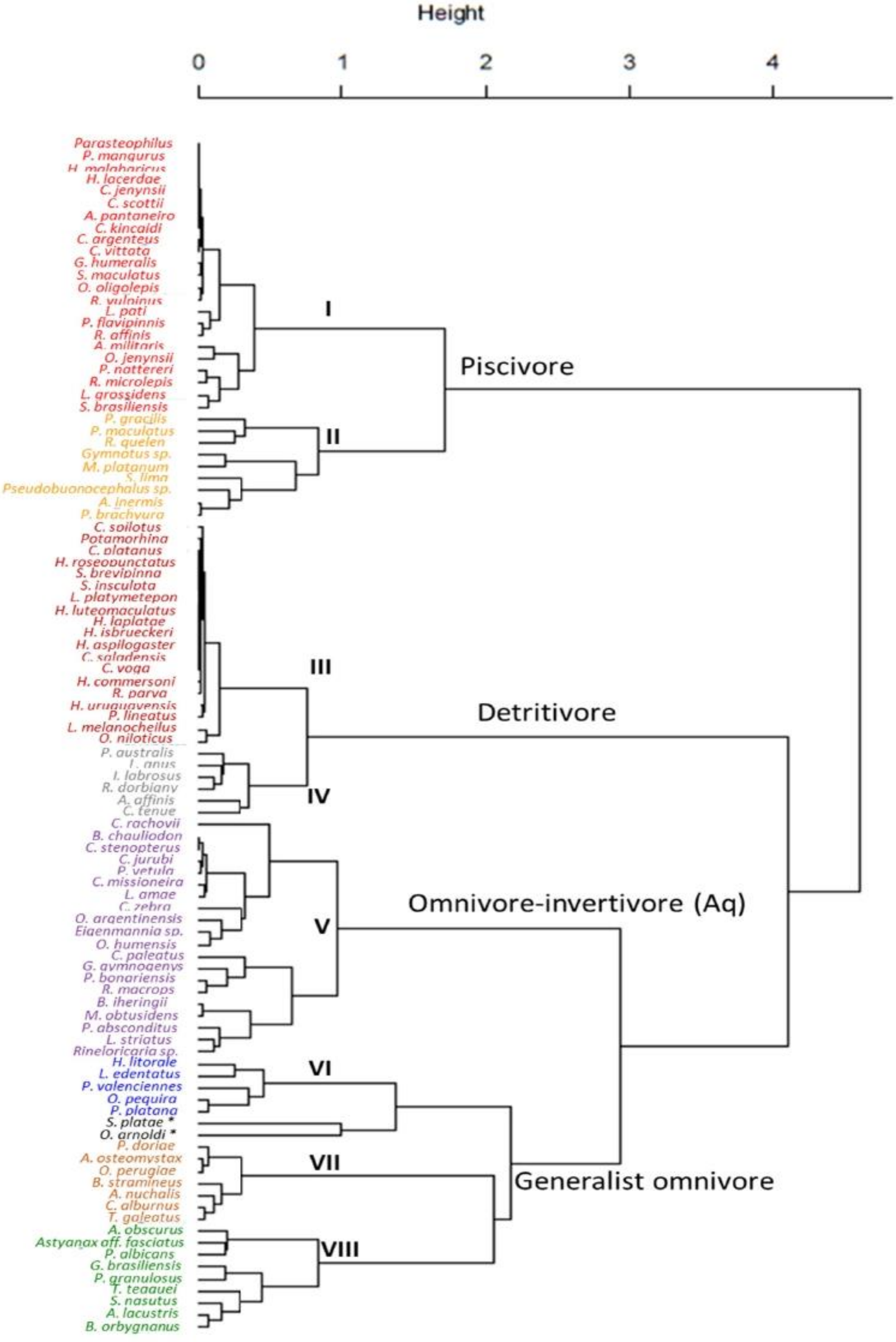


**Figure 2.** Cluster analysis showing trophic classification of 100 fish species along the Uruguay River. The text in the main tree branches corresponds to the broad scale trophic classification into four large trophic groups. Within each group, a statistically significant separation into more detailed sub-groups is made and marked with numbers and different text font colours. The final eight trophic groups are: I: Piscivore; II: Piscivore-invertivore; III: Detritivore; IV: Omnivore-detritivore; V: Omnivore-invertivore—(Aq.); VI: Omnivore-planktivore; VII: Omnivore-invertivore—(Terr.); and VIII: Omnivore-herbivore—(Terr.). The two species with * were excluded from groups due to their unique diet composition. Species abbreviations are shown, for full species names and detailed dietary characterization see Table 1.

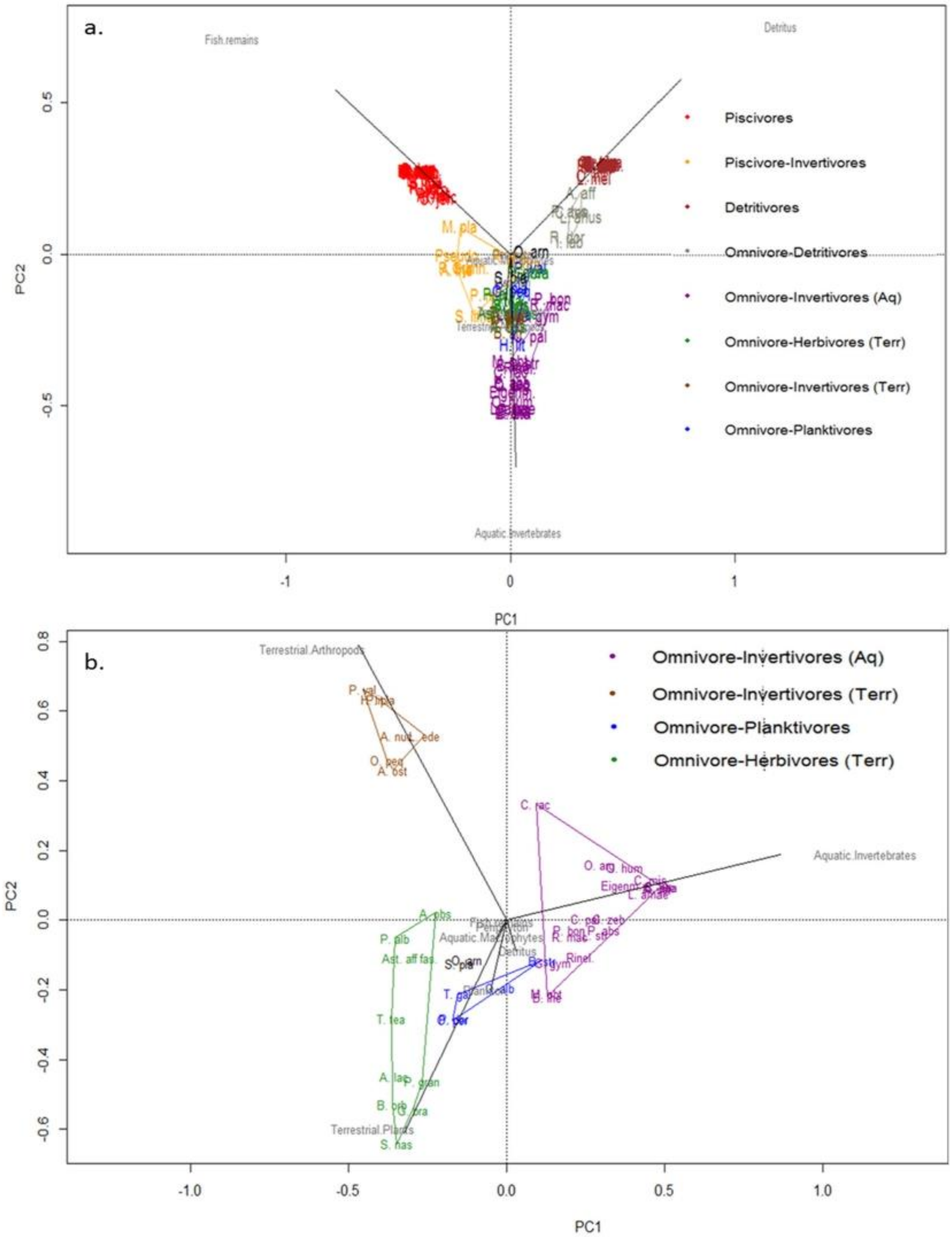


**Figure 3.** Principal component analysis: (**a**) showing all fish species assemblages in trophic groups according main food item in diet; PCA axes 1 and 2 explained 40% and 27% of the variance, respectively; (**b**) PCA (without the piscivore and detritivore groups) showing omnivorous fish specialization and grouped in trophic groups; PCA axes 1 and 2 explained 43% and 24% of the variance, respectively. Each colored polygon represents one trophic group. To see the full name of the species, see Figure 2 and/or Table 1.

The combination of the IRI values of each dietary item (detailed in Table 1) used in the cluster analysis allowed classifying species into four coarse-level trophic groups: Piscivore (32% of the species), detritivore (24% of the species), omnivore-invertivore (aquatic) (20% of the species, being omnivores mostly feeding on aquatic macroinvertebrates) and generalist-omnivore (23% of the species being omnivores mostly feeding on terrestrial material) groups (Figure 2, Table 1). When visualising this data in principal component analysis (PCA) the separation of this same four broad trophic groups was as clearly evident as in the cluster analysis of Figure 2, with the first two axis explaining 67% of the variation in the data (PC1 = 40% and PC2 = 27%) (Figure 3a). The PERMANOVA test gave strong statistical support to this broad level classification into four groups, showing significant differences in the IRI index value for the multiple dietary items between every group ($F_{3, 96} = 58.22$; $P = 0.001$).

Furthermore, data exploration using both PCA and cluster analysis suggested the suitability of increasing the resolution of the four broad trophic groups. For instance, piscivore and detritivore groups could be separated into two groups each (Figures 2 and 3a, Table 1), including the strictly piscivorous and detritivorous groups of species, and those that while feeding mostly on fish and detritus respectively also include other diet items to a lesser extent (Figure 3, Table 1). To perform this finer scale classification a PCA using exclusively the omnivorous groups was made to better resolve and classify them into four trophic subgroups (Figure 3b). In this case, 67% of the variation in the data was explained (PC1 = 43% and PC2 = 24%). The PERMANOVA test also showed consistent statistical support to this finer separation of omnivores into four subgroups ($F_{1, 41} = 16.16$; $P = 0.001$).

Altogether, the ordination methods supported the separation into eight trophic groups:

I. Piscivore: Diet dominated by entire fishes, fish remains, scales and fins.
II. Piscivore-invertivore: Diet dominated by fishes, fish remains, scales and fins, with inclusion of aquatic macroinvertebrates and terrestrial arthropods.
III. Detritivore: Diet dominated by detritus.
IV. Omnivore-detritivore: A combination of vegetal and animal sources, with dominance of detritus.
V. Omnivore-invertivore (Aquatic): A combination of species with either a diet largely dominated by aquatic macroinvertebrates and generally a minor inclusion of vegetal components.
VI. Omnivore-planktivore: Combination of vegetal and animal sources, with dominance of planktonic items (mostly zooplankton).
VII. Omnivore-invertivore (Terrestrial): A combination of species with either a diet largely dominated by terrestrial arthropods and generally a minor inclusion of vegetal components.
VIII. Omnivore-herbivores (Terrestrial): Diet dominated by terrestrial seeds and fruits, but with minor inclusion of terrestrial arthropods.

Finally, a one-way PERMANOVA performed with all eight subgroups supported the trophic classification, showing significant between each group ($F_{8, 91} = 101.42$; $P = 0.001$). Two species were excluded (although appeared related to the Omnivore-planktivore group in the cluster analysis) due to their unique diet: *Otocinclus arnoldi*, that fed mostly on periphyton with minor inclusion of detritus, and *Schizodon platae*, with a diet almost entirely composed of aquatic macrophytes (Table 1).

The trophic composition of the assemblages did not differ significantly between the three river sections in term of relative biomass (PERMANOVA $F_{7, 111} = 1.4$, $P = 0.18$), relative abundance (PERMANOVA $F_{7, 111} = 1.03$, $P = 0.41$) or relative species richness (PERMANOVA $F_{7, 111} = 1.18$, $P=0.31$) of trophic groups. The three sites in the upper portion of the river were particularity variable in its trophic composition in terms of relative abundance and biomass (Table S1, Figure 4). Moreover, no significant difference in the relative biomass, abundance or species richness of any of the trophic groups was found between the three river sections; the only exception being the relative species richness of the omnivores species feeding on terrestrial invertebrates, which was greater in the middle than in the lower Uruguay River section (ANOVA $F_{2, 13} = 12.6$; $P = 0.001$; 6 species in the middle vs. 3 in the lower section).

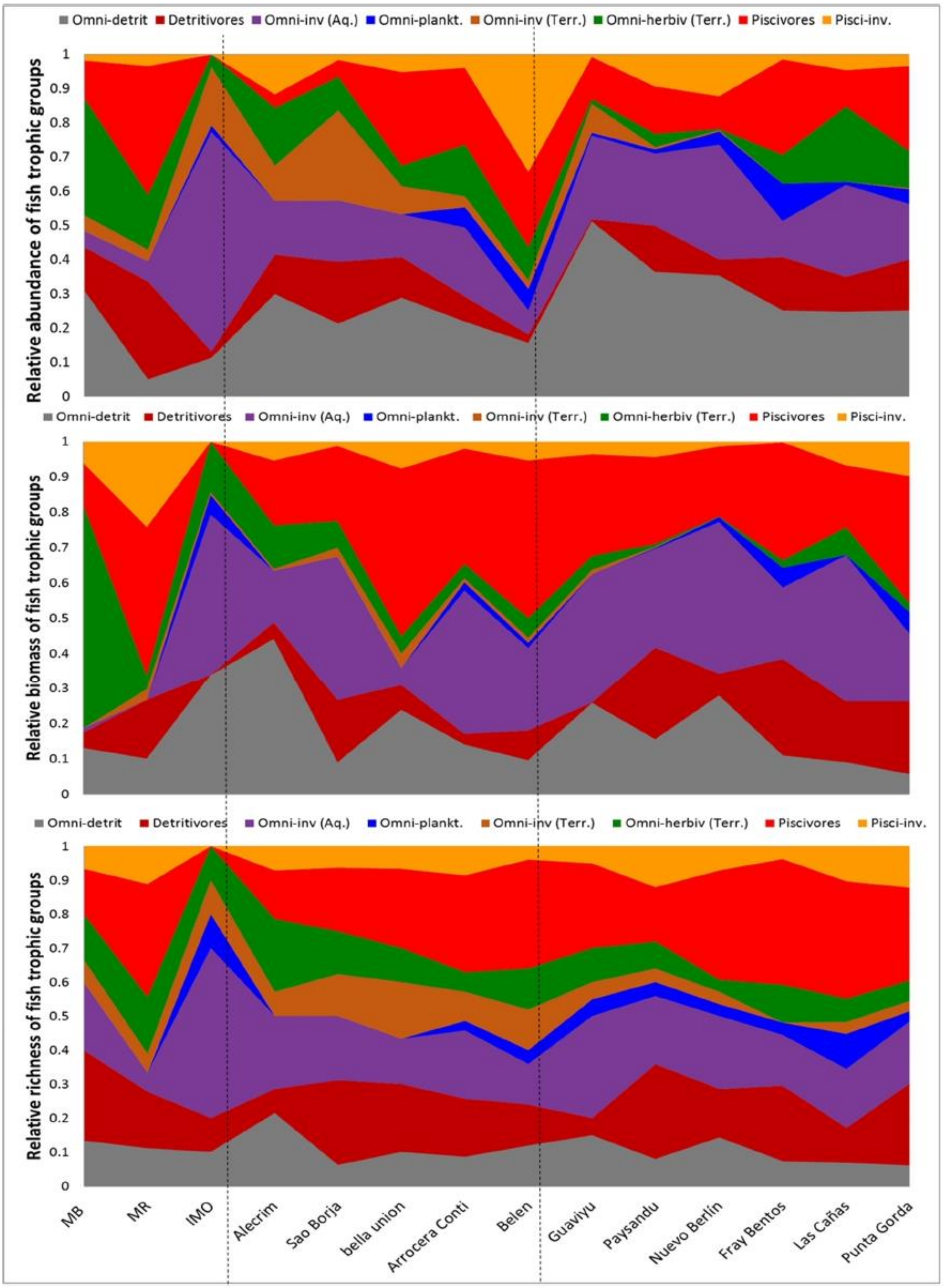


**Figure 4.** Longitudinal variability in trophic structure of the fish assemblages in sampled locations of Uruguay River from upper (MB, MR, IMO) to middle (Alecrim, Sao Borja, Bella Unión, Isla del Zapallo, Belén) and lower (Guaviyú, Paysandú, Nuevo Berlín, Fray Bentos, Las Cañas and Punta Gorda) river sections. Dashed lines represent the division between river sections. Above: Relative biomass; middle panel: Relative abundance; and below relative richness of each trophic group.

In terms of relative abundance of individuals, the assemblages along the river were generally dominated by omnivore-detritivore (26 ± 11% of total abundance, mean and Standard Deviation), followed by the omnivore-invertivore feeding mostly on aquatic prey (20 ± 15%, mean and SD) and the piscivores (16 ± 11%, mean and SD). Meanwhile, detritivore and omnivore-herbivore groups represented about 10% of the total abundance each, whereas the remaining trophic groups represented less than 5% of the total abundance (Table S1, Figure 4).

In contrast, both in terms of relative biomass and relative species richness, the trophic structure of the assemblages was clearly dominated by the piscivore group (representing 27 ± 13% of total biomass and 24 ± 10% of total richness), followed by the omnivore-invertivore group that feed on aquatic macroinvertebrates (representing 26 ± 16% of the total biomass and 20 ± 10% of the total richness). The omnivore-detritivore conformed the third most important group (18 ± 11% of total biomass), while the remaining groups represented 10% or less of the total biomass. In terms of relative species richness, omnivore-detritivore groups occupied the third place in importance, representing 20 ± 10% of all the species present on average. Each of the remaining trophic groups hosted about 10% of the total species number or less (Table S1, Figure 4). Remarkably, the trophic group with less relative biomass, density and species richness was the omnivore-planktivores—composed by five species feeding on copepods, cladocerans and/or ostracods mostly (see Table 1)—present in only one third of the upper and middle river section localities, but being always present in the lower river section.

## 4. Discussion

A total of one hundred species were recorded in a single sampling campaign comprising 14 localities spread along the main course of Uruguay River. This elevated taxa number illustrates the high biodiversity of the river, especially because this is a 12-h gillnet sampling in each site (in comparison with larger studies), but approximates to the total number of species historically registered for the river [43,165]. Moreover, the species richness seems to be at a similar level than that found for tropical rivers of comparable discharge. For example a study performed within a river stretch of a similar length in the Teles Pires River, located in Central Brazil and with similar characteristics to the Uruguay River (1600 km extension, c.a. 4000 $m^3$/s of average discharge) in a year of sampling, 90 species were collected [82]. Another example is the Miranda River, a tropical river located in Pantanal, Brazil, where 101 species were recorded over two years of sampling [166].

Moreover, the abundance and the movement of migrating species is controlled by seasonality, spatial and temporal environmental variability, and the hydrological regime [167]; therefore, it is not likely that all species that inhabit the main course of the river would be collected at the same time. However, according to previous sampling experience (e.g., [28]) and general literature for the region (e.g., [168,169]) we argue that our sampling was representative of the most common and frequent species in the river.

This study represents the first standardized fish assemblage description published and trophic classification of the species of the entire Uruguay River. Regarding the fish species present registered, it becomes of particular interest to highlight the presence of one exotic invasive fish species that represents a global threat to native biodiversity in the upper Uruguay River: The Nile Tilapia (*Oreochromis niloticus*). This species is one of the most commonly used in freshwater pisciculture production worldwide [170], and often generates great negative ecological consequences, particularly competing with native species [170]. The proliferation of these and other exotic species could affect local biodiversity by predation and competition with native species that share the same trophic niche.

Furthermore, this is the first dietary description for 29 fish species, despite that some of them are of elevated importance in fisheries (e.g., *Luciopimelodus pati*, being one of the most captured species by artisanal-commercial fisheries in the region) [171–173] and aquaculture (e.g., *Hoplias lacerdae* with lack of published field diet studies) (e.g., [174]). The other species with a previously unknown diet are rare species that are not usually collected in large numbers (e.g., *Otocinclus arnoldi* and most of the *Hypostomus* species). All this new information contributes to the knowledge of the trophic structure of fish assemblage. Moreover, when reviewing literature of the previously studied species, it most generally falls within a similar trophic classification; but one (*Leporinus striatus)* shows contrasting diet differences. *L. striatus* analyzed in this study lie well within the omnivore-invertivore trophic group, with important contribution of aquatic invertebrates (mostly invasive golden mussel, *Limnoperna fortunei)* to its diet. However, previous studies describe the species as an herbivore. This evidence suggest that the trophic classification of this species should be reassigned in the Uruguay River following our study. The reason behind this change might be the contrasting food availability between study sites (Amazon River Basin vs. Uruguay River) after the invasion of the golden mussel into the Uruguay River. The invasive golden mussel is nowadays known to represent a key dietary item in some Anostomid fish species (e.g., *M. obtusidens* and *L. striatus*), formerly classified as herbivorous ([175], González-Bergonzoni et al., in Prep).

Regarding the general trophic classification made here, it must be held in mind that the Uruguay River has a great spatial and temporal variability along its length, which could mean a high intra-specific variability in diet—particularly in the species with feeding plasticity—responding to flood pulses, seasonality, or local habitat conditions (e.g., [176,177]). This kind of spatial and individual size variability was not considered in the current analyses, because the main objective of this study consisted in a broad-scale classification for each species that surpassed local particularities or a particular life stage. Although diet analysis of some rare species that only presented one or few individuals was also performed, those were still kept into the analyses because their diets were sometimes completely unknown in the region. The aspects outlined above must be taken into account if an objective to describe food webs at a fine resolution or at a local level is to be addressed. However, a broad classification of fishes into feeding groups such as this one is an important tool in ecology, allowing comparisons among different environments, river basins or regions, based on fish assemblage structure [178].

The trophic structure of fish assemblages did not generally differ among the three river sections, being the piscivores dominant in terms of relative biomass and richness and the omnivore-detritivore dominant in terms of abundance. This partly reflects the contrasting size structure of species within those trophic groups, being the piscivores usually larger and with higher biomass in the assemblage. Much of the dominance in abundance of the omnivorous-detritivorous group responds to the high frequency and abundance of the *Iheringichthys labrosus* species, sampled along of most of the river length. This ubiquitous species is highly plastic in its diet [40] and digestive morphological features [179], being a constantly dominant species across the entire river.

The observed significantly higher relative species richness of omnivorous species feeding on terrestrial invertebrates towards the middle section of the river may correspond to the dominant environmental characteristics of that zone. In particular, the middle section hosts several large floodplains in which the river channel contacts grasslands and forest areas during floods where terrestrial invertebrates become highly available (e.g., [180]). In this context, it needs to be mentioned that sampling took place during a high river flow scenario, with significant floods, particularly in the middle and lower stretches. Most of the species within this trophic group have morphological adaptations to feed on the water surface (e.g., supra-terminal mouth), where arthropods derived from the land drift in the water surface. This evidence generally agrees with large river theories (e.g. "The flood pulse concept") in which increased land-water contact increases terrestrial subsidies for fish biomass [180]. Moreover, it matches well with the observed in studies arrayed at diverse scales, where the terrestrial food intake of fish increase whenever the land-water interphase increases, e.g., towards flooded forests (e.g., [181]), or towards stream ecosystems with riparian forests [182]. Thus, this study finding probably remarks that terrestrial carbon input and flow in aquatic ecosystem food webs might be increased in regions with high terrestrial-aquatic habitat connectivity.

The relative importance of trophic groups such as piscivore and omnivore-herbivore did not increase downstream as previously evidenced for smaller fluvial ecosystems (at least at the coarse level defined here) [12–14]. The change in the scale of analysis (large river vs. middle size rivers and streams in the evidence fueling most river theories) may account for the absence of strong changes in the fish assemblage trophic structure from headwaters to mouth, probably because, even in the upper section, the system may be already large and productive enough to sustain high trophic diversity. However, and remarkably, the omnivorous-planktivorous fish trophic group was far more frequent in the lower than in the middle and upper sections, probably reflecting that the river velocity and turbulent flow decrease downstream as the river widens up allowing establishment of planktonic communities (as postulated by Horwitz 1978, and Vannote 1980 [12,13]).

Several anthropogenic factors may affect fish assemblages, such as the agrochemical inputs from the basin, fisheries, industrial and domestic sewage [183] and habitat fragmentation caused by hydroelectric dams [27,184]. This anthropogenic intervention in freshwater ecosystems typically results in the reduction of local biodiversity and affected community structure, particularly of fish [185,186]. For example, the low species richness and high spatial variability in the relative representation of different trophic groups in the upper Uruguay River might well be attributed to the presence of three hydroelectric dams between sampling sites (being this, a well-known impact of dams) [27,184,187]. Unfortunately, as there is a lack of baseline information on fish trophic structure it became impossible to disentangle the anthropogenic and natural effects driving fish trophic structure along the Uruguay River gradient. In a global scenario of increased anthropogenic pressure to aquatic ecosystems, and particularly of river fragmentation by dam construction [186,188–190] there is an increasing need for the generation of appropriate information about the ecology and biology of fishes, particularly in South America, to achieve better understanding of the ecosystems and improve management plans for the entire continent [34].

This research contributes with basic knowledge that allows interpreting how food webs are structured within this ecosystem, enabling predictions about the roles of particular trophic groups and fish species in the system. Moreover, a proper management of natural resources (such as many of this species that are target for fisheries) demands baseline knowledge on trophic interactions between species, previously inexistent along the entire Uruguay River. Future standardized monitoring programs along the river longitudinal gradient may increase the understanding of these observed patterns across seasons and long temporal scales including the effects of climate variability. Furthermore, in a global scale, the information about trophic classification of fishes generated in this study contributes to the knowledge of ecosystem functioning in this scarcely studied region, and may allow for comparisons with other climate regions.

**Supplementary Materials:** The following are available online at http://www.mdpi.com/2073-4441/11/7/1374/s1, Table S1: Fish assemblage trophic structure along a longitudinal gradient in Uruguay River. Sites are arranged from headwaters to mouth from left to right columns in the table. Values represent the relative abundance / relative biomass (%) of each species and trophic group (as the sum of all species within a group) at each study site. Values are only shown for the species collected in standardized samplings; species presence is marked with "X" in the case of individuals obtained from local fishermen or in previous samplings. The species with * have not been grouped due to unique dietary characteristics, Table S2: Fish species sampled along a longitudinal gradient in the Uruguay River. Taxonomic identification, minimum-maximum standard length (and number of guts analyzed) for each species and site are shown. Sites are arranged from headwaters to mouth from right to left columns in the table. Note that for some species the number of fish is very low and were kept in the analysis for being rare species from which information is highly novel. Use that information with special care.

**Author Contributions:** Conceptualization, A.L.-R. and I.G.-B.; data curation, A.L.-R., I.S. and I.G.-B.; formal analysis, A.L.-R., I.S., S.d.Á.-S., S.S., R.B., J.P., G.T. and I.G.-B.; funding acquisition, F.T.d.M., A.D. and I.G.-B.; investigation, A.L.-R. and I.G.-B.; methodology, A.L.-R., I.S., S.d.Á.-S., S.S., R.B., M.V.M., J.P., G.T., F.T.d.M., A.D., N.V., M.M., D.A.R.-T., E.Z.-F. and I.G.-B.; project administration, A.D. and I.G.-B.; resources, F.T.d.M., A.D. and I.G.-B.; supervision, F.T.d.M., A.D., N.V., M.M. and I.G.-B.; visualization, A.L.-R., I.S. and I.G.-B.; writing—original draft, A.L.-R. and I.G.-B.; writing—review and editing, A.L.-R., I.S., S.d.Á.-S., S.S., R.B., M.V.M., J.P., G.T., F.T.d.M., A.D., N.V., M.M., D.A.R.-T., E.Z.-F. and I.G.-B.

**Funding:** This research project was funded partly by Scientific Research Sectorial Commission (Uruguay) project CSIC I+D_2016_577-348 and the National Agency for Innovation and Research (ANII) project ANII FCE_ 2_2016_1_126780. ALR and IS received financial support from the Postgraduate Academic Commission (CAP) scholarship programme. R.B, M.V.M and D.A.R.-T. received financial support by FAPERGS: Fundação de Amparo a Pesquisa do Estado do Rio Grande do Sul. IGB, AD, NV, MM and FTM received financial support by the ANII National System of Researchers (SNI), and IGB also from the ANII scholarship ANII PD_NAC_2015_1_108121.

**Acknowledgments:** We gratefully thank the many students and researchers that helped along with fish sampling campaigns and sample processing such as Nicolas Boullosa, Patricia Correa, Renata Maria Guereschi, Samara Hermes-Silva, Ronaldo da Silva and Pedro Iaczinski. We also thank artisanal fishermen Lito López, Elbio Russo, Jorge Fagúndez, Mario Britos, Rogelio Zunini, J. Tajes, Pablo Conti, Jorge Franchini, and the wildlife park ranger from Nuevo Berlín: Ángel Rosano for their constant support and collaboration with fish samplings. We also thank three anonymous reviewers whose contribution improved the manuscript considerably.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Elton, C.S. *Animal Ecology*; Sigwick and Jackson: London, UK, 1927.
2. Paine, R.T. Food Webs: Linkage, Interactions Strength and Community Infrastructure. *J. Anim. Ecol.* **1980**, *49*, 666–685. [CrossRef]
3. Thompson, R.M.; Dunne, J.A.; Woodward, G. Freshwater food webs: Towards a more fundamental understanding of biodiversity and community dynamics. *Freshw. Biol.* **2012**, *57*, 1329–1341. [CrossRef]
4. Woodward, G. Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. *Freshw. Biol*. **2009**, *54*, 2174–2187. [CrossRef]
5. Power, M.E. Effects of fish in river food webs. *Science* **1990**, *250*, 811–814. [CrossRef] [PubMed]
6. Delong, M.; Thorp, J.M.; Thons, M.S.; Mcintosh, L. Trophic niche dimensions of fish communities as a function of historical hydrological conditions in a Plains river. *River Syst.* **2011**, *19*, 177–187. [CrossRef]
7. Vander Zanden, M.J.; Vadeboncoeur, Y. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* **2002**, *83*, 2152–2161. [CrossRef]
8. Vidotto-Magnoni, A.P.; Carvalho, E.D. Aquatic insects as the main food resource of fish the community in a Neotropical reservoir. *Neotrop. Icthyol.* **2009**, *7*, 701–708. [CrossRef]
9. Tonella, L.H.; Fugi, R.; Vitorino, O.B.; Suzuki, H.I.; Gomes, L.C.; Agostinho, A.A. Importance of feeding strategies on the long-term success of fish invasions. *Hydrobiologia* **2018**, *817*, 239–252. [CrossRef]
10. Teixeira-de Mello, F.; Vidal, N.; González-Bergonzoni, I.; Iglesias, C. Length–weight relationships of eight fish species from the lower section of the Uruguay River (Río Negro, Uruguay). *J. Appl. Ichthyol.* **2009**, *25*, 128–129. [CrossRef]
11. González-Bergonzoni, I.; Meerhoff, M.; Davidson, T.A.; Teixeira-de Mello, F.; Baattrup-Pedersen, A.; Jeppesen, E. Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. *Ecosystems* **2012**, *15*, 492–503. [CrossRef]
12. Horwitz, R.J. Temporal variability patterns and the distributional patterns of stream fishes. *Ecol. Monogr.* **1978**, *48*, 307–321. [CrossRef]
13. Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **1980**, *37*, 130–137. [CrossRef]
14. Ibañez, C.; Belliard, J.; Hughes, R.M.; Irz, P.; Kamdem-Toham, A.; Lamorouroux, N.; Tedesco, P.A.; Oberdoff, T. Convergence of temperate and tropical stream fish assemblages. *Ecography* **2009**, *32*, 658–670. [CrossRef]
15. Winemiller, K.O.; Hoeinghaus, D.J.; Pease, A.A.; Esselman, P.C.; Honeycutt, R.L.; Gbanaador, D.; Carrera, E.; Payne, J. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. *Riv. Res. Applic.* **2010**, *27*, 791–803. [CrossRef]
16. Li, J.; Huang, L.; Sato, T.; Zou, L.; Jiang, K.; Yahara, T.; Kano, Y. Distribution pattern, threats and conservation of fish biodiversity in the East Tiaoxi, China. *Environm. Biol. Fish.* **2013**, *96*, 519–533. [CrossRef]
17. Pease, A.A.; González-Díaz, A.A.; Rodiles-Hernández, R.; Winemiller, K.O. Functional diversity and trait–environment relationships of stream fish assemblages in a large tropical catchment. *Freshw. Biol*. **2012**, *57*, 1060–1075. [CrossRef]
18. Lévêque, C.; Oberdorff, T.; Paugy, D.; Stiassny, M.L.J.; Tedesco, P.A. Global diversity of fish (Pisces) in freshwater. In *Freshwater Animal Diversity Assessment*; Bailan, E.V., Lévêque, C., Segers, H., Martens, K., Eds.; Springer: Dordrecht, The Netherlands, 2007; pp. 545–567.

19. Reis, R.E.; Albert, J.S.; Di Dario, F.; Mincarones, M.M.; Petry, P.; Rocha, L.A. Fish biodiversity and conservation in South America. *J. Fish Biol.* **2016**, *89*, 12–47. [CrossRef]
20. Reis, R.E.; Kullander, S.O.; Ferraris, C.J., Jr. *Check List of the Freshwater Fishes of South and Central America*; Edipucrs: Porto Alegre, Brazil, 2003; ISBN 85-7430-361-5.
21. Reynalte-Tataje, D.A.; Agostinho, A.A.; Bialetzki, A.; Hermes-Silva, S.; Fernandes, R.; Zaniboni-Filho, E. Spatial and temporal variation of the ichthyoplankton in a subtropical river in Brazil. *Environ. Biol. Fishes* **2012**, *94*, 403–419. [CrossRef]
22. Petry, P.; Bayley, P.B.; Markle, D.F. Relationship between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *J. Fish. Biol.* **2003**, *63*, 547–579. [CrossRef]
23. Röpke, C.P.; Amadio, S.; Zuanon, J.; Ferreira, E.J.; De Deus, C.P.; Pires, T.H.; Winemiller, K.O. Simultaneous abrupt shifts in hydrology and fish assemblage structure in a floodplain lake in the central Amazon. *Sci. Rep.* **2017**, *7*, 40170. [CrossRef] [PubMed]
24. Agostinho, A.A.; Pelicice, F.M.; Petry, A.C.; Gomes, L.C.; Júlio, H.F., Jr. Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. *Aquat. Ecosyst. Health* **2007**, *10*, 174–186. [CrossRef]
25. Rodríguez, M.A.; Winemiller, K.O.; Lewis, W.M., Jr.; Taphorn Baechle, D.C. The freshwater habitats, fishes, and fisheries of the Orinoco River basin. *Aquat. Ecosyst. Health* **2007**, *10*, 140–152. [CrossRef]
26. Zaniboni-Filho, E.; Ribolli, J.; Hermes-Silva, S.; Nuñer, A.P.O. Wide reproductive period of a long-distance migratory fish in a subtropical river, Brazil. *Neotrop. Ichthyol.* **2017**, *15*, e160135. [CrossRef]
27. Schork, G.; Zaniboni-Filho, E. Structure dynamics of a fish community over ten years of formation in the reservoir of the hydroelectric power plant in upper Uruguay River. *Braz. J. Biol.* **2017**, *77*, 710–723. [CrossRef]
28. González-Bergonzoni, I.; D'Anatro, A.; Vidal, N.; Stebniki, S.; Tesitore, G.; Silva, I.; Teixeira-de Mello, F. Origin of fish biomass in a diverse subtropical river: An allochthonic-supported biomass increase following flood pulses. *Ecosystems* **2019**. [CrossRef]
29. Agostinho, A.A.; Gomes, L.C.; Santos, N.C.L.; Ortega, J.C.G.; Pelicice, F.M. Fish assemblages in Neotropical reservoirs: Colonization patterns, impacts and management. *Fish. Res.* **2016**, *173*, 26–36. [CrossRef]
30. Oliveira, A.G.; Baumgartner, M.T.; Gomes, L.C.; Agostinho, A.A. Long-term effects of flow regulation by dams simplify fish functional diversity. *Freshw. Biol.* **2018**, *63*, 293–305. [CrossRef]
31. Pelicice, F.M.; Azevedo-Santos, V.M.; Esguicero, A.L.H.; Agostinho, A.A.; Arcifa, M.S. Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil. *Neotrop. Ichthyol.* **2018**, *16*, 1–18. [CrossRef]
32. Ávila-Simas, S.; Reynalte-Tataje, D.A.; Zaniboni-Filho, E. Pools and rapids as spawning and nursery areas for fish in a river stretch without floodplains. *Neotrop. Ichthyol.* **2014**, *12*, 611–622. [CrossRef]
33. Reynalte-Tataje, D.A.; Zaniboni-Filho, E.; Bialetzki, A.; Agostinho, A.A. Temporal variability of fish larvae assemblages: influence of natural and anthropogenic disturbances. *Neotrop. Ichthyol.* **2012**, *10*, 837–846. [CrossRef]
34. Barletta, M.; Jaureguizar, A.J.; Baigun, C.; Fontoura, N.F.; Agostinho, A.A.; Almeida-Val, V.M.; Val, A.L.; Torres, R.A.; Jimenes-Segura, L.F.; Giarrizzo, T.; et al. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. *J. Fish. Biol.* **2010**, *76*, 2118–2176. [CrossRef]
35. Nuñer, A.P.O.; Zaniboni-Filho, E. Length-weight relationships of fish species caught in the Upper Uruguay River, Brazil. *J. Appl. Ichthyol.* **2009**, *25*, 362–364. [CrossRef]
36. Zarucki, M.; González-Bergonzoni, I.; Teixeira-de Mello, F.; Duarte, A.; Serra, S.; Quintans, F.; Loureiro, M. New records of freshwater fish for Uruguay. *Check List.* **2010**, *6*, 191–194. [CrossRef]
37. Serra, W.S.; Teixeira-de Mello, F.; DÁnatro, A.; Vidal, N.; González-Bergonzoni, I.; García, D.; Masdeu, M.; Lenzi, J.; Tana, J. New records and distribution extension of *Pimelodus absconditus* Azpelicueta, 1995 (Siluriformes: Pimelodidae) and Triportheus nematurus (Kner, 1985) (Characiformes: Triportheidae). *Bol. Soc. Zool. Uruguay (2a época)* **2017**, *26*, 16–20.
38. Reynalte-Tataje, D.A.; Barcellos, R.P.; Hartmann, P.B.; Scherer, J.B.; Martine, G.; Vlieger, I.T.; Zaniboni-Filho, E.; Hermes-Silva, S.; Pelicice, F.M. O médio rio Uruguai como importante área de reprodução do surubim-pintado *Pseudoplatystoma corruscans* (Siluriformes: Pimelodidae). *Bol. Soc. Ictiol. Londrina* **2017**, *122*, 10–15.
39. González-Bergonzoni, I.; Teixeira-de Mello, F.; Vidal, N.; D'Anatro, A.; Masdeu, M. Reappearence and diet of juvenile armado catfish (*Pterodoras granulosus*) in Lower Uruguay River, (Río Negro, Uruguay). *Bol. Soc. Zool. Uruguay (2a época)* **2010**, *19*, 42–46.

40. Masdeu, M.; Teixeira-de Mello, F.; Loureiro, M.; Arim, M. Feeding habits and morphometry of Iheringichthys labrosus (Lütken, 1874) in the Uruguay River (Uruguay). *Neotrop. Ichthyol.* **2011**, *9*, 657–664. [CrossRef]
41. Meurer, S.; Zaniboni-Filho, E. Reproductive and feeding biology of *Acestrorhynchus pantaneiro* Menezes, 1992 (Osteichthyes: Acestrorhynchidae) in areas under the influence of dams in the upper Uruguay River, Brazil. *Neotrop. Ichthyol.* **2012**, *10*, 159–166. [CrossRef]
42. Ferriz, R.A.; Arrieta, P.M.; Dmánico, A.A. Trophic characterization of nine species of fishes in Middle and Lower Uruguay River. In *Historia Natural*; Azara, Fundación de Historia Natural, Universidad Maimónides: Buenos Aires, Argentina, 2016; Volume 6, pp. 41–53.
43. Di Persia, D.H.; Neiff, J.J.; Olazarri, J. The Uruguay River System. In *The Ecology of River Systems*; Davies, B.R., Walker, K.F., Eds.; Monographiae Biologicae, Springer: Dordrecht, The Netherlands, 1986; pp. 599–629.
44. Bischoff, S.A.; García, N.O.; Vargas, W.M.; Jones, P.D.; Conway, D. Climatic variability and Uruguay River Flows. *Water Int.* **2000**, *25*, 446–456. [CrossRef]
45. Zaniboni-Filho, E.; Schulz, U.H. Migratory fishes of the Uruguay River. In *Migratory Fishes of the South America: Biology, Fisheries and Conservation Status*; Carolsfeld, J., Harvey, B., Ross, C., Baer, A., Eds.; World Fisheries Trust: Victoria, BC, Canada; World Bank: Washington, DC, USA; IDRC: Otawa, ON, Canada, 2003; pp. 135–168, e-ISBN 1552501140.
46. Krepper, C.M.; Garcia, N.O.; Jones, P.D. Interannual variability in the Uruguay River basin. *Intern. J. Climatol.* **2003**, *23*, 103–115. [CrossRef]
47. González-Bergonzoni, I.; Jeppesen, E.; Vidal, N.; Teixeira-de Mello, F.; Goyenola, G.; López-Rodríguez, A.; Meerhoff, M. Potential drivers of seasonal shifts in fish omnivory in a subtropical stream. *Hydrobiologia* **2016**, *768*, 183–196. [CrossRef]
48. Hyslop, E.J. Stomach contents analysis—A review of methods and their application. *J. Fish Biol.* **1980**, *17*, 411–429. [CrossRef]
49. Pinkas, L.; Oliphant, M.S.; Iverson, I.L.K. Food habits of Albacore Bluefin Tuna and Bonito in California Waters. *Calif. Fish Game.* **1971**, *152*, 1–105.
50. Nielsen, J.M.; Clare, E.L.; Hayden, B.; Brett, M.T.; Kratina, P. Diet tracing in ecology: Method comparison and selection. *Methods Ecol. Evol.* **2017**, *12*, 1–14. [CrossRef]
51. Pouilly, M.; Yunoki, T.; Rosales, C.; Torres, L. Trophic structure of fish assemblages from Mamoré River floodplain lakes (Bolivia). *Ecol. Freshw. Fish* **2004**, *13*, 245–257. [CrossRef]
52. Anderson, M.J. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* **2001**, *26*, 32–46.
53. Pimm, S.L. Food webs. In *Food Webs*; Springer: Dordrecht, The Netherlands, 1982; pp. 1–11.
54. Polis, G.A. Food webs, trophic cascades and community structure. *Aust. J. Ecol.* **1994**, *19*, 121–136. [CrossRef]
55. Oksanen, J.; Kindt, R.; Legendre, P.; O'Hara, B.; Stevens, M.H.H.; Oksanen, M.J. The Vegan Package. *Comm. Ecol. Pack.* **2007**, *10*, 631–637.
56. Cantanhêde, G.; Fugi, R.; Hahn, N.S. Variation in prey selection of a piscivores fish after the impoundment of a neotropical reservoir: Prey size and type. *J. Fish Biol.* **2009**, *75*, 75–86. [CrossRef] [PubMed]
57. Krinski, D. Diet of the dog fish *Acestrorhynchus pantaneiro* Menezes, 1992 (Characidae: Acestrorhynchinae) from Pantanal of Poconé, Mato Grosso State, Brazil. *Biosci. J.* **2010**, *26*, 287–295.
58. Catella, A.C.; Petrere, M. Body-shape and food habits of fish from Baía da Onçca, a Pantanal flood plain lake, Brazil. *Verh. Int. Verein. Limnol.* **1998**, *26*, 2203–2208. [CrossRef]
59. Novakowski, G.C.; Cassemiro, F.A.; Hahn, N.S. Diet and ecomorphological relationships of four cichlid species from the Cuiabá River basin. *Neotrop. Ichthyol.* **2016**, *14*, e150151. [CrossRef]
60. Corrêa, C.E.; Petry, A.C.; Hahn, N.S. Influência do ciclo hidrológico na dieta e estrutura trófica da ictiofauna do rio Cuiabá, Pantanal Mato-Grossense. *Iheringia Sér. Zool.* **2009**, *99*, 456–463. [CrossRef]
61. de los Angeles Bistoni, M.; Haro, J.G.; Gutiérrez, M. Feeding of *Hoplias malabaricus* in the wetlands of Dulce river (Córdoba, Argentina). *Hydrobiologia* **1995**, *316*, 103–107. [CrossRef]
62. Fernández, E.M.; Ferriz, R.A.; Bentos, C.A.; López, G.R. Dieta y ecomorfología de la ictiofauna del arroyo Manantiales, provincia de Buenos Aires, Argentina. *Rev. Mus. Argent. Cienc. Nat.* **2012**, *14*, 1–13. [CrossRef]
63. Loureiro, V.E.; Hahn, N.S. Dieta e atividade alimentar da traíra, *Hoplias malabaricus* (Bloch, 1794) (Osteichthyes, Erythrinidae), nos primeiros anos de formação do reservatório de Segredo-PR. *Acta Limnol. Bras.* **1996**, *8*, 195–205.

64. de Almeida, V.L.L.; Hahn, N.S.; Vazzoler, A.D.M. Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). *Ecol. Freshw. Fish* **1997**, *6*, 123–133. [CrossRef]
65. Carvalho, L.N.; Fernandes, C.H.V.; Moreira, V.S.S. Alimentação de *Hoplias malabaricus* (Bloch, 1794) (Osteichthyes, Erythrinidae) no rio Vermelho, Pantanal Sul Mato-Grossense. *Rev. Bras. Zoociências* **2002**, *4*, 227–236.
66. Pereira, C.C.G.; Smith, W.S.; Espíndola, E.L.G. Hábitos alimenticios de nueve especies de peces del embalse de Três Irmãos, São Paulo, Brasil. *Univ. Cien.* **2004**, *1*, 33–38.
67. Bortoluzzi, T.; Aschenbrenner, A.D.C.; da Silveira, C.D.R.; Roos, D.C.; Lepkoski, E.D.; Martins, J.A.; Goulart, M.G.; Querol, E.; Querol, M.V. Hábito alimentar da Sardinha Prata, *Lycengraulis grossidens* (Spix & Agassiz, 1829), (Pisces, Engraulidae), Rio Uruguai Médio, Sudoeste do Rio Grande do Sul, Brasil. *Biodivers. Pampeana* **2006**, *4*, 11–23.
68. Mai, A.C.G.; Vieira, J.P. Review and consideration on habitat use, distribution and life history of *Lycengraulis grossidens* (Agassiz, 1829) (Actinopterygii, Clupeiformes, Engraulididae). *Biota Neotrop.* **2013**, *13*, 121–130. [CrossRef]
69. Hartz, S.M.; Martins, A.; Barbieri, G. Dinâmica da alimentação e dieta de *Oligosarcus jenynsii* (Günther, 1864) na lagoa Caconde, Rio Grande do Sul, Brasil (TELEOSTEI, CHARACIDAE). *Bol. Inst. Pesca* **1996**, *23*, 21–29.
70. Silva, S.H.; Meurer, S.; Zaniboni-Filho, E. Biologia alimentar e reprodutiva do peixe-cachorro (*Oligosarcus jenynsii* Günther, 1864) na região do alto rio Uruguai-Brasil. *Acta Sci. Biol. Sci.* **2004**, *26*, 175–179. [CrossRef]
71. Nunes, D.M.; Hartz, S.M. Feeding dynamics and ecomorphology of *Oligosarcus jenynsii* (Gunther, 1864) and *Oligosarcus robustus* (Menezes, 1969) in the Lagoa Fortaleza, southern Brazil. *Braz. J. Biol.* **2006**, *66*, 121–132. [CrossRef] [PubMed]
72. Barros, S.E. Alimentación de Oligosarcus jenynsii (Characiformes: Characidae) en dos embalses sobre el río Juramento, Salta, Subtrópico de Argentina. *Rev. Aquatic* **2016**, *20*, 44–50.
73. Bonato, K.O.; Burres, E.D.; Fialho, C.B. Dietary differentiation in relation to mouth and tooth morphology of a neotropical characid fish community. *Zool. Anz.* **2017**, *267*, 31–40. [CrossRef]
74. Zarucki, M.; González-Bergonzoni, I.; Teixeira-de Mello, F.; Loureiro, M. Fish diversity loss in an urban stream of Uruguay throughout the last century. *PANAMJAS* **2011**, *6*, 71–75.
75. Gonzalez, N.; Vispo, C. Aspects of the diets and feeding ecologies of fish from nine floodplain lakes of the lower Caura, Venezuelan. *Scient. Guaian.* **2003**, *12*, 329–366.
76. Moreira-Hara, S.S.; Zuanon, J.A.; Amadio, S.A. Feeding of *Pellona flavipinnis* (Clupeiformes, Pristigasteridae) in a Central Amazonian floodplain. *Iheringia Sér. Zool.* **2009**, *99*, 153–157. [CrossRef]
77. Behr, E.R.; Signor, C.A. Distribution and feeding of two sympatric species of piranhas *Serrasalmus maculatus* and *Pygocentrus nattereri* (Characidae, Serrasalminae) of the Ibicuí river, State of Rio Grande do Sul, Brazil. *Iheringia Sér. Zool.* **2008**, *98*, 501–507. [CrossRef]
78. Ferreira, F.S.; Vicentin, W.; Costa, F.E.; Súarez, Y.R. Trophic ecology of two piranha species, *Pygocentrus nattereri* and *Serrasalmus marginatus* (Characiformes, Characidae), in the floodplain of the Negro River, Pantanal. *Acta Limnol. Bras.* **2014**, *26*, 381–391. [CrossRef]
79. Peterson, C.C.; McIntyre, P. Ontogenetic diet shifts in *Roeboides affinis* with morphological comparisons. *Environ. Biol. Fishes* **1998**, *53*, 105–110. [CrossRef]
80. Novakowski, G.C.; Fugi, R.; Hahn, N.S. Diet and dental development of three species of *Roeboides* (Characiformes: Characidae). *Neotrop. Ichthyo.* **2004**, *2*, 157–162. [CrossRef]
81. Novakowski, G.C.; Hahn, N.S.; Fugi, R. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotrop. Ichthyol.* **2008**, *6*, 567–576. [CrossRef]
82. Nunes, M.E. Alimentação de Juvenis de Dourado *Salminus Brasiliensis* e Piava *Megaleporinus Obtusidens* no Médio rio Uruguai. Bachelor's Thesis, Universidade Federal de Santa Catarina, Florianópolis, Brazil, 2017; 30p.
83. Dary, E.P.; Ferreira, E.; Zuanon, J.; Röpke, C.P. Diet and trophic structure of the fish assemblage in the mid-course of the Teles Pires River, Tapajós River basin, Brazil. *Neotrop. Ichthyol.* **2017**, *15*, e160173. [CrossRef]
84. Hahn, N.S.; Fugi, R.; Peretti, D.; Russo, M.R.; Loureiro-Crippa, V.E. Estrutura trófica da ictiofauna da planície de inundação do alto rio Paraná. In *A planície de inundação do alto Rio Paraná*; Agostinho, A.A., Thomaz, S.M., Rodrigues, L., Gomes, L.C., Eds.; Programa PELD/CNPq: Maringá, Brazil, 2002; pp. 123–126.
85. Sazima, I. Similarities in feeding behavior between some marine and freshwater fishes in two tropical communities. *J. Fish Biol.* **1986**, *29*, 53–65. [CrossRef]

86. Horeau, V.; Cerdan, P.; Champeau, A.; Richard, S. Importance of aquatic invertebrates in the diet of rapids-dwelling fish in the Sinnamary River, French Guiana. *J. Trop. Ecol.* **1998**, *14*, 851–864. [CrossRef]
87. Bonato, K.O.; Delariva, R.L.; da Silva, J.C. Diet and trophic guilds of fish assemblages in two streams with different anthropic impacts in the northwest of Paraná, Brazil. *Zoologia* **2012**, *29*, 27–38. [CrossRef]
88. Lolis, A.A.; Andrian, I.D.F. Alimentação de Pimelodus maculatus Lacépède 1803 (Siluriformes, Pimelodidae), na planície de inundação do alto Rio Paraná, Brasil. *Boletim do Instituto de Pesca* **1996**, *23*, 23–28.
89. Lima-Junior, S.E.; Goitein, R. Ontogenetic diet shifts of a Neotropical catfish, *Pimelodus maculatus* (Siluriformes, Pimelodidae): An ecomorphological approach. *Environ. Biol. Fishes* **2003**, *68*, 73–79. [CrossRef]
90. Lobón-Cerviá, J.; Bennemann, S. Temporal trophic shifts and feeding diversity in two sympatric, Neotropical, omnivorous fishes: Astyanax bimaculatus and Pimelodus maculatus in Río Tibagi (Paraná, Southern Brazil). *Arch. Hydrobiol.* **2000**, *149*, 285–306. [CrossRef]
91. Bonato, K.O.; Fialho, C.B. Evidence of niche partitioning under ontogenetic influences among three morphologically similar Siluriformes in small subtropical streams. *PLoS ONE* **2014**, *9*, e110999. [CrossRef] [PubMed]
92. Hawlitschek, O.; Yamamoto, K.C.; Carvalho-Neto, F.G.M. Diet composition of fish assemblage of Lake Tupe, Amazonas, Brazil. *Ver. Colombiana Cienc. Anim.* **2013**, *5*, 313–326. [CrossRef]
93. Rodrigues, G.G.; Hartz, S.M. Food dynamics of fish and the interaction with macroinvertebrates from a shallow lake in Southern Brazil. *Verh. Int. Verein. Limnol.* **2001**, *27*, 3309–3314. [CrossRef]
94. Corrêa, F. Estrutura Trófica da Assembléia de Peixes Numa Área de Banhado do Parque Nacional da Lagoa do Peixe (RS). Ph.D. Thesis, Universidade Federal do Rio Grande, Rio Grande, Brazil, 2011.
95. Saccol-Pereira, A. Variação Sazonal e Estrutura Trófica da Assembléia de Peixes do Delta do Rio Jacuí, RS, Brasil. Ph.D. Thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, 2008.
96. González Sagrario, M.; Ferrero, L. The trophic role of *Cyphocharax voga* (Hensel, 1869) according to foraging area and diet analysis in turbid shallow lakes. *Fundam. Appl. Limnol.* **2013**, *183*, 75–88. [CrossRef]
97. Corrêa, F.; Piedras, S.R.N. Alimentação de *Cyphocharax voga* (Hensel, 1869) (Characiformes, Curimatidae) no arroio Corrientes, Pelotas, Rio Grande Do Sul, Brasil. *Biotemas* **2008**, *21*, 117–122. [CrossRef]
98. Angelescu, V.; Gneri, F.S. Adaptaciones del aparato digestivo al régimen alimenticio de algunos peces del rio Uruguay y rio de La Plata. *Inst. Nac. Investig. Cienc. Nat.* **1949**, *1*, 161–281.
99. Dourado, E.C.d.S.; Benedito-Cecilio, E.; Latini, J.D. O grau de trofia do ambiente influencia a quantidade de energia dos peixes. In *Biocenoses em Reservatórios: Padrões Espaciais e Temporais*; Rodrigues, L., Thomaz, S.M., Agostinho, A.A., Gomes, L.C., Eds.; Rima Editora: São Carlos, Brazil, 2005; pp. 211–222.
100. Delariva, R.L.; Agostinho, A.A. Relationship between morphology and diets of six Neotropical Loricariids. *J. Fish Biol.* **2001**, *58*, 832–847. [CrossRef]
101. Hahn, N.S.; Fugi, R.; Loureiro-Crippa, V.E.; Peretti, A.C.; Russo, M.R. Trophic structure of the fish fauna. In *Structure and Functioning of the Paraná River and its Floodplains*; Agostinho, A.A., Rodrigues, L., Gomes, L.C., Thomaz, S.M., Miranda, L.E., Eds.; EDUEM: Maringá, Brazil, 2004; pp. 139–143.
102. Zardo, É.L.; Behr, E.R. Trophic ecology of *Loricariichthys melanocheilus* Reis & Pereira, 2000 (Siluriformes: Loricariidae) in Ibicuí river, southern Brazil. *Acta Sci. Biol. Sci.* **2016**, *38*, 10.4025.
103. Fugi, R.; Hahn, N.S.; Agostinho, A.A. Feeding styles of five species of bottom-feeding fishes of the high Paraná River. *Environ. Biol. Fish.* **1996**, *46*, 297–307. [CrossRef]
104. Fugi, R.; Agostinho, A.A.; Hahn, N.S. Trophic morphology of five benthic-feeding fish species of a tropical floodplain. *Rev. Brasil. Biol.* **2001**, *61*, 27–33. [CrossRef]
105. Khallaf, E.A.; Alne-na-ei, A.A. Feeding ecology of *Oreochromis niloticus* (Linnaeus) & *Tilapia zillii* (Gervias) in a Nile canal. *Hydrobiologia* **1987**, *146*, 57–62.
106. Monaco, I.d.A.; Resende, E.K. Alimentação de *Liposarcus anisitsi* e *Potamorhina squamoralevis*, peixes abundantes na Baía Tuiuiú, Pantanal, Mato Grosso do Sul, Brasil. In Proceedings of the 5° Simpósio sobre Recursos Naturais e Socioeconômicos do Pantanal, Corumba, MS, Brazil, 9–12 November 2010.
107. Pereira, R.A.C.; Resende, E.K. Peixes detritívoros da planície inundável do Rio Miranda, Pantanal, Mato Grosso Do Sul, Brasil. *Embrapa Bol. Pesq.* **1998**, *12*, 1–50.
108. Giora, J.; Fialho, C.B. Feeding biology of *Steindachnerina brevipinna* (Characiformes, Curimatidae) in the Ibicuí-mirim river, Rio Grande do Sul, Brazil. *Iheringia Sér. Zool.* **2003**, *93*, 277–281. [CrossRef]
109. Flores, S.; Hirt, L.; Araya, P. Estructura y dinámica de la comunidad íctica del arroyo Yabotí, Reserva de Biosfera Yabotí, Misiones, Argentina. *Rev. Mex. Biodiv.* **2015**, *86*, 386–395. [CrossRef]

110. Casatti, L.; Mendes, H.F.; Ferreira, K.M. Aquatic macrophytes as feeding site for small fishes in the Rosana Reservoir, Paranapanema River, Southeastern Brazil. *Braz. J. Biol.* **2003**, *63*, 213–222. [CrossRef] [PubMed]
111. Santin, M.; Bialetzki, A.; Nakatani, K. Mudanças ontogênicas no trato digestório e dieta de *Apareiodon affinis* (Steindachner, 1879) (Osteichthyes, Parodontidae). *Acta Sci. Biol. Sci.* **2004**, *26*, 291–298.
112. Abes, S.D.S.; Agostinho, A.A.; Okada, E.K.; Gomes, L.C. Diet of *Iheringichthys labrosus* (Pimelodidae, Siluriformes) in the Itaipu Reservoir, Paraná River, Brazil-Paraguay. *Braz. Archiv. Biol. Technol.* **2001**, *44*, 101–105. [CrossRef]
113. Makrakis, M.C.; Nakatani, K.; Bialetzki, A.; Sanches, P.V.; Baumgartner, G.; Gomes, L.C. Ontogenetic shifts in digestive tract morphology and diet of fish larvae of the Itaipu Reservoir, Brazil. *Environ. Biol. Fish.* **2005**, *72*, 99–107. [CrossRef]
114. Teixeira, I.; Bennemann, S.T. Ecomorfologia refletindo a dieta dos peixes em um reservatório no sul do Brasil. *Biota Neotrop.* **2007**, *7*, 67–76. [CrossRef]
115. Fagundes, C.K.; Behr, E.R.; Kotzian, C.B. Diet of *Iheringichthys labrosus* (Siluriformes, Pimelodidae) in the Ibicuí river, southern Brazil. *Iheringia Sér. Zool.* **2008**, *98*, 60–65. [CrossRef]
116. García, M.L.; Protogino, L.C. Invasive freshwater molluscs are consumed by native fishes in South America. *J. Appl. Ichthyol.* **2005**, *21*, 34–38. [CrossRef]
117. López Cazorla, A.C.; Durán, W.; Tejera, L. Alimentación de la ictiofauna del río Sauce Grande, provincia de Buenos Aires, Argentina. *Biol. Acuat.* **2003**, *20*, 73–79.
118. Loureiro-Crippa, V.E.; Hahn, N.S. Use of food resources by the fish fauna of a small reservoir (rio Jordão, Brazil) before and shortly after its filling. *Neotrop. Ichthyol.* **2006**, *4*, 357–362. [CrossRef]
119. Bastos, R.F.; Miranda, S.F.; Garcia, A.M. Diet and feeding strategy of *Characidium rachovii* (Characiformes, Crenuchidae) in coastal plain streams of southern Brazil. *Iheringia Sér. Zool.* **2013**, *103*, 335–341. [CrossRef]
120. González-Bergonzoni, I. Dieta de Peces de Agua Dulce: Efectos de Factores Climáticos y Complejidad del Hábitat. Master's Thesis, Universidad de la República, Pedeciba, Uruguay, 2011; 67p.
121. de Mérona, B.; Vigouroux, R.; Horeau, V. Changes in food resources and their utilization by fish assemblages in a large tropical reservoir in South America (Petit-Saut Dam, French Guiana). *Acta Oecol.* **2003**, *24*, 147–156. [CrossRef]
122. de Mérona, B.; Vigouroux, R.; Tejerina-Garro, F.L. Alteration of fish diversity downstream from Petit-Saut Dam in French Guiana. Implication of ecological strategies of fish species. *Hydrobiologia* **2005**, *551*, 33–47. [CrossRef]
123. Sánchez, R.M.; Galvis, G.; Victoriano, P.F. Relationship between digestive tract characteristics and diets of fishes from Yucao River, Meta River system (Colombia). *Gayana* **2003**, *67*, 75–86. [CrossRef]
124. Longoni, L.S. Biologia alimentar e reprodutiva do cará *Gymnogeophagus gymnogenys* (Perciformes: Cichlidae) na Região do Delta do Jacuí, Rio Grande do Sul. Bachelors Thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, 2009; 42p.
125. Selmo, A.T. Estudo comparado da dieta de duas espécies simpátricas de *Gymnogeophagus* (Perciformes, Cichlidae) em um riacho no sul do Brasil. Bachelors Thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, 2010; 29p.
126. Ibañez, C.; Tedesco, P.A.; Bigorne, R.; Hugueny, B.; Pouilly, M.; Zepita, C.; Zubieta, J.; Oberdorff, T. Dietary-morphological relationship in fish assemblages of small forested streams in the Bolivian Amazon. *Aquat. Living Resour.* **2007**, *20*, 131–142. [CrossRef]
127. Rodrigues, F.L.; Bemvenuti, M.A. Hábito alimentar e osteologia da boca do peixe-rei, *Odontesthes humensis* de Buen (Atheriniformes, Atherinopsidae) na Lagoa Mirim, Rio Grande do Sul, Brasil. *Rev. Bras. Zool.* **2001**, *18*, 793–802. [CrossRef]
128. Fugi, R.; Hahn, N.S.; Novakowski, G.C.; Balassa, G.C. Feeding ecology of *Pachyurus bonariensis* (Perciformes, Sciaenidae) in two bays of the Pantanal, Mato Grosso State, Brazil. *Iheringia Sér. Zool.* **2007**, *97*, 343–347. [CrossRef]
129. Lima, D.O.; Behr, E.R. Feeding ecology of *Pachyurus bonariensis* Steindachner, 1879 (Sciaenidae: Perciformes) in the Ibicuí River, Southern Brazil: Ontogenetic, seasonal and spatial variations. *Braz. J. Biol.* **2010**, *70*, 503–509. [CrossRef] [PubMed]
130. de Mérona, B.; Dos Santos, G.M.; De Almeida, R.G. Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. *Environ. Biol. Fishes* **2001**, *60*, 375–392. [CrossRef]

131. Barili, E.; Fugi, R.; Novakowski, G.C.; Agostinho, A.A. Impoundment effects in the population of *Auchenipterus osteomystax* (Siluriformes: Auchenipteridae): A Neotropical reservoir case. *Rev. Biol. Trop.* **2012**, *60*, 699–708. [CrossRef] [PubMed]
132. Demétrio, J.A.; Gomes, L.C.; Latini, J.D.; Agostinho, A.A. Influence of net cage farming on the diet of associated wild fish in a Neotropical reservoir. *Aquaculture* **2012**, *330*, 172–178. [CrossRef]
133. Strictar-Pereira, L.; Agostinho, A.A.; Gomes, L.C. Cage culture with tilapia induces alteration in the diet of natural fish populations: The case of *Auchenipterus osteomystax*. *Braz. J. Biol.* **2010**, *70*, 1021–1030. [CrossRef] [PubMed]
134. Suiberto, M.R.; Galuch, A.V.; Bialetzki, A.; Nakatani, K. Ontogenetic shifts in the digestive tube and diet of *Bryconamericus stramineus* Eigenmann, 1908 (Osteichthyes, Characidae). *Acta Limnol. Bras.* **2009**, *21*, 465–472.
135. Brandão-Gonçalves, L.; Lima-Junior, E.; Suarez, Y.R. Feeding habits of *Bryconamericus stramineus* Eigenmann, 1908 (Characidae), in different streams of Guiraí River Sub-Basin, Mato Grosso do Sul, Brazil. *Biota Neotrop.* **2009**, *9*, 135–143. [CrossRef]
136. Artioli, L.G.S.; Prates-Júnior, P.H.S.; Diefenthaeler, F.; Fontoura, N.F. Período reprodutivo e alimentação de *Astyanax alburnus* no canal cornélios, capão da canoa, Rio Grande do Sul (Teleostei, Characiformes, Characidae). *Biociências* **2003**, *11*, 115–122.
137. Delariva, R.L.; Hahn, N.S.; Kashiwaqui, E.A.L. Diet and trophic structure of the fish fauna in a subtropical ecosystem: Impoundment effects. *Neotrop. Ichthyol.* **2013**, *11*, 891–904. [CrossRef]
138. Vilella, F.S.; Becker, F.G.; Hartz, S.M. Diet of *Astyanax* species (Teleostei, Characidae) in an Atlantic forest river in Southern Brazil. *Braz. Arch. Biol. Technol.* **2002**, *45*, 223–232. [CrossRef]
139. Bemvenuti, M.A. Silversides in South Brazil: Morphological and ecological aspects. *Biocell* **2006**, *30*, 111–118. [PubMed]
140. Brancolini, F.; Maroñas, M.E.; Sendra, E.D. Dieta de *Pseudocorynopoma doriae* (Characiformes: Characidae) en el arroyo de La Choza, Buenos Aires, Argentina. *Biol. Acuática* **2015**, *30*, 259–265.
141. Ferriz, R.A.; Fernandez, E.M.; López, G.R.; Bentos, C.A. Alimentación de *Pseudocorynopoma doriai* (Pisces: Characidae) en el arroyo El Portugués, provincia de Buenos Aires, Argentina. *Rev. Mus. Arg. Cienc. Nat.* **2012**, *14*, 243–251. [CrossRef]
142. Andrade-López, J.; Machado-Allison, A. Morphological and ecological aspects of the Heptapteridae and *Auchenipteridae* species in the Morichal Nicolasito (Aguaro River, Guárico State, Venezuela). *Bol. Acad. C Fís Mat. Nat.* **2009**, *69*, 35–52.
143. Santin, M.T.M.; Baggio, M.M.; Agostinho, A.A.; Bialetzki, A. Mudanças ontogênicas no trato digestório e na dieta de *Trachelyopterus galeatus*. *Bol. Inst. Pesca São Paulo* **2015**, *41*, 57–68.
144. Mol, J.H. Ontogenetic diet shifts and diet overlap among three closely related Neotropical armoured catfishes. *J. Fish Biol.* **1995**, *47*, 788–807. [CrossRef]
145. Winemiller, K.O. Feeding and reproductive biology of the currito, *Hoplosternum littorale*, in the Venezuelan llanos with comments on the possible function of the enlarged male pectoral spines. *Environ. Biol. Fishes* **1987**, *20*, 219–227. [CrossRef]
146. Dias, T.S. Estudo da Dieta de Oito Espécies da Subfamília Cheirodontinae (Characiformes: Characidae) em Diferentes Sistemas Lacustres nos Estados do Rio Grande do Norte e Rio Grande do Sul. Unpublished M.Sc. Dissertation, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, 2007; 89p.
147. Scanferla, A.F.L.; Súarez, Y.R. Flood pulse are the main determinant of feeding dynamics and composition of *Odontostilbe pequira* (Characiformes: Characidae) in southern Pantanal, Brazil. *Acta Limnol. Bras.* **2016**, *28*, e19. [CrossRef]
148. Fiori, L.F.; Alves, G.H.Z.; Hahn, N.S.; Benedito, E. Influence of feeding plasticity on the fitness of small Neotropical characids. *Iheringia. Sér. Zool.* **2016**, *106*, 1–6. [CrossRef]
149. Santos, C.L.; Dos Santos, I.A.; Da Silva, C.J. Ecologia trófica de peixes ocorrentes em bancos de macrófitas aquáticas na baia Caiçara, Pantanal Mato-Grossense. *Braz. J. Biosci.* **2009**, *7*, 473–476.
150. Aguiaro, T.; Caramaschi, É.P. Trophic guilds in fish assemblages in three coastal lagoons of Rio de Janeiro State (Brazil). *Verh. Int. Verein. Limnol.* **1998**, *26*, 2166–2169. [CrossRef]
151. Aguiaro, T.; Castelo Branco, C.W.; Verani, J.R.; Caramaschi, É.P. Diet of the clupeid fish *Platanichthys platana* (Regan, 1917) in two different Brazilian coastal lagoons. *Braz. Arch. Biol. Technol.* **2003**, *46*, 215–222. [CrossRef]

152. Pereira, L.S.; Agostinho, A.A.; Delariva, R.L. Effects of river damming in Neotropical piscivores and omnivorous fish: Feeding, body condition and abundances. *Neotrop. Ichthyol.* **2016**, *14*, e150044. [CrossRef]
153. Esteves, K.E. Feeding ecology of three *Astyanax* species (Characidae, Tetragonopterinae) from a floodplain lake of Mogi-Guaçú River, Paraná River basin, Brazil. *Environ. Biol. Fishes* **1996**, *46*, 83–101. [CrossRef]
154. Wolff, L.L.; Abilhoa, V.; Rios, F.S.A.; Donatti, L. Spatial, seasonal and ontogenetic variation in the diet of *Astyanax aff. fasciatus* (Ostariophysi: Characidae) in an Atlantic Forest river, Southern Brazil. *Neotrop. Ichthyol.* **2009**, *7*, 257–266. [CrossRef]
155. Arcifa, M.S.; Northcote, T.G.; Froehlich, O. Interactive ecology of two cohabiting characin fishes (*Astyanax fasciatus* and *Astyanax bimaculatus*) in an eutrophic Brazilian reservoir. *J. Trop. Ecol.* **1991**, *7*, 257–268. [CrossRef]
156. Barbosa, P.M.M.; Matsumura-Tundisi, T. Consumption of zooplanktonic organisms by *Astyanax fasciatus* Cuvier, 1819 (Osteichthyes, Characidae) in Lobo (Broa) Reservoir, São Carlos, SP, Brazil. *Hydrobiologia* **1984**, *113*, 171–181. [CrossRef]
157. Abelha, M.C.F.; Goulart, E. Oportunismo trófico de *Geophagus brasiliensis* (Quoy & Gaimard, 1824) (Osteichthyes, Cichlidae) no reservatório de Capivari, Estado do Paraná, Brasil. *Acta Sci. Biol. Sci.* **2004**, *26*, 37–45. [CrossRef]
158. Bastos, R.F.; Condini, M.V.; Varela Junior, A.S.; Garcia, A.M. Diet and food consumption of the pearl cichlid *Geophagus brasiliensis* (Teleostei: Cichlidae): Relationships with gender and sexual maturity. *Neotrop. Ichthyol.* **2011**, *9*, 825–830. [CrossRef]
159. Moraes, M.F.P.; de Freitas Barbola, I.; Duboc, L.F. Feeding habits and morphometry of digestive tracts of *Geophagus brasiliensis* (Osteichthyes, Cichlidae), in a lagoon of high Tibagi River, Paraná State, Brazil. *Publ. UEPG Biol. Health Sci.* **2004**, *10*, 37–45. [CrossRef]
160. Cantanhêde, G.; Hahn, N.S.; Gubiani, É.A.; Fugi, R. Invasive molluscs in the diet of *Pterodoras granulosus* (Valenciennes, 1821) (Pisces, Doradidae) in the Upper Paraná River floodplain, Brazil. *Ecol. Freshw. Fish* **2008**, *17*, 47–53. [CrossRef]
161. de Souza-Stevaux, M.C.; Negrelle, R.R.; Citadini-Zanette, V. Seed dispersal by the fish *Pterodoras granulosus* in the Paraná River Basin, Brazil. *J. Trop. Ecol.* **1994**, *10*, 621–626. [CrossRef]
162. Arcifa, M.S.; Froehlich, O.; Northcote, T.G. Distribution and feeding ecology of fishes in a tropical Brazilian reservoir. *Soc. Cienc. Nat. La Salle* **1988**, *48*, 301–326.
163. Villares Junior, G.A.; Gomiero, L.M.; Goitein, R. Biological aspects of *Schizodon nasutus* Kner, 1858 (Characiformes, Anostomidae) in the low Sorocaba river basin, São Paulo state, Brazil. *Braz. J. Biol.* **2011**, *71*, 763–770. [CrossRef] [PubMed]
164. Zardo, É.L.; da Rosa, V.M.; Behr, E.R. Distribution and feeding of fish from Anostomidae family in Ibicuí River, Río Grande do Sul, Brazil. *Bol. Inst. Pesca São Paulo* **2016**, *42*, 156–166. [CrossRef]
165. Sverlij, S.B.; López, H.L.; Schenke, R.L.D.; Ros, A.E. *Peces del Río Uruguay: Guía ilustrado de las especies más comunes del rio Uruguay inferior y el embalse de Salto Grande*; CARU: Montevideo, Uruguay, 1998; 89p.
166. de Resende, E.K. Trophic structure of fish assemblages in the lower Miranda river, Pantanal, Mato Grosso do Sul State, Brazil. *Rev. Bras. Biol.* **2000**, *60*, 389–403. [CrossRef]
167. Winemiller, K.O. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* **1989**, *8*, 225–241. [CrossRef]
168. Zaniboni-Filho, E.; Meurer, S.; Schibatta, O.A.; Nuñer, A.P.O. *Catálogo ilustrado de peixes do alto rio Uruguai*; Editora da UFSC: Florianópolis, Brazil, 2000.
169. Teixeira-de Mello, F.; Gonzalez-Bergonzoni, I.; Viana, F.; Saizar, C. Length–weight relationships of 26 fish species from the middle section of the Negro River (Tacuarembó-Durazno, Uruguay). *J. Appl. Ichthyol.* **2011**, *27*, 1413–1415. [CrossRef]
170. Canonico, G.C.; Arthington, A.; McCrary, J.K.; Thieme, M.L. The effects of introduced tilapias on native biodiversity. *Aquat. Conserv.* **2005**, *15*, 463–483. [CrossRef]
171. Vidal, N.; DÁnatro, A.; Stebniki, S.; González-Bergonzoni, I.; Teixeira-de Mello, F. *Monitoreo de la pesca artesanal en el Rïo Uruguay a través de información generada por pescadores de la zona de Nuevo Berlín, Fray Bentos y Las Cañas (Período 2007–2017)*; UPM: Montevideo, Uruguay, 2018.
172. Iwaszkiw, J.; Lacoste, F. La pesca artesanal en la Cuenca del Plata (Argentina) y sus implicancias en la conservación de la biodiversidad. *Rev. Mus. Arg. Cienc. Nat.* **2011**, *13*, 21–25. [CrossRef]

173. Vidal, N.; DÁnatro, A.; Stebniki, S.; González-Bergonzoni, I.; Teixeira-de Mello, F. *Monitoreo de la pesca artesanal en el Rïo Uruguay a través de información generada por pescadores de la zona de Nuevo Berlín, Fray Bentos y Las Cañas (Período 2007–2016)*; UPM: Montevideo, Uruguay, 2017.
174. Luz, R.K.; Portella, M.C. Freqüencia alimentar na larvicultura do trairão (*Hoplias lacerdae*). *Rev. Bras. Zootec.* **2005**, *34*, 1442–1448. [CrossRef]
175. Penchaszadeh, P.E.; Darrigran, G.; Angulo, C.; Averbuj, A.; Brogger, M.; Dogliotti, A.; Pirez, N. Predation of the invasive freshwater mussel Limnoperna fortunei (Dunker 1857) (Mytilidae) by the fish Leporinus obtusidens Valenciennes, 1846 (Anostomidae) in the Rio de la Plata, Argentina. *J. Shelfish Res.* **2000**, *19*, 229–231.
176. Luz-Agostinho, K.D.G.; Agostinho, A.A.; Gomes, L.C.; Júlio, H.F., Jr. Influence of flood pulses on diet composition and trophic relationship among piscivorous fish in the upper Paraná River floodplain. *Hydrobiologia* **2008**, *607*, 187–198. [CrossRef]
177. Freitas, T.M.S.; Almeida, V.H.D.; Valente, R.D.; Montag, I.F.D. Feeding ecology of *Auchenipterichthys longimanus* (Siluriformes: Auchenipteridae) in a riparian flooded forest of Eastern Amazonia, Brazil. *Neotrop. Ichtiol.* **2011**, *9*, 629–636. [CrossRef]
178. Brejão, G.C.; Gerhard, P.; Zuanon, J. Functional trophic composition of the ichthyofauna of forest streams in eastern Brazilian Amazon. *Neotrop. Ichthyol.* **2013**, *11*, 361–373. [CrossRef]
179. D'Anatro, A.; Vidal, N.; Gonzalez-Bergonzoni, I.; Teixeira de Mello, F.; Tana, J.; Naya, D. Geographic and seasonal variation analysis of digestive morphology in the catfish *Iheringichthys labrosus* along lower Río Uruguay. *Animal Physiol.* **2013**, *5*, 9–13.
180. Junk, W.J.; Bayley, P.B.; Sparks, R.E. The flood pulse in river-floodplain systems. In *Proceedings of International Large River Symposium*; Dodge, D.P., Ed.; Canadian Special Publication of Fisheries and Aquatic Sciences, 0706-6481; Department of Fisheries and Oceans: Ottawa, ON, Canada, 1989; Volume 106, pp. 110–127.
181. Winemiller, K.O.; Jepsen, D.B. Effects of seasonality and fish movement on tropical river food webs. *J. fish Biol.* **1998**, *53*, 267–296. [CrossRef]
182. Baxter, C.V.; Fausch, K.D.; Carl Saunders, W. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. *Freshw. Boil.* **2005**, *50*, 201–220. [CrossRef]
183. Malmqvist, B.; Rundle, S.D.; Covich, A.P.; Hildrew, A.G.; Robinson, C.T.; Townsend, C.R. Prospects for streams and rivers: An ecological perspective. In *Aquatic Ecosystems: Trends and Global Prospects*; Polunin, N.V.C., Ed.; Cambridge University Press: Cambridge, UK, 2008; pp. 19–29. ISBN 978-0-521-83327-1.
184. Agostinho, A.A.; Pelicice, F.M.; Gomes, L.C. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Braz. J. Biol.* **2008**, *68*, 1119–1132. [CrossRef]
185. Dudgeon, D.; Arthington, A.H.; Gessner, M.O.; Kawabata, Z.I.; Knowler, D.J.; Léveque, C.; Naiman, R.J.; Prieur-Richard, A.-H.; Soto, D.; Stiassny, M.L.; et al. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* **2005**, *81*, 163–182. [CrossRef] [PubMed]
186. Winemiller, K.O.; McIntyre, P.B.; Castello, L.; Fluet-Chouinard, E.; Giarrizzo, T.; Nam, S.; Baird, I.G.; Darwan, W.; Lujan, N.K.; Harrison, I.; et al. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* **2016**, *351*, 128–129. [CrossRef] [PubMed]
187. Lopes, C.A.; Zaniboni-Filho, E. Mosaic environments shape the distribution of Neotropical freshwater ichthyoplankton. *Ecol. Freshw. Fish* **2019**. [CrossRef]
188. Dudgeon, D. Large-Scale hydrological changes in tropical Asia: Prospects for riverine biodiversity. The construction of large dams will have an impact on the biodiversity of tropical Asian rivers and their associated wetlands. *BioScience.* **2000**, *50*, 793–806. [CrossRef]
189. Ormerod, S.J.; Dobson, M.; Hildrew, A.G.; Townsend, C.R. Multiple stressors in freshwater ecosystems. *Freshw. Biol.* **2010**, *55*, 1–4. [CrossRef]
190. Zarfl, C.; Lumsdon, A.E.; Berlekamp, J.; Tydecks, L.; Tockner, K. A global boom in hydropower dam construction. *Aquat. Sci.* **2015**, *77*, 161–170. [CrossRef]

# 5. Artículo 2

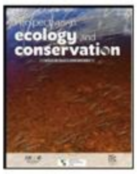
Perspectives in Ecology and Conservation xxx (xxxx) xxx–xxx

ABECO ASSOCIAÇÃO BRASILEIRA DE CIÊNCIA ECOLÓGICA E CONSERVAÇÃO

Perspectives in ecology and conservation

Supported by Instituto Tecnológico Vale and CEPAN

www.perspectecolconserv.com



Research Letters

## Longitudinal changes on ecological diversity of Neotropical fish along a 1700 km river gradient show declines induced by dams

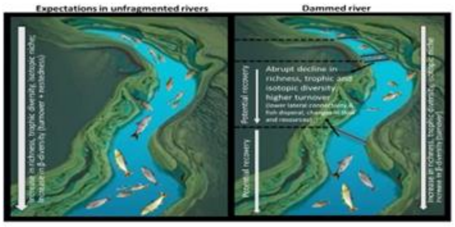
Anahí López-Rodríguez[a,b,c,*], Mariana Meerhoff[a,d,1], Alejandro D'Anatro[e], Sunshine de Ávila-Simas[f], Ivana Silva[b], Joaquín Pais[b], Franco Teixeira de Mello[a], David Augusto Reynalte-Tataje[g], Evoy Zaniboni-Filho[f], Iván González-Bergonzoni[b,1]

[a] *Department of Ecology and Environmental Management, Centro Universitario Regional del Este, Universidad de la República, Tacuarembó s/n, 2000, Maldonado, Uruguay*
[b] *Departamento de Ciencias Biológicas, CENUR Litoral Norte, Universidad de la República, Ruta 3 Km 363 EEMAC, Paysandú, Uruguay*
[c] *Departamento de Ecología y Biología Evolutiva, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay*
[d] *Department of Ecoscience, Aarhus University, Denmark*
[e] *Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Iguá 4225, Malvín Norte, 11400, Montevideo, Uruguay*
[f] *Laboratório de Biologia e Cultivo de Peixes de Água Doce (LAPAD), Departamento de Aquicultura, Universidade Federal de Santa Catarina (UFSC), 88066-260 Florianópolis, SC, Brazil*
[g] *Campus Cerro Largo, Universidade Federal da Fronteira Sul (UFFS), Av. Jacob Reinaldo Haupenthal, 1580, 97900-000 Cerro Largo, RS, Brazil*

### HIGHLIGHTS

- Dams promote ecological changes on rivers tackled by the Serial Discontinuity Concept.
- Multidimensional diversity of fish was studied along a 1700 km river stretch.
- Species richness and trophic and isotopic diversity increased towards the river mouth.
- Dam cascades caused declines in fish species richness and ecological diversity and higher turnover.
- Long dam-free stretches of rivers were key for the recovery of ecological diversity.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

*Article history:*
Received 3 October 2023
Accepted 18 March 2024
Available online xxx

*Keywords:*
Longitudinal gradient
Habitat fragmentation
Fish diversity
Beta diversity
Isotopic niche
Trophic diversity

### ABSTRACT

In naturally flowing waters, communities are expected to increase their taxonomic and functional diversity as well as increase the complexity of food web architecture along the longitudinal gradient from headwaters to mouth. However, these theories do not necessarily apply to dammed rivers. We analysed fish communities at 12 locations along the 1700 km stretch of the transnational Uruguay River. We determined species richness, beta-diversity and its components (turnover and nestedness), trophic diversity, and isotopic niches at community level, with particular focus on areas upstream and downstream of the four existing dams. We estimated trophic diversity metrics based on diet analysis, and isotopic niche breadth based on Bayesian isotopic niche models. We detected consistent longitudinal changes, supporting predictions from the River Continuum Concept. However, taxonomic richness, trophic diversity, and isotopic niche decreased abruptly immediately downstream of dams, and the component contributing the most to beta diversity was turnover, with the highest values occurring mainly after the cascade of

---

* Corresponding author.
*E-mail addresses:* alopez@fcien.edu.uy (A. López-Rodríguez), merluz@fcien.edu.uy (M. Meerhoff), passer@fcien.edu.uy (A. D'Anatro), sunshine.avila@ufsc.br (S. de Ávila-Simas), isilva@fcien.edu.uy (I. Silva), jpais@fcien.edu.uy (J. Pais), frantei@fcien.edu.uy (F. Teixeira de Mello), david.tataje@uffs.edu.br (D.A. Reynalte-Tataje), evoy@lapad.ufsc.br (E. Zaniboni-Filho), ivg@fcien.edu.uy (I. González-Bergonzoni).

[1] Mariana Meerhoff and Iván González-Bergonzoni are co-senior author.

https://doi.org/10.1016/j.pecon.2024.03.003

Please cite this article as: A. López-Rodríguez, M. Meerhoff, A. D'Anatro et al. Longitudinal changes on ecological diversity of Neotropical fish along a 1700 km river gradient show declines induced by dams, Perspectives in Ecology and Conservation, https://doi.org/10.1016/j.pecon.2024.03.003

dams in the upper Uruguay River, fitting expectations from the Serial Discontinuity Concept. The dam-free stretches of the Uruguay River allowed the recovery of ecological diversity as fish richness and trophic and isotopic niche increased. The negative impacts of dams should urgently be considered in the Neotropics, where many large dams are projected.

---

## Introduction

Several theories have been proposed to explain the functioning of river systems, predicting changes in communities and the architecture of food webs along the longitudinal gradients (e.g., Vannote et al., 1980; Junk et al., 1989; Thorp et al., 2008). One of the earliest theories, known as the River Continuum Concept (RCC) (Vannote et al., 1980), predicts longitudinal gradients in community composition, food webs, and ecosystem-scale processes from headwaters to mouth. Evidence from different climatic regions shows increasing ecological diversity (e.g., increase in species richness and number of links in trophic webs) from headwaters to mouth (e.g., Pease et al., 2012). However, most large river basins in different parts of the world have been significantly altered in their hydrology and geomorphology due to dam construction (Dudgeon et al., 2005) and South America is no exception (Agostinho et al., 2007; Winemiller et al., 2016). The Serial Discontinuity Concept (SDC) (Ward and Stanford, 1983; 1995) arose as a modification of the RCC to explain the functioning of flow-regulated ecosystems. This theory postulates that fluvial ecosystems have a predictable longitudinal gradient in biophysical conditions, which depend on environmental conditions and the position, functioning, and distance to dams (Ward and Stanford, 1983; 1995). Often, river stretches are interrupted by a series of consecutive dams. The spatial distribution of barriers along the longitudinal gradient of the river (i.e., dam cascades) can strongly affect downstream ecological patterns (e.g., Barbosa et al., 1999; Santos et al., 2018). The cumulative effects of such series of dams on changes in hydrology, sediment and nutrient retention, and physico-chemical processes represent a stronger impact than the combined effects of independent dams (Santos et al., 2018). These environmental changes can affect local communities, including shifts in fish composition (Barletta et al., 2010), and the structure of food webs (Ruhí et al., 2016). Some studies have found pauperization of some functional groups upstream and downstream of dams (e.g., de Bem et al., 2021), and an increase in the proportion of generalist species of fishes after dams (Turgeon et al., 2019). Declines in downstream diversity, population sizes, and genetic diversity in upstream reaches of the dam cascade due to isolation caused by habitat fragmentation have also been reported (Ribolli et al., 2021). Moreover, habitat fragmentation due to dams could result in species loss but also the addition of other species downstream of the dams, thus altering beta diversity (i.e., changes in species diversity between communities within a region) by modifying longitudinal patterns of turnover (degree of species replacement) and nestedness (subset of species present in the most diverse site) (Ganassin et al., 2021).

The presence of dams also affects the availability of basal food sources, leading to changes in the ecological niche utilized by the species (Guo et al., 2023). Stable isotope analyses (SIA) facilitate the study of global changes in ecological niches using, for example, isotopic niches areas as proxies of trophic diversity in food webs (Newsome et al., 2007) over a relatively long-time span (as stated originally by Layman et al., 2007a). In particular, SIA has enabled the identification of changes in community functioning indirectly induced by the presence of dams (primarily changes in hydrological flows affecting basal resources) (Guo et al., 2023).

The aim of this work was to determine the changes in ecological fish diversity, as a combination of different metrics of diversity (i.e., species richness, beta-diversity, trophic and isotopic diversity) along the fluvial gradient of a major South American river, the Uruguay River, within the framework of existing theories for regulated and unregulated rivers. We hypothesized that, in contrast to expectations from unregulated systems, dams would promote a decline in ecological niche, species diversity and a higher species turnover along this long river longitudinal gradient.

## Methods

### Study area

This research was conducted along a stretch of approximately 1700 km of the main course of the Uruguay River, which originates in Brazil and whose middle and lower sections separate Argentina and Uruguay (for more information see Appendix S1 in Supporting Material [SM]). Four hydroelectric dams operate along the Uruguay River: three in the upper section: Machadinho (1140 MW/h capacity; opening date: 2002), Itá (1450 MW/h; opening date: 2000), and Foz de Chapecó (855 MW/h; opening date: 2010), and one in the lower section, Salto Grande Dam (1890 MW/h; opening date: 1979) (Table S1in SM).

The middle as well as the final section of the upper section of the river remain largely undisturbed in terms of hydrology, with an unfragmented section of ca. 1,000 km. The upper Uruguay River and the upper part of the Middle Uruguay River are characterized by a channelized system (sites 1, 2, 3, 4) without floodplains and a few low-flow tributaries. The largest floodplains and main tributaries occur in the lower part of the Middle (sites 5, 6, 7, 8) and in the Lower sections (sites 9, 10, 11, 12) of the Uruguay River. The latter has high productivity, associated with floodplains and the formation of marginal pools (Zaniboni-Filho and Schulz, 2003) (Appendix S1 in SM).

### Fish sampling

Fish communities were sampled during the austral autumn of 2017 (May-early June) at 12 sites along the main course. Three sites were sampled in the upper river section, five in the middle, and four in the lower section (Fig. 1; Table S2 in SM). Some of the sites are located in the areas of influence of the dams, in transition zones between the lentic-lotic environment (e.g., sites 1, 2 and 8), while others are located in running sections (Table 1). The sampling sites were chosen considering available monitoring programs along the river to facilitate logistics.

In the upper section of the Uruguay River (sites 1-MPB, 2-MR, 3-IMO, Brazil), ongoing monitoring programs utilized a combination of gillnets and trammel nets (Appendix S1, SM). Both sets of nets were deployed in the littoral zone in the evening and left in place for ca. 12 h. Also, a seine net trawl and 3 casts of cast nets (with a mesh size of 8.0 mm) were placed in the littoral zone during the daytime. The fish community of the middle and lower sections was sampled using multi-mesh Nordic gillnets (Appendix S1 in SM). At each site, eight sets of gillnets were placed, four in the littoral zone and four in the pelagic zone at 2–5.0 m depth, and left in place for ca. 12 h from sunset to sunrise. Whenever possible, commercially important large fish specimens were obtained from local fishermen (at sites 6, 7, 8, 11, and 12) to supplement the sampling, wherever

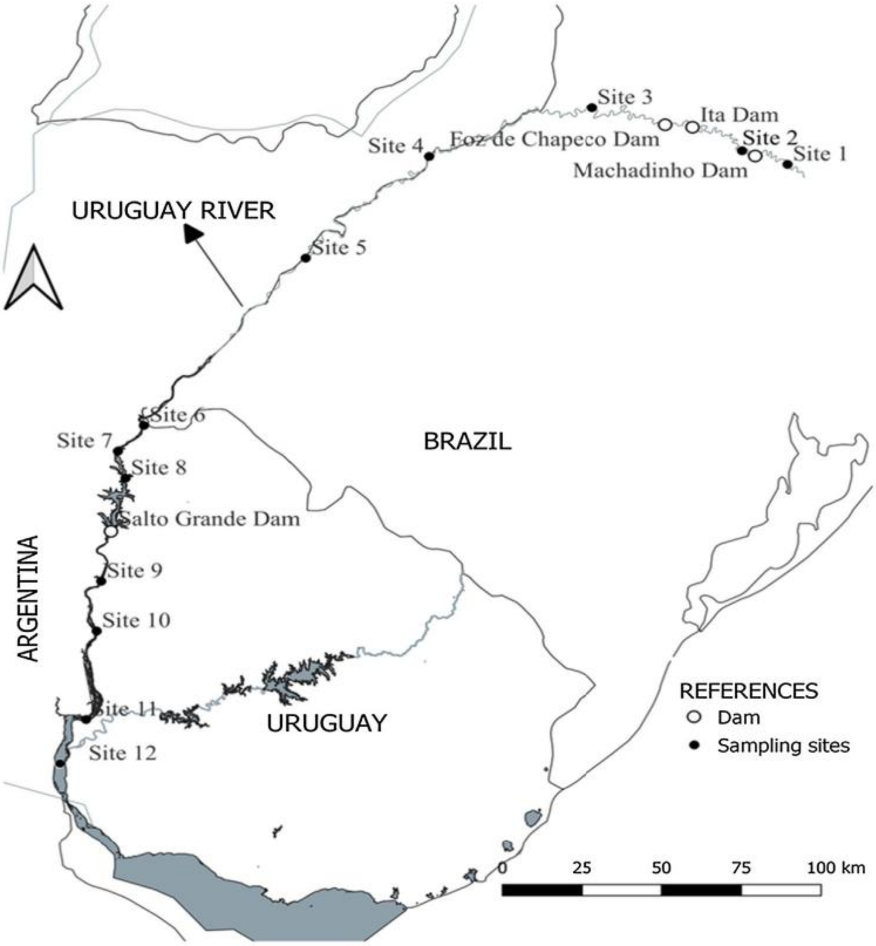


**Fig. 1.** Location of the 12 sampling sites along the Uruguay River. From headwaters to mouth: site 1-MPB: Barracão; Site 2-MR: Marcelino Ramos; Site 3-IMO: Mondaí; Site 4-ALE: Alecrim; Site 5-SB: São Borja; site 6- BU: Bella Unión; Site 7-IZ: Isla del Zapallo; Site 8-BEL: Belén; Site 9-GVY: Guaviyú; Site 10-PAY: Paysandú; Site 11-LC: Las Cañas; Site 12- PG: Punta Gorda. The location of sampling sites is represented by black circles; the location of dams is represented by white circles. Sites 1 to 5 are in Brazil, sites 6 to 12 were sampled from the Uruguayan side of the river.

these species (known to be present along the entire river) were not captured with the Nordic multi-mesh gillnets.

All fishes collected were identified in the field to the lowest taxonomic level possible (Table S3 and S4 in SM).

### *Sampling for stable isotope analyses*

Flank muscle samples were collected from N = 5 individuals (or all individuals if less than 5) per species per site, aiming to cover a wide range of body sizes (Table S3 in SM). After processing (Appendix S1 in SM), samples were sent to the Center for Stable Isotopes, University of New Mexico for stable isotopes analysis. The results of stable isotopes ratios were expressed as ‰ (parts per thousand) and were calculated using the standard formula:

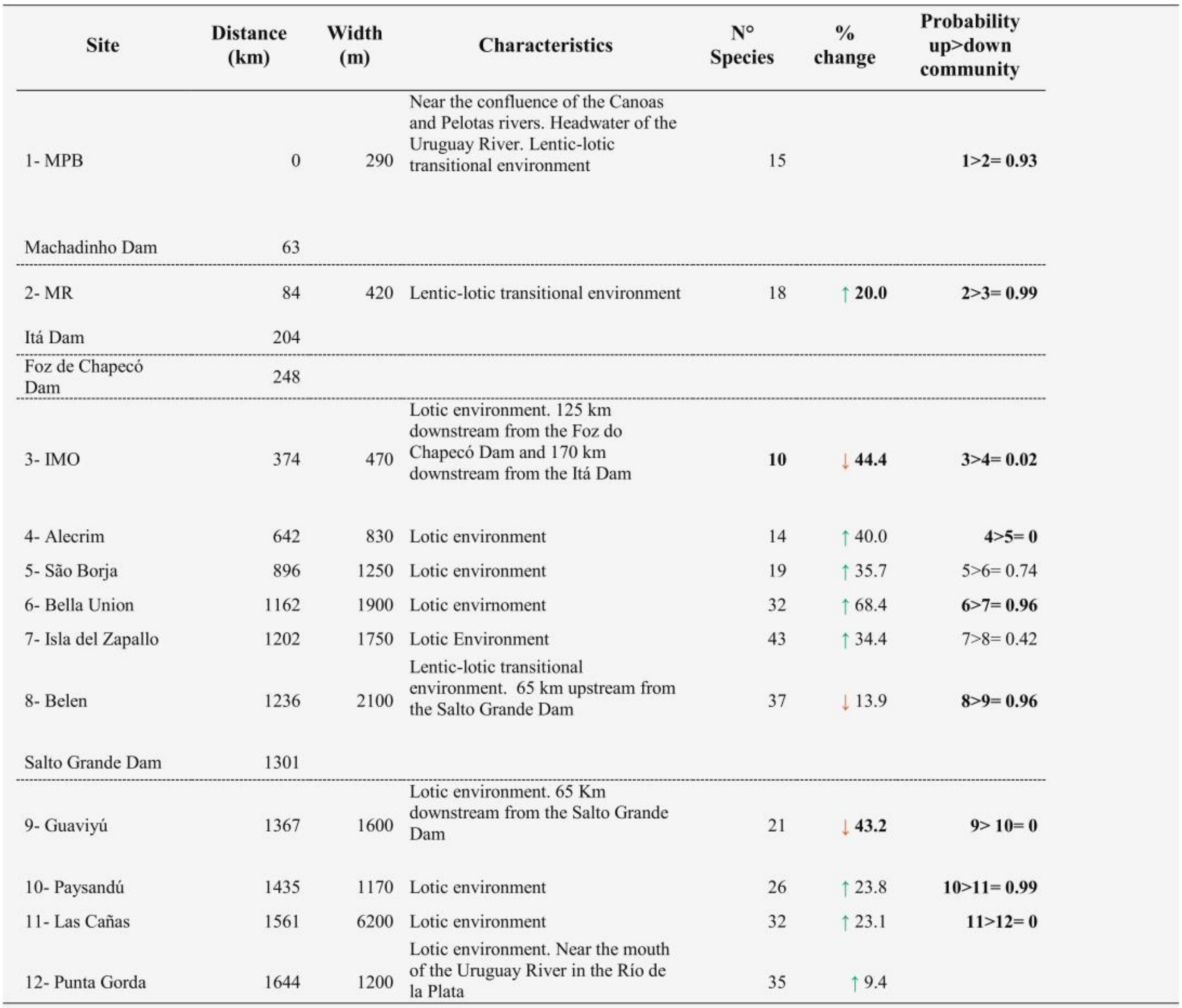
$$\delta X = \left[\left(\frac{Rsample}{Rstandard}\right) - 1\right] * 1000$$

where δX represents $\delta^{15}N$ or $\delta^{13}C$, R sample is the ratio of heavy to light isotopes of element X and R standard is that isotopic ratio in a standard. The C:N ratio was verified with laboratory results, and if greater than 3.5, the lipid isotopic signal was arithmetically corrected using the equations suggested for aquatic animals by Post et al. (2007).

### *Taxonomic richness and β-diversity*

The number of species captured at each sampling site (α diversity) was used to describe longitudinal patterns. Based on the presence-absence matrix of species per sampling site (Table S4 in SM), we calculated beta (β) diversity and its components (turnover and nestedness) for both the entire system (i.e., multiple beta diversity) and between particular pairs of sites (i.e., pairwise beta diversity), using the Sørensen dissimilarity index (Baselga and Orme, 2012; Appendix S1, SM). The pairwise beta diversity analysis results in three matrices: the Sørensen dissimilarity index matrix (βsor) that represents the total compositional variation (between 0 and 1); the Simpson dissimilarity index matrix (βsim) that indicates changes of species due to species turnover, and the nestedness matrix (βnes) resulting from βsor − βsim. From these matrices, we analyzed pairwise beta diversity at two levels: (1) across the entire longitudinal gradient, comparing pairs of sites with reference to site 1 at the headwaters (hereafter referred as "pairwise

**Table 1**
Sampling sites and dams' location, fish species richness with change relative to the upstream site (%) and probability of differences in SEAc between sites along the longitudinal gradient of the Uruguay River.



| Site | Distance (km) | Width (m) | Characteristics | N° Species | % change | Probability up>down community |
|---|---|---|---|---|---|---|
| 1- MPB | 0 | 290 | Near the confluence of the Canoas and Pelotas rivers. Headwater of the Uruguay River. Lentic-lotic transitional environment | 15 | | **1>2= 0.93** |
| Machadinho Dam | 63 | | | | | |
| 2- MR | 84 | 420 | Lentic-lotic transitional environment | 18 | ↑ **20.0** | **2>3= 0.99** |
| Itá Dam | 204 | | | | | |
| Foz de Chapecó Dam | 248 | | | | | |
| 3- IMO | 374 | 470 | Lotic environment. 125 km downstream from the Foz do Chapecó Dam and 170 km downstream from the Itá Dam | **10** | ↓ **44.4** | **3>4= 0.02** |
| 4- Alecrim | 642 | 830 | Lotic environment | 14 | ↑ 40.0 | **4>5= 0** |
| 5- São Borja | 896 | 1250 | Lotic environment | 19 | ↑ 35.7 | 5>6= 0.74 |
| 6- Bella Union | 1162 | 1900 | Lotic envirnoment | 32 | ↑ 68.4 | **6>7= 0.96** |
| 7- Isla del Zapallo | 1202 | 1750 | Lotic Environment | 43 | ↑ 34.4 | 7>8= 0.42 |
| 8- Belen | 1236 | 2100 | Lentic-lotic transitional environment. 65 km upstream from the Salto Grande Dam | 37 | ↓ 13.9 | **8>9= 0.96** |
| Salto Grande Dam | 1301 | | | | | |
| 9- Guaviyú | 1367 | 1600 | Lotic environment. 65 Km downstream from the Salto Grande Dam | 21 | ↓ **43.2** | **9> 10= 0** |
| 10- Paysandú | 1435 | 1170 | Lotic environment | 26 | ↑ 23.8 | **10>11= 0.99** |
| 11- Las Cañas | 1561 | 6200 | Lotic environment | 32 | ↑ 23.1 | **11>12= 0** |
| 12- Punta Gorda | 1644 | 1200 | Lotic environment. Near the mouth of the Uruguay River in the Río de la Plata | 35 | ↑ 9.4 | |

Distance = distance from each site to site 1, located at the headwaters of the Uruguay River (km); the green arrow represents species gained; the red arrow represents species lost. Probability up > down* = Probability that a given site has a higher SEAc than the site immediately downstream. Significant probabilities (i.e., higher than 90%) in Bayesian analysis are shown in bold. Dotted lines indicate the presence of dams.
*Probability in Bayesian statistics models is a degree of plausibility of occurrence of a specific event, based on prior distribution that depends on previous knowledge.

beta diversity"); and (2) step-wise beta diversity, comparing pairs of neighboring sites (e.g., site 1 vs. 2; site 2 vs. 3, and so on along the entire longitudinal gradient).

### *Trophic web metrics, trophic and ecological niche diversity analyses*

Based on the information from the stomach content analysis conducted by López-Rodríguez et al. (2019), the relative abundance of each food item consumed was calculated for each species at each sampling site. This information was used to calculate the trophic position of each fish species/site, following the modified equations of Winemiller (1990) (Appendix S1 in SM). The trophic positions of the consumed items were estimated according to the literature. Food webs were reconstructed and the number of nodes in the food web, number of trophic links, and linkage density (number of links/species) were calculated (Appendix S1 in SM). Due to the high correlation between these three metrics (Fig. S1 in SM), we chose to work with trophic links, since this is the trophic diversity metric most widely used in the literature (e.g., Pease et al., 2012) and hereafter refer to it as trophic diversity.

The isotopic niche breadth calculation was performed within a Bayesian model framework (Jackson et al., 2011; Appendix S1 in SM)). Since a large isotopic niche area implies a wide diversity in the use of the environment by the consumers, it is considered more accurate to use the standard ellipse area corrected for sample size (SEAc) as an indicator of ecological niche diversity (Newsome et al., 2007). We used isotopic signatures from consumers (fish) as input for the models.

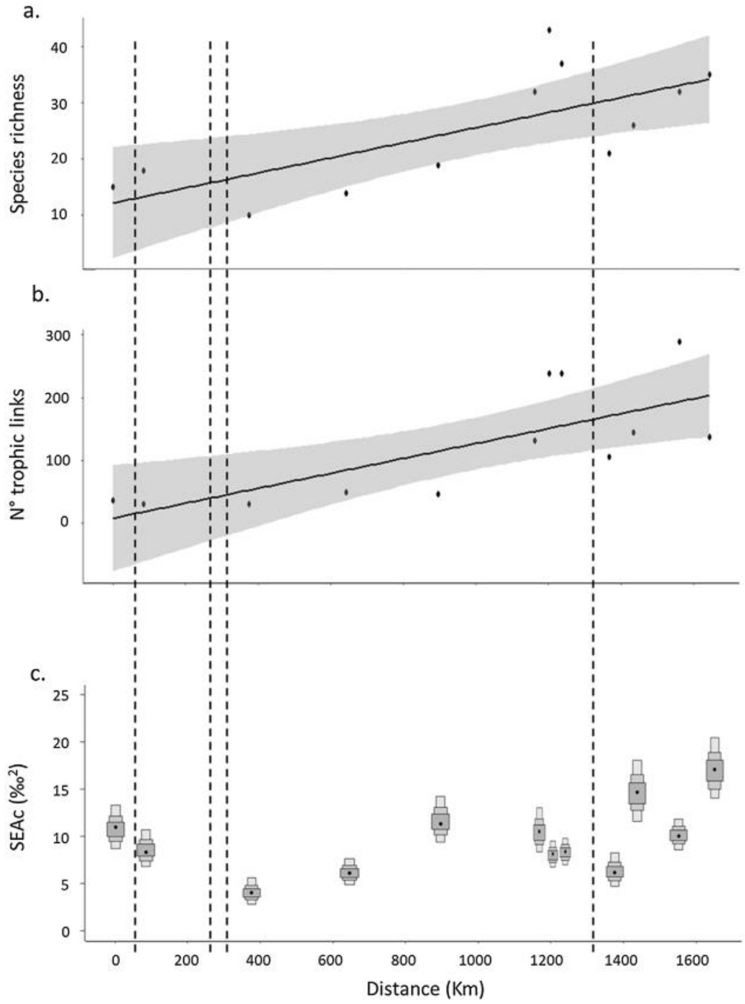


**Fig. 2.** Changes in fish ecological diversity at community level along the longitudinal gradient of Uruguay River: a. Species richness; b. Trophic diversity (number of trophic links); and c. Mean standard ellipse area (SEAc- refering to the isotopic niche breadth), at each sampling sites. Boxes indicate the SEAc with Bayesian models and 50, 75, and 95% credibility intervals. Dashed lines indicate the location of dams.
The parameters of the Bayesian model were: 95% confidence intervals, number of chains = 2; iterations = 200000; burning = 10000, and thins = 10, and the ellipse built considered 40% of data points, as implied by SEAc.

The combination of diet analysis and SIA provides different temporal information, from the last few hours (diet analysis; Muñoz et al., 2009) to the past 15–60 days (SIA in muscle; Buchheister and Latour, 2010).

### *Statistical analyses*

We adjusted linear regressions between captured species richness with the positions of each site along the longitudinal gradient of the river. To assess changes in species richness between sites, we calculated the percentage change (gain or loss) between a given site and the site immediately upstream. As a complementary approach, we fitted linear regression models between beta diversity and its components (turnover and nestedness) with the position in the longitudinal river gradient, both for values obtained from pairwise comparisons between each site and the reference site (site 1), as well as between neighbouring sites. Prior to the analyses, data in the dissimilarity matrix were standardized.

For trophic diversity (number of trophic links) we also fitted linear models.

For the ecological niche analyses, we pairwise tested the probabilities of SEAc being higher in one site than in another site of interest (e.g., pre vs. post dam) (Jackson et al., 2011).

All the statistical analyses were done using the open-source Statistical Software Package R (R Development Core Team).

## Results

92 fish species were collected in total from all sampled sites, accounting for 1364 samples for stable isotopes and 2309 for dietary analysis (Table S3 in SM).

In general, fish species richness (alfa diversity) increased along the longitudinal gradient ($R^2 = 0.49$; $p = 0.01$) but showed sharp declines in the sites located downstream of the dams. The greatest loss of species occurred downstream of the dam between sites 2 and 3, with a loss of 44% of the species, and downstream of the Salto Grande Dam, between sites 8 and 9, with a loss of 43% of the species (Table 1; Fig. 2a). The migratory species *Megaleporinus obtusidens* and *Prochilodus lineatus* occurred from site 5 and downstream, while *Salminus brasiliensis* was found at site 7 and

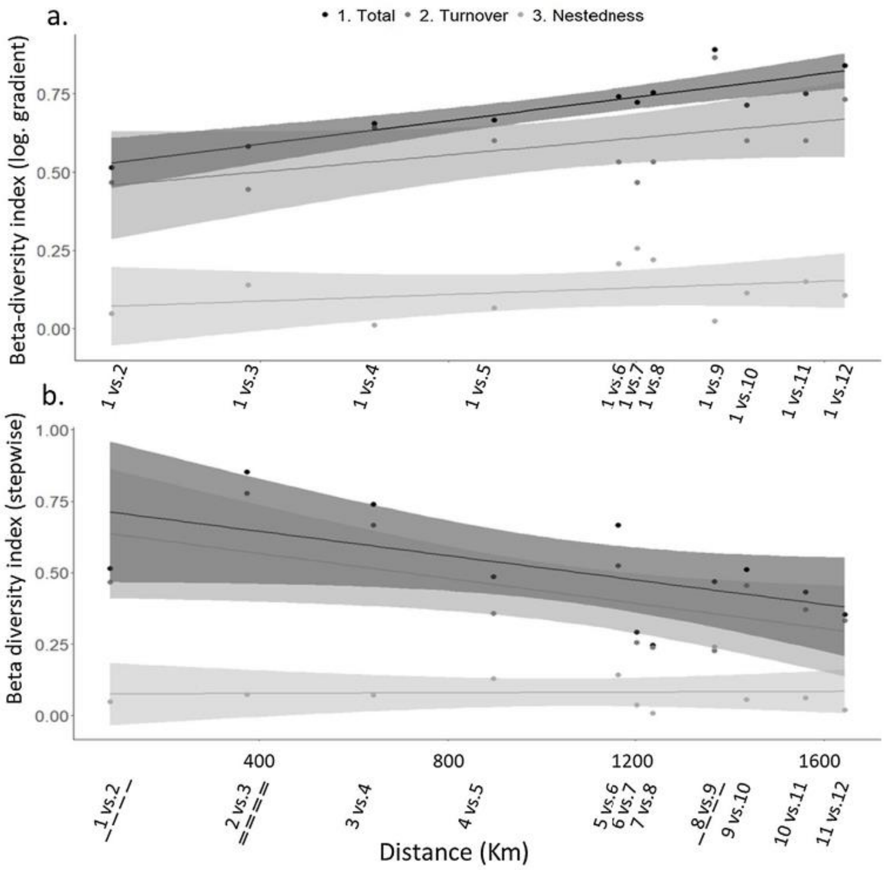


**Fig. 3.** Changes in pairwise beta-diversity and its components (turnover and nestedness) along the longitudinal gradient of the Uruguay River: a. Pairwise comparison between each site and the first site (site 1) at the headwaters; b. Step-wise: pairwise comparison between each site and the neighbor site, located downstream. Dashed lines indicate the presence of dams between those sites.

distributed downstream along the rest of the longitudinal gradient (Table S3 in SM).

Remarkably, despite the sampling effort being greater in the upper section (by performing three different methods), we found lower species richness there than in the middle and lower sections. Also, despite the relatively low number of sampling points in space and time, the patterns found were strong and aligned with expectations.

Of the three different beta-diversity estimation, two of them, multiple beta-diversity and turnover, provided support to the hypothesis that longitudinal trends in diversity existed and were interrupted by dams. Multiple beta-diversity ($\beta_{SOR}$, estimated as the multiple comparison of all possible pairs of sites) was high ($\beta_{SOR} = 0.82$), with turnover being the component with the highest contribution ($\beta_{SIM} = 0.72$), while nestedness had a low contribution to the difference in species composition between local communities along the gradient ($\beta_{NES} = 0.10$). In the analysis comparing each site with the reference site (i.e., site 1), pairwise beta diversity also increased along the longitudinal gradient, showing a marginally significant relationship with the distance to the headwaters ($R^2 = 0.259$; $p = 0.06$). Turnover also significantly increased along the longitudinal gradient ($R^2 = 0.305$; $p = 0.04$), but nestedness did not show a clear pattern ($R^2 = 0.110$; $p > 0.05$) (Fig. 3a; Table S5 in SM). The highest pairwise beta diversity (i.e., the highest differences between communities) and species turnover were found between sites 1 and 9 (downstream of Salto Grande Dam). In contrast, beta diversity and species turnover from the step-wise comparison between consecutive sites decreased along the longitudinal gradient, with a significant relationship with the distance to the headwaters ($R^2 = 0.864$; $p < 0.001$ and $R^2 = 0.571$; $p < 0.004$, for total beta diversity and species turnover, respectively), while nestedness again did not show a significant pattern with the distance to the headwaters ($R^2 = 0.044$; $p > 0.05$) (Fig. 3b; Table S5, SM). In this case, the highest beta-diversity and turnover were observed between sites 2 and 3 (i.e., the sites separated by two dams), whereas the lowest beta diversity was observed in the stretch between sites 6 and 8.

Trophic diversity (expressed as the number of trophic links) followed a similar pattern to taxonomic richness, i.e., a general trend of increase along the longitudinal gradient showing interruptions in the areas with dams. The number of trophic links recorded in the network ranged from 31 to 289, with the minimum reported at sites 2 and 3 and the maximum at site 12, showing an increase along the longitudinal gradient ($R^2 = 0.55$, $p = 0.006$), and decreased after the dams (i.e., from 36 to 31 between site 1 and 2, with the strongest decline observed after the Salto Grande dam, from 238 to 105 trophic links) (Fig. 2b).

In the case of isotopic niche area, SEAc presented a strong decrease in the upper reaches coinciding with the presence of the dam cascade (99% probability of having a higher SEAc in site 2 than in site 3, site located downstream the dam cascade), followed downstream by increases and a more even distribution of the isotopic niche in the middle and lower stretches of the river (Table 1; Fig. 2c). Similarly to species richness and trophic diversity, the SEAc showed a reduction after Salto Grande, with a 96% probability of

SEAc being higher in the pre-Salto Grande site than in the post-Salto Grande location.

## Discussion

The general longitudinal patterns found (i.e., increased species richness, beta-diversity and turnover of species, trophic diversity, and ecological niche diversity) support the general framework proposed by the River Continuum Concept (Vannote et al., 1980). However, we also found clear evidence of the negative impacts of dams on fish diversity as predicted by the SDC (Ward and Stanford, 1983; 1995), shown by the sharp declines in species richness, trophic diversity, and ecological niche diversity in the sections immediately downstream of the dams, as well as the changes in turnover in paired sites around dams.

Similar evidence partially supporting the RCC was found in the Tennessee River (USA) and major tributaries (23 reservoirs), where fish species richness and the number of functional attributes increased longitudinally (ca. 1500 km) despite being highly dammed (Besson et al., 2023). However, fish species richness and abundance often decrease at sites located further downstream of a cascade of dams, as found in three Brazilian basins (Iguaçu, Paranapanema, and São Francisco River basins) (Ganassin et al., 2021). The decrease in species richness after the dams may be a consequence of the changes in environmental conditions (Pelicice et al., 2018). In the dam cascades located in the upper Uruguay River, we observed an abrupt reduction in species richness from site 2 to site 3, with the latter having the lowest species richness of the entire river. This likely reflects the limitation of fish migration upstream of the dams, as suggested elsewhere (e.g., de Bem et al., 2021; Ribolli et al., 2021). In this sense, we observed the presence of migratory species in the middle reach of the Uruguay River, from site 5 to the mouth, which are sites located downstream of the dam cascades. This had been observed in previous studies where richness of migratory species increased towards downstream reaches of dammed rivers (Pelicice et al., 2018).

The negative impacts on fish ecological diversity indicators, along with their recovery as the distance to the dams increased, align with the predictions of the Serial Discontinuity Concept (SDC) and its modifications (Ward and Stanford, 1983; 1995), thus supporting our hypothesis.

Furthermore, the predominant influence of species turnover on beta diversity among all sites support the notion that dams act as environmental filters, promoting species sorting (López-Delgado et al., 2020) and the introduction of new ones. The step-wise beta-diversity decreasing along the longitudinal gradient suggests that the variation in species composition among neighboring sites decreased as the river potentially receives new species from tributaries in the longitudinal gradient. However, we observed that the highest beta-diversity and turnover occurred downstream of the dam cascade in the upper part of the river. There, we observed the effects of dams preventing the accumulation of species, altering the downstream composition as found in other dammed rivers (Agostinho et al., 2008).

These findings align with our findings at the species richness level, underscoring the impact of dam-induced habitat fragmentation on beta diversity (Edge et al., 2017). Similar patterns have been observed in studies on fish (e.g., Lansac-Tôha et al., 2019; Ganassin et al., 2021) and macroinvertebrates (Wang et al., 2021a).

Empirical evidence shows that taxonomic diversity is usually high in sites located in a highly connected longitudinal gradient (i.e., more central locations), but beta diversity is often low as species compositions are similar due to the absence of dispersal restric-

**Box 1: Synthesis of factors that may operate promoting changes in isotopic signal and ratios, either due to local characteristics without changes in fish diet (i.e., processes that may be considered artifacts in SIA), or by processes leading to true changes in diet and energy acquisition and flow within communities. Several of these factors can respond to direct or indirect environmental changes promoted by dams.**

| Type of variability | Factors leading to higher isotopic diversity of consumers | Mechanisms | Literature example | Potentially operating in this study |
|---|---|---|---|---|
| Biotic factors | High taxonomic and functional diversity of basal resources. | A greater variety of resources may be consumed by individuals | Layman et al., 2007a | yes |
| | Different origins of similar basal resources (e.g., detritus). | Resources of different origins (e.g., C3 vs. C4 dominant terrestrial vegetation producing detritus) are consumed by individuals within a species and/or individuals from different species at the community level. | Fry, 2006 | |
| | Higher fish taxonomic richness | Often correlates with high functional richness, and/or differential use of space. E.g., more specialist species can use more resources. | Layman et al., 2007b | yes |
| | Long movement of fish | Implies the integration during weeks of different and distant resources with potentially different isotopic ratios. | Rasmussen et al., 2009; Wang et al., 2021b | yes (mainly in the uninterrupted stretch and near the river mouth) |
| Abiotic factors | High environmental heterogeneity at different spatial scales | Greater variety of resources offered by different habitats at one time (e.g., riffles and pools, floodplain lakes connected to the river) | Silva-Azevedo et al., 2021 | yes (mainly in the middle and lower sections) |
| | High environmental heterogeneity in time | Greater temporal variability of isotopic ratios of benthic algae due to changing flow, either naturally or by dam operation | Trudeau and Rasmussen, 2003; Wang et al., 2021b | yes |
| Type of variability | Lower isotopic diversity of consumers | Mechanisms | Literature | Potential |
| Abiotic factors | Low environmental heterogeneity (including hydrological homogenization) | Dams may promote homogenization of limnological conditions in the transition zone and reservoir homogenizing isotopic values of resources. | Turner et al., 2015 | yes |
| | Pollution | Loss of sensitive taxa and homogenization of basal resources | Wang et al., 2021b | |

tions (Gianluca et al., 2017; Henriques-Silva et al., 2019). These central communities seemed to be present in our study system in the dam-free areas, primarily between sites 6 and 8, where we found high alpha diversity and low differences in community composition. These stretches may also act as species hubs that facilitate biodiversity recovery (Pachla et al., 2022).

The longitudinal patterns in the isotopic niche area were less clear than those observed with alpha and beta-diversity. Several not mutually exclusive factors might be operating on the variability of the isotopic signal. A series of both biotic and abiotic factors directly or indirectly promoted by dams (not analyzed in this work), can promote either high or low isotopic diversity (Box 1). The main abiotic factors potentially affecting ecological diversity include spatial and temporal environmental heterogeneity (Layman et al., 2007b; Turner et al., 2015) and hydrological heterogeneity determined by variability in water flows (Trudeau and Rasmussen, 2003). Biotic factors mainly include a high diversity of basal resources, a local increase in species richness, and the use of a wide diversity of environments and food sources (Delong et al., 2011). Also, the arrival of individuals that move long distances allows for the incorporation of isotopic signals from diverse environments, increasing the isotopic niche area in a given location (Rasmussen et al., 2009; Wang et al., 2021b). This phenomenon could well explain the higher isotopic niche area found for the fish community at the areas near the river mouth and at site 5, where fish could freely move and assimilate resources with potentially contrasting isotopic values along a stretch of 1000 km. Some of these factors could have operated in the long unregulated and thus highly variable stretch in the middle section of the Uruguay River.

The dimensions of our river (ca. 1800 km long, with an average discharge above 4000 $m^3$/s) and the scale of our study allowed us to detect the recovery of the system after the negative impacts of dams.

Our results suggest that the dam-free stretches of the Uruguay River play a crucial role in maintaining the river's ecological diversity, as suggested by the recovery of ecological niche areas, mainly in the middle section. Fish passage constructions often fail as upstream movements are allowed but the return of adults and their offspring is not (Agostinho et al., 2007). Therefore, the maintenance of long dam-free reaches and undammed tributaries in the watershed is key to maintaining fish diversity in impacted rivers (López-Delgado et al., 2020). Tributaries can provide food resources and serve as a refuge and feeding areas (Santos et al., 2020; Pachla et al., 2022) and can be used as spawning areas for migratory fish (Reynalte-Tataje et al., 2012) and nursery (Corrêa et al., 2011).

## Conclusions

Our results contribute to enriching theoretical frameworks such as RCC and SDC by evidencing a general pattern of longitudinal increases in fish species richness, beta diversity and ecological functions, but also clear negative effects of dams, mainly of the cascade of dams in the upper section of the river. Our findings highlight the need to consider diverse dimensions of diversity (e.g., species richness, beta-diversity, trophic diversity, ecological niche), as dams' effects go beyond the loss of species. The size and flow of this river, as well as the focus on the entire longitudinal gradient, enabled us to detect ecosystem recoveries within the dam-free section. In the Neotropics, numerous large dams are projected in the coming decades (Winemiller et al., 2016; Pelicice and Castello, 2021). Notably, in the Uruguay River, two additional consecutive hydroelectric dams, Garabí (planned operational power: 2700 MW/h) and Panambí (1800 MW/h), are scheduled in the middle section (1000 km stretch where the river currently flows freely), coinciding with the highest ecological diversity of fish. This calls for attention from the relevant authorities in the different countries involved. The Uruguay River is situated at a triple multinational border, which also implies that environmental monitoring data may be collected at different times and at a specific number of sites and may imply differences in fishing techniques and effort. Through this work, we identified the need to establish and sustain standardized transnational monitoring programs to generate scientific knowledge that properly informs policy and management.

## Author contributions

Conceptualization: AL-R, MM, IG-B; Methodology: AL-R, IG-B; Investigation: AL-R, AD, SdAS, JP, FTM, DR-T, EZ-F, IG-B; Resources: DR-T, EZ-F, IG-B; Data curation: AL-R, SdAS, IS, JP, IG-B; Formal analysis: AL-R; Writing-original draft: AL-R, MM, IG-B; Writing review & editing: all; Visualization: ALR; Supervision: MM, IG-B; Project administration & Funding acquisition: DR-T, EZ-F, IG-B.

## Funding

This research project was partly funded by the Scientific Research Sectorial Commission (Uruguay) (Project CSIC I+D_2016_577-348) and the National Agency for Innovation and Research (ANII) (Project ANII-FCE_2_2016_1_126780).

## Conflict of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We thank the artisanal fisherman Elbio Russo for his support and collaboration with sampling and fisheries data. We deeply thank the very constructive comments from reviewers and editor. AL-R, MM, IGB, AD, FTM are supported by ANII and PEDECIBA. AL-R received support from CAP-UDELAR. AL-R, MM, IGB also acknowledge the funding from CSIC Groups-2022 #882442 and #883452. MM also acknowledges the support by the Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany, during a stay as senior researcher. EZF thanks CNPq, grant 302860/2014–2, and Engie (Tractebel Energia), Consórcio Itá, and Consórcio Machadinho for financial support.

Fish sampling and handling procedures were approved by the Honorary Commission of Animal Experimentation, Uruguay (CHEA, Permit-ID 309) and the ethics committee of the Federal University of Fronteira Sul, Brazil (permit-ID 23.205.004977/2015-90).

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pecon.2024.03.003.

## References

Agostinho, A.A., Marques, E.E., Agostinho, C.S., Almeida, D.A., Oliveira, R.J., Melo, J.R., 2007. Fish ladder of Lajeado Dam: migrations on one-way routes? Neotrop. Ichthyol. 5, 121130, http://dx.doi.org/10.1590/S1679-62252007000200005.

Agostinho, A.A., Pelicice, F.M., Gomes, L.C., 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz. J. Biol. 68, 1119–1132, http://dx.doi.org/10.1590/S1519-69842008000500019.

Barbosa, F.A.R., Padisák, J., Espíndola, E.L.G., Borics, G., Rocha, O., 1999. The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-basin, São Paulo State, Brazil. In: Tundisi, J.G., Straskraba, M. (Eds.), Theoretical reservoir ecology and its applications. Backhuys Publishers, Leiden, pp. 425–437.

Barletta, M., Jaureguizar, A.J., Baigun, C., Fontoura, N.F., Agostinho, A.A., Almeida-Val, V.M., Val, A.L., Torres, R.A., Jimenes-Segura, L.F., Giarrizzo, T., Fabré, N.N., Batista, V.S., Lasso, C., Taphorn, D.C., Costa, M.F., Chaves, P.T., Vieira, J.P., Correa, M.F., 2010. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. J. Fish Biol. 76, 2118–2176, http://dx.doi.org/10.1111/j.1095-8649.2010.02684.x.

Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. Meth. Ecol. Evol. 35, 808–812, http://dx.doi.org/10.1111/j.2041-210X.2012.00224.x.

Besson, J.C., Neary, J.J., Stafford, J.D., Dunn, C.G., Miranda, L.E., 2023. Fish functional gradients along a reservoir cascade. Freshw. Biol. 00, 1–13, http://dx.doi.org/10.1111/fwb.14087.

Buchheister, A., Latour, R.J., 2010. Turnover and fractionation of carbon and nitrogen stable isotopes in tissues of a migratory coastal predator, summer flounder (*Paralichthys dentatus*). Can. J. Fish. Aquat. Sci. 67, 445–461, http://dx.doi.org/10.1139/F09-196.

Corrêa, R.N., Hermes-Silva, S., Reynalte-Tataje, D.A., Zaniboni-Filho, E., 2011. Distribution and abundance of fish eggs and larvae in three tributaries of the Upper Uruguay River (Brazil). Environ. Biol. Fishes. 91, 51–61, http://dx.doi.org/10.1007/s10641-010-9759-x.

de Bem, J., Ribolli, J., Röpke, C., Winemiller, K.O., Zaniboni-Filho, E., 2021. A cascade of dams affects fish spatial distributions and functional groups of local assemblages in a subtropical river. Neotrop. Ichthyol. 19, e200143, http://dx.doi.org/10.1590/1982-0224-2020-0133.

Delong, M.D., Thorp, J.H., Thoms, M.C., McIntosh, L.M., 2011. Trophic niche dimensions of fish communities as a function of historical hydrological conditions in a Plains River. Riv. Syst. 19, 177–187, http://dx.doi.org/10.1127/1868-5749/2011/019-0036.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, L.J., Sullivan, C.A., 2005. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81, 163–182, http://dx.doi.org/10.1017/S1464793105006950.

Edge, C.B., Fortin, M.J., Jackson, D.A., Lawrie, D., Stanfield, L., Shrestha, N., 2017. Habitat alteration and habitat fragmentation differentially affect beta diversity of stream fish communities. Landscape Ecol. 32, 647–662, http://dx.doi.org/10.1007/s10980-016-0472-9.

Fry, B., 2006. Stable isotope ecology. Springer, New York, pp. 318, 521.

Ganassin, M.J.M., Muñoz-Mas, R., Oliveira, F.J.M., Muniz, C.M., Santos, N.C.L., García-Berthou, E., Gomes, L.C., 2021. Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins. Sci. Tot. Environ. 778, 146246, http://dx.doi.org/10.1016/j.scitotenv.2021.146246.

Gianluca, A.T., Declerck, S.A.J., Lemmens, P., De Meester, L., 2017. Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β-diversity. Ecology. 98, 525–533, http://dx.doi.org/10.1002/ecy.1666.

Guo, F., Fry, B., Yan, K., Huang, J., Zhao, Q., O'Mara, K., Li, F., Gao, W., Kainz, M.J., Brett, M.T., Bunn, S.E., Zhang, Y., 2023. Assessment of the impact of dams on aquatic food webs using stable isotopes: current progress and future challenges. Sci. Tot. Environ. 904, 167097, http://dx.doi.org/10.1016/j.scitotenv.2023.167097.

Henriques-Silva, R., Logez, M., Reynaud, N., Tedesco, P.A., Brosse, S., Januchowski-Hartley, S.R., Oberdorff, T., Argillier, C., 2019. A comprehensive examination of the network position hypothesis across multiple river metacommunities. Ecography 42 (2), 284–294, http://dx.doi.org/10.1111/ecog.03908.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602, http://dx.doi.org/10.1111/j.1365-2656.2011.01806.x.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. Can. J. Fish. Aquat. 106, 110–127.

Lansac-Tôha, F.M., Heino, J., Quirino, B.A., Moresco, G.A., Peláez, O., Meira, B.R., Rodrigues, L.C., Jati, S., Lansac-Tôha, F.A., Velho, L.F.M., 2019. Differently dispersing organism groups show contrasting beta diversity patterns in a dammed subtropical river basin. Sci. Tot. Environ. 691, 1271–1281, http://dx.doi.org/10.1016/j.scitotenv.2019.07.236.

Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007a. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology. 88, 42–48, http://dx.doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2.

Layman, C.A., Quattrochi, J.P., Peyer, C.M., Allgeier, J.E., 2007b. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecol. Lett. 10, 937–944, http://dx.doi.org/10.1111/j.1461-0248.2007.01087.x.

López-Delgado, E.O., Winemiller, K.O., Villa-Navarro, F.A., 2020. Local environmental factors influence beta-diversity patterns of tropical fish assemblages more than spatial factors. Ecology. 101, e02940, http://dx.doi.org/10.1002/ecy.2940.

López-Rodríguez, A., Silva, I., de Ávila-Simas, S., Stebniki, S., Bastian, R., Massaro, M.V., Pais, J., Tesitore, G., Teixeira de Mello, F., D'Anatro, A., Vidal, N., Meerhoff, M., Reynalte-Tataje, D.A., Zaniboni-Filho, E., González-Bergonzoni, I., 2019. Diets and trophic structure of fish assemblages in a large and unexplored subtropical river: the Uruguay River. Water. 11, 1374, http://dx.doi.org/10.3390/w11071374.

Muñoz, I., Ramaní, A.M., Rodrígues-Capítulo, A., González Esteban, J., García-Berthou, E., 2009. Trophic relations in fluvial ecosystems. In: Elosegui, A., Sabater, S. (Eds.), Concepts and techniques in fluvial ecology (in Spanish). Fundación BBVA, Bilbao, pp. 347–366.

Newsome, S.D., Martínez del Río, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429–436, http://dx.doi.org/10.1890/060150.01.

Pachla, L.A., Hartmann, P.B., Massaro, M.V., Pelicice, F.M., Reynalte-Tataje, D.A., 2022. Recruitment of migratory fish in free-flowing rivers with limited floodplain development. Aquat. Conserv.: Mar. Freshw. 32, 1888–1900, http://dx.doi.org/10.1002/aqc.3860.

Pease, A.A., González-Díaz, A.A., Rodiles-Hernández, R., Winemiller, K.O., 2012. Functional diversity and trait-environment relationship of stream fish assemblages in a large tropical catchment. Freshw. Biol. 57, 1060–1075, http://dx.doi.org/10.1111/j.1365-2427.2012.02768.x.

Pelicice, F.M., Castello, L., 2021. A political tsunami hits Amazon conservation. Aquat. Conserv.: Mar. Freshw. 31, 1221–1229, http://dx.doi.org/10.1002/aqc.3565.

Pelicice, F.M., Azevedo-Santos, V.M., Esguícero, A.L.H., Agostinho, A.A., Arcifa, M.S., 2018. Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil. Neo. Ichthyol. 16, e170150, http://dx.doi.org/10.1590/1982-0224-20170150.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montaña, C.G., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189, http://dx.doi.org/10.1007/s00442-006-0630-x.

Rasmussen, J.B., Trudeau, V., Morinville, G., 2009. Estimating the scale of fish feeding movements in rivers using δ13C signature gradients. J. Anim. Ecol. 78, 674–685, http://dx.doi.org/10.1111/j.1365-2656.2008.01511.x.

Reynalte-Tataje, D.A., Nuñer, A.P., Nunes, M.C., Garcia, V., Lopes, C.A., Zaniboni-Filho, E., 2012. Spawning of migratory fish species between two reservoirs of the upper Uruguay River, Brazil. Neotrop. Ichthyol. 10, 829–835, http://dx.doi.org/10.1590/S1679-62252012000400016.

Ribolli, J., Zaniboni-Filho, E., Barros Machado, C., de Souza Guerreiro, T.C., Domínguez de Freitas, P., Galetti Jr., P.M., 2021. Anthropogenic river fragmentation reduces long-term viability of the migratory fish *Salminus brasiliensis* (Characiforme:Bryconidae) populations. Neotrop. Ichthyol. 19, e200123, http://dx.doi.org/10.1590/1982-0224-2020-0123.

Ruhí, A., Muñoz, I., Tornes, E., Batalla, R.J., Vericat, D., Ponsatí, L., Acuña, V., Von Schiller, D., Marcé, R., Bussi, G., Francés, F., Sabater, S., 2016. Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. Freshw. Biol 61, 1536–1549, http://dx.doi.org/10.1111/fwb.12794.

Santos, N.C.L., Garcia-Berthou, E., Dias, J.D., Lopes, T.M., Affonso, I.D.P., Severi, W., Gomes, L.C., Agostinho, A.A., 2018. Cumulative ecological effects of a Neotropical reservoir cascade across multiple assemblages. Hydrobiologia. 819, 77–91, http://dx.doi.org/10.1007/s10750-018-3630-z.

Santos, N.C.L., Dias, R.M., Alves, D.C., de Melo, B.A.R., Ganassin, M.J.M., Gomes, L.C., Servi, W., Agostinho, A.A., 2020. Trophic and limnological changes in highly fragmented rivers predict the decreasing abundance of detritivorous fish. Ecol. Indic. 110, 105933.

Silva-Azevedo, L., Pestana, I.A., Almeida, M.G., Bastos, W.R., Souza, C.M.M., 2021. Do fish isotopic niches change in an Amazon floodplain lake over the hydrological regime? Ecol. Freshw. Fish. 31, 72–80, http://dx.doi.org/10.1111/eff.12609.

Thorp, J.H., Thoms, M.C., Delong, M.D., 2008. The riverine ecosystem synthesis. Towards Conceptual Cohesiveness in River Science. Academic Press/Elsevier, Amsterdam, the Netherlands.

Trudeau, V., Rasmussen, J.B., 2003. The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. Limnol. Oceanogr. 48, 2194–2199, http://dx.doi.org/10.4319/lo.2003.48.6.2194.

Turgeon, K., Turpin, C., Gregory-Eaves, I., 2019. Dams have varying impacts on fish communities across latitudes: a quantitative synthesis. Ecol. Lett. 22, 1501–1516, http://dx.doi.org/10.1111/ele.13283.

Turner, T.F., Krabbenhoft, T.J., Collyer, M.L., Krabbenhoft, C.A., Edwards, M.S., Sharp, Z.D., 2015. Retrospective stable isotope analysis reveals ecosystem responses to river regulation over the last century. Ecology. 96, 3213–3226, http://dx.doi.org/10.1890/14-1666.1.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37, 130–137, http://dx.doi.org/10.1139/f80-017.

Wang, J., Ding, C., Tao, J., Jiang, X., Heino, J., Ding, L., Su, W., Chen, M., Zhang, K., He, D., 2021a. Damming affects riverine macroinvertebrate metacommunity dynamics: Insights from taxonomic and functional beta diversity. Sci. Tot. Environ. 763, 142945, http://dx.doi.org/10.1016/j.scitotenv.2020.142945.

Wang, S., Luo, B.K., Qin, Y.J., Zhao, J.G., Wang, T.T., Stewart, S.D., Yang, Y., Chen, Z.-B., Qiu, H.X., 2021b. Fish isotopic niches associated with environmental indicators and human disturbance along a disturbed large subtropical river in China. Sci. Tot. Environ. 750, 141667, http://dx.doi.org/10.1016/j.scitotenv.2020.141667.

Ward, J.V., Stanford, J.A., 1983. The serial discontinuity concept of lotic ecosystems. In: Fontaine, T.D., Bartell, S.M. (Eds.), Dynamic of Lotic Ecosystems. Ann Arbor Science, Ann Arbor, MI, pp. 347–356.

Ward, J.V., Stanford, J.A., 1995. The serial discontinuity concept: extending the model to floodplain rivers. Regul. Riv. Res. Manage. 10, 159–168, http://dx.doi.org/10.1002/rrr.3450100211.

Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. Ecol. Monogr. 60, 331–367, http://dx.doi.org/10.2307/1943061.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I.G., Darwan, W., Lujan, N.K., Harrison, I., Stiassny, M.L., Silvano, R.A., Fitzgerald, D.B., Pelicice, F.M., Agostinho, A.A., Gomes, L.C., Albert, J.S., Baran, E., Petrere Jr., M., Zarfl, C., Mulligan, M., Sullivan, J.P., Arantes, C.C., Sousa, L.M., Koning, A.A., Hoeignghaus, D.J., Sabaj, M., Lundberg, J.G., Armbruster, J., Thieme, M.L., Petry, P., Zuanon, J., Torrente Vilara, G., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C.S., Akama, A., van Soesbergen, A., Sáenz, L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351, 128–129, http://dx.doi.org/10.1126/science.aac7082.

Zaniboni-Filho, E., Schulz, U.H., 2003. Migratory Fishes of the Uruguay River. In: Carolsfeld, J., Harvey, B., Ross, C., Baer, A. (Eds.), Migratory Fish of South America. Biology, Fisheries and Conservation Status. World Fisheries Trust/Word Bank/International Development Research Centre, Washington D.C., U.S.A. and Ottawa, Canada, pp. 157–194.

# 6. Artículo 3

## Dams modify energetic pathways for fish along a large subtropical river

Anahí López-Rodríguez [a,b,c*], Mariana Meerhoff [a,d,1], Alejandro D'Anatro [e], Sunshine de Ávila-Simas [f], Ivana Silva [b], Franco Teixeira de Mello [a], David Augusto Reynalte-Tataje [g], Evoy Zaniboni-Filho [f], Iván González-Bergonzoni [b,1]

[a] Departamento de Ecología y Gestión Ambiental, Centro Universitario Regional del Este, Universidad de la República, Tacuarembó s/n, 2000, Maldonado, Uruguay

[b] Departamento de Ciencias Biológicas, CENUR Litoral Norte, Universidad de la República, Ruta 3 Km 363 EEMAC, Paysandú, Uruguay

[c] Departamento de Ecología y Biología Evolutiva, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay

[d] Department of Ecoscience, Aarhus University, Denmark

[e] Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Iguá 4225, Malvín Norte, 11400, Montevideo, Uruguay

[f] Laboratório de Biologia e Cultivo de Peixes de Água Doce (LAPAD), Departamento de Aquicultura, Universidade Federal de Santa Catarina (UFSC), 88066-260 Florianópolis, SC, Brazil

[g] Campus Cerro Largo, Universidade Federal da Fronteira Sul (UFFS), Av. Jacob Reinaldo Haupenthal, 1580, 97900-000 Cerro Largo, RS, Brazil

* Correspondence to: A. López-Rodríguez, Departamento de Ecología y Gestión Ambiental, CURE, Universidad de la República, Tacuarembó s/n, 20000, Maldonado, Uruguay. E-mail: alopez@fcien.edu.uy

[1] Mariana Meerhoff and Iván González-Bergonzoni are equal senior authors

## Abstract

The world's rivers face significant anthropogenic pressures that are leading to loss of biodiversity and major changes in ecosystem functioning. Understanding the role of autochthonous and allochthonous subsidy pathways in supporting fish biomass is crucial for determining which ecosystems to prioritize for biodiversity conservation. Most theoretical frameworks addressing fluvial ecosystem functioning have limitations, as some are based on low-order ecosystems in temperate regions, or, alternatively, on large rivers with seasonal flow variation and the presence of floodplains. Most theories also fail to consider the impacts of dam construction, a major anthropogenic stressor currently affecting most rivers worldwide.

Our study aimed to assess the energetic subsidies to fish biomass along a large subtropical river (Uruguay River), using stable isotope analysis and fish biomass data from 12 sites along the longitudinal gradient. Additionally, we tested the potential effects of the four current dams on fish energy subsidy by comparing the contribution of autochthonous and allochthonous pathways between pre- and post-dam sites. We found that the coupling of energy pathways seems to be the rule in this river, rather than the dominance of one pathway over the other. The total biomass of the fish community along the Uruguay River was sustained by coupling both energetic pathways in a similar proportion, with a slight predominance of allochthonous subsidy, but showing an increase in the relative importance of autochthonous subsidy as the river increased in width in the only long unregulated reach. Allochthonous material was particularly important in subsidizing the top of the food web.

Dams appeared to alter the longitudinal patterns, with one pathway losing relevance around dam sites. The direction of such changes seemed, however, to depend on local environmental characteristics. These changes in energetic pathways coincide with observed impacts on fish trophic and taxonomic diversity observed in previously published research in this same river system, providing further evidence of the effects of dams on both fish community structure and functionality. Also, we provide empirical evidence of the importance of both energy sources for maintaining food webs and, therefore, ecosystem-scale processes.

**Keywords:** Uruguay River; habitat fragmentation; fish biomass; fuelling resources; allochthonous support; autochthonous support

## 1. Introduction

The rivers of the world, particularly those in the neotropics, represent one of the most productive ecosystems globally (Dudgeon et al., 2005; Lévêque et al., 2008). Additionally, they are among the freshwater ecosystems facing the greatest anthropogenic pressures (Dudgeon, 2000; Agostinho et al., 2008; Ormerod et al., 2010; Vörösmarty et al., 2010), mainly due to the exponential growth of dam construction and the planning of many more in the coming decades (Agostinho et al., 2007; Winemiller et al., 2016; Pelicice & Castello, 2021; Flecker et al., 2022).

The effects of dams on the environment impact local communities (Junk et al., 1989; Barletta et al., 2010), with primarily those species able to tolerate the physical conditions of the environment persisting (Cross et al., 2011), as well as by altering available resources, thereby affecting food webs (Sabo et al., 2010; Ruhí et al., 2016). Therefore, understanding the patterns of energy circulation, especially the transformation of organic matter and its uptake into food webs, is crucial for maintaining biodiversity (Winemiller et al., 2010). As a consequence, the relative importance of autochthonous (i.e., originated via instream- productivity such as benthic algae) and allochthonous (i.e., arising from terrestrial subsidies of organic matter) basal resources in supporting riverine food webs has been a topic of debate for decades (e.g., Vannote et al., 1980; Junk et al., 1989; Thorp & Delong, 1994; Humphries et al., 2014; Guo et al., 2022; Leal et al., 2023).

Several theoretical frameworks have been proposed on this topic. One of the earliest theories in recent fluvial ecology, the River Continuum Concept (RCC) (Vannote et al., 1980), connects the physical and geomorphological characteristics of running waters with biodiversity patterns and community dynamics. It describes predictable longitudinal shifts in community composition, food webs, and ecosystem-scale processes from headwaters to mouth. According to this theory, headwaters are strongly influenced by riparian vegetation, which contributes with allochthonous organic matter (detritus) to the system but reduces algal production due to restriction of light penetration by dense canopy cover. Consequently, headwater food webs are subsidized by allochthonous resources, and this allochthonous subsidy decreases along the longitudinal gradient, with an increase in the relative contribution of benthic algae (autochthonous fuelling) in the middle and lower reaches due to increased openness and better light conditions (Vannote et al., 1980). However, some limitations of this theory include its focus mainly on macroinvertebrate communities and constructing generalized predictions based solely on temperate low-order systems (streams). Additionally, this theory does not incorporate the lateral dimension (i.e., connection with floodplains) in fluvial ecosystems (Junk et al., 1989). This led to the development of the Flood Pulse Concept (FPC), which suggests that fluvial ecosystems are connected to their floodplains through prolonged and often predictable pulses, increasing the exchange of matter and energy between terrestrial and aquatic ecosystems, thus shaping the assemblages of local communities. According to this theory, most of the energetic subsidy for riverine food webs comes from terrestrial organic matter (Junk et al., 1989). The Riverine Productivity Model (RPM) (Thorp & Delong, 1994; 2002) and the Riverine Ecosystem Synthesis (RES) (Thorp et al., 2006; 2008) contradict the Flood Pulse Concept (FPC) in that assumption. According to these theories, the biomass subsidizing consumers in rivers has a predominantly autochthonous origin. The RES proposes that the only exception would be for some species and seasons in patches with a significant input of terrestrial detritus, such as shallow areas with dense canopy cover (Thorp et al., 2006).

In the last decade, a theory that reconciles previous theoretical frameworks has been proposed: The River Wave Concept (RWC-Humphries et al., 2014). It postulates that in river sections with high flow biomass will be mainly subsidized by carbon from the terrestrial environment, as under these conditions autotrophic production should be limited by low light input (Humphries et al., 2014). The same is expected in periods of flood pluses. All these theories present limitations, as some originated in low-order ecosystems in temperate regions (e.g., Vannote et al., 1980) or on large rivers with seasonal flow variation and the presence of floodplains (e.g., Junk et al., 1989; Thorp & Delong, 1994; Thorp et al., 2006; Humphries et al., 2014). Furthermore, these theories propose contrasting scenarios, all of them suggesting that river geomorphology and its interaction with the hydrological regimes are drivers of changes in the energy sources of riverine food webs.

However, all these theories have been formulated for systems without interruptions in their hydrology. The importance of hydrology and of dams-promoted environmental modifications as key determinants of food webs has been widely recognized (e.g., Bunn & Arthington, 2002; Humpries et al., 2014), indicating the need to address these gaps.

The construction of dams alters the structure and functioning of running waters by modifying the physical conditions of the environment, both in the riverine ecosystem and the surrounding terrestrial habitats (Bunn & Arthington, 2002; Dudgeon et al., 2005). The primary changes in the biophysical environment are associated with reductions in water flow variability and overall changes to the hydrological regime, decreased transport of matter and nutrients downstream of the reservoirs (due to increased retention in reservoir sediments), and alterations in water transparency (e.g., Baxter, 1977; Nilsson et al., 2005; Barletta et al., 2010; Cross et al., 2011). Dams also reduce both longitudinal and lateral connectivity, decreasing the input of allochthonous material from the surrounding environment and interfering in the energy transfer trough the food web (Cross et al., 2011) and across habitats. All these changes can have effects on the available resources that support trophic pathways in dam-affected sites (Sabo et al., 2010; Winemiller et al., 2010; Roach & Winemiller, 2015; Ruhí et al., 2016).

Some studies have investigated the origin of biomass fuelling food webs in dammed rivers, analysing riverine regions upstream and downstream of dams, as well as the lacustrine zone of the reservoir, showing contrasting results. The energetic subsidy for consumers in reservoirs and downstream areas often derives from autochthonous organic matter (e.g., Hoeinghaus et al., 2007; Doi et al., 2008; Roach, 2013; Wellard-Kelly et al., 2013; Pease et al., 2019), while other studies have observed allochthonous subsidy in food webs in reservoirs or downstream regions (e.g., Wang et al., 2014; Kaymak et al., 2015; Felden et al., 2020). Despite the contrasting evidence, a review conducted by Guo et al. (2023), analyzing studies comparing regulated vs. unregulated rivers as well as pre-post dam sites (both spatially and temporally), observed that in hydrologically regulated systems due to the presence of dams, the trophic web support is predominantly of autochthonous origin.

Despite significant progress has been made in recent years, the debate about the potential effects of dams on changes on the origin of resources subsidizing fish biomass continues among ecologists (e.g., Guo et al., 2023; Leal et al., 2023). Several knowledge gaps have been identified, including the need for more work at higher biological organization levels (e.g., community and all trophic network levels) (Guo et al., 2023).

In this context, the objective of this study was to describe the origin of energetic subsidies to the fish biomass in the longitudinal gradient of a large subtropical river in South America (Uruguay River), combining stable isotope analysis and information on the biomass of fish species that comprise the community at each sampling site. Additionally, we tested the potential effects of the four dams located in this river on fish energy subsidy by comparing the contribution of autochthonous and allochthonous resources between pre- and post-dam sites. In this context, we hypothesized that dams located on the Uruguay River have an effect on the availability of food resources for fish, as a result of increased water residence and reductions in water velocity and suspended sediments in the reservoir and its tail, and as a result of the reduced downstream sediment transport and thus allowing greater penetration of light, favouring local primary production (autochthonous basal resources). Therefore, we expected that in regions of the Uruguay River affected by dams, the greater contribution to fish biomass would come from aquatic carbon (i.e., autochthonous origin). Furthermore, we also expected that the accumulation of effects caused by the presence of cascade dams would accentuate the expected effects of a single dam, thus we expected to find low proportion of species subsidizing by allochthonous pathway.

## 2. Methods

### *2.1. Study area*

This research was carried out along an approximately 1700 km stretch of the main course of the Uruguay River, the second largest tributary of Río de la Plata River drainage basin, spanning 1,800 km from its origin in Brazil, in the confluence of Canoas and Pelotas rivers, to its mouth in La Plata River (Saccol-Pereira, 2008). Its middle and lower sections serve as the boundary between Argentina and Uruguay. The Uruguay River can be divided into three main sections based on its geological characteristics: upper, middle, and lower. The Yucuma Falls in Brazil are the natural division between the upper and middle sections, while the Salto Grande Dam marks the boundary between the river's middle and lower sections (Zaniboni-Filho & Schulz, 2003). Over the past 20 years, the upper section of the Uruguay River has seen a development of hydroelectric dams, with the construction of three dams in that section of the river. Along the entire longitudinal gradient spanning 1800 km, there are four hydroelectric dams in operation. Three of these dams are located in the upper section: Machadinho (capacity: 1140 MW/h; operated since 2002), Itá (capacity: 1450 MW/h; opening date: 2000), and Foz de Chapecó (capacity: 855 MW/h; opened in 2010). In the lower section, there is the Salto Grande Dam (capacity: 1890 MW/h; opened in 1979). The upper Uruguay River is situated within a confined subtropical valley, and it is characterized by the absence of floodplains in its landscape (Reynalte-Tataje et al., 2012). The final sections of the upper part of the river and the middle Uruguay River largely remain undisturbed in terms of hydrology, with an unfragmented stretch spanning approximately 1,000 km. The middle section of the Uruguay River is characterized by a long, undisturbed section with a significant presence of riparian forest on both margins (Argentina and Brazil). In the upper part of this section, we find on the right margin, in Argentina, the Yabotí Biosphere Reserve, and on the left margin, in Brazil, the Turvo State Park, some of the last relicts of the Atlantic Forest Biome (Zaniboni-Filho & Schulz, 2003). In the lower part of the middle section, as the river enters in the pampa's biome, extensive floodplains can be observed. The lower section of the Uruguay River begins downstream of the Salto Grande Dam. In this section, in the upper part, there is an area with a significant presence of native riparian forest along the Uruguay River (Saladero Guaviyú). In the middle part of the lower Uruguay River, there are urban areas as well as sections of islands and marginal wetlands, primarily along the Argentine bank. Towards the lower part, the river begins to widen until it reaches its mouth in the Rio de la Plata Estuary.

The fish communities in the main rivers in the La Plata River basin have a high species and functional richness, including resident and migratory species (Menni, 2004; Bertaco et al., 2016). In particular, the Uruguay River is characterized by commercially important species, such as *Prochilodus lineatus* (Prochilodontidae, local name sabalo or grumata), *Megaleporinus obtusidens* (Characidae, local name boga or piava) and *Salminus brasiliensis* (Characidae, local name dorado) (López-Rodríguez et al., 2019).

### *2.2. Fish sampling*

Fish communities were sampled at 12 sites along the main course of the Uruguay River, during the austral autumn of 2017 (May-early June). Three sites were sampled in the upper river section, five in the middle, and four in the lower section (Fig. 1). Some of the sites are located in areas influenced by dams, representing transition zones between lentic and lotic environments (e.g., sites 1, 2, and 8), while others are situated in flowing sections with diverse characteristics of the surrounding terrestrial environment (Table 1). The selection of sampling sites took into account available monitoring programs along the river to facilitate logistical operations. We sampled during autumn because a higher diversity of fish size ranges and stage in the life cycle could be expected, as most species usually spawn in spring-summer and thus both juveniles and adults could be collected during autumn (Pachla et al., 2022).

In sites 1, 2 and 3 (sites located in the upper section of the Uruguay River in Brazil), ongoing monitoring programs employed a combination of gillnets and trammel nets (gillnets mesh sizes ranging from 15.0 to 80.0 mm knot to knot and lengths that varied between 20 and 120 m, with heights ranging from 1.6 to 8.0 m; trammel nets had inner mesh sizes ranging from 15.0 to 80.0 mm and outer meshes of 200.0 mm knot to knot, with lengths between 30 and 40 m and a height of 1.8 m). Both sets of nets were deployed in the littoral zone in the evening and left in place for approximately 12 hours. Additionally, at all three sites, a seine net trawl and three casts of cast nets (with a mesh size of 8.0 mm) were conducted in the littoral zone during the daytime. In the middle and lower sections of the Uruguay River, we employed multi-mesh Nordic gillnets (30 m long and 1.5 m high, consisting of 12 mesh sizes ranging from 5.0 to 55 mm knot to knot) to sample fish communities. At each site, eight sets of gillnets were placed in the littoral zone, with four sets positioned at depths of 1.5-2.0 m and four in deeper waters (pelagic zone: 2-5.0 m deep), leaving them in place from sunset to sunrise (approximately 12 hours). Fish assemblage and taxonomic richness data are detailed in Lopez-Rodríguez et al. (2019). Additionally, we supplemented our sampling efforts by obtaining commercially important large fish specimens from local fishermen (at sites 6, 7, 8, 11, and 12) whenever these species, known to inhabit the entire river, were not captured using the Nordic multi-mesh gillnets.

All collected fish were identified in the field to the lowest possible taxonomic level, measured for total and standard length in cm, and weighed for total fresh biomass in g.

In Uruguay, fish sampling and handling procedures were approved by the Honorary Commission of Animal Experimentation (CHEA, Permit ID 309). In Brazil, procedures were approved by the ethics committee of the Federal University of Fronteira Sul, Brazil (permit ID 23.205.004977/2015-90).

Fig. 1. Location of the 12 sampling sites along the Uruguay River. From headwaters to mouth: site 1-MPB: Barracão; Site 2-MR: Marcelino Ramos; Site 3-IMO: Mondaí; Site 4-ALE: Alecrim; Site 5-SB: São Borja; site 6- BU: Bella Unión; Site 7-IZ: Isla del Zapallo; Site 8-BEL: Belén; Site 9-GVY: Guaviyú; Site 10-PAY: Paysandú; Site 11-LC: Las Cañas; Site 12- PG: Punta Gorda. The location of sampling sites is represented by black circles; location of dams is represented by white circles. Sites 1 to 5 are in Brazil, sites 6 to 12 were sampled from the Uruguayan side of the river.

Table 1. Sampling sites and dams' location along the longitudinal gradient of the Uruguay River. Riparian cover: % of riparian cover in a radius of 2km for site (information extracted from Google Earth). Dotted lines indicate the presence of dams.

| Site | Width (m) | Characteristics | Riparian cover |
|---|---|---|---|
| 1- MPB | 290 | Near the confluence of the Canoas and Pelotas rivers. Headwater of the Uruguay River. Lentic-lotic transitional environment. No floodplains. | 67 % |
| Machadinho Dam | | | |
| 2- MR | 420 | Lentic-lotic transitional environment | 17 % |
| Itá Dam | | | |
| Foz de Chapecó Dam | | | |
| 3- IMO | 470 | Lotic environment. 60 km downstream from the Foz do Chapecó Dam and 170 km downstream from the Itá Dam | 7 % |
| 4- Alecrim | 830 | Lotic environment. Presence of pools. Turvo State Park (riparian forest and canopy) | 56 % |
| 5- São Borja | 1250 | Lotic environment. Floodplains and pools | 23 % |
| 6- Bella Union | 1900 | Lotic environment. | 10 % |
| 7- Isla del Zapallo | 1750 | Lotic Environment. Floodplains. | 17 % |
| 8- Belen | 2100 | Lentic-lotic transitional environment. 65 km upstream from the Salto Grande Dam. Tail of the Salto Grande Dam | 3 % |
| Salto Grande Dam | | | |
| 9- Guaviyú | 1600 | Lotic environment. 65 Km downstream from the Salto Grande Dam | 26 % |
| 10- Paysandú | 1170 | Lotic environment | 22 % |
| 11- Las Cañas | 6200 | Lotic environment. 65 km downstream from the protected National Park Area: Esteros de Farrapos (riparian forest) | 5 % |
| 12- Punta Gorda | 1200 | Lotic environment. Near the mouth of the Uruguay River in the Río de la Plata | 10 % |

### *2.3. Sampling for stable isotope analyses*

During the sampling campaign, a subset of each fish species collected at each site was selected for stable isotope analysis (SIA). When feasible, flank muscle samples were collected from N=5 individuals per species per site, with the aim of covering a broad size range. If 5 individuals of a species were not captured, flank muscle samples were collected from all individuals caught per species per site.

Moreover, during the field campaigns, samples from potential resources for fish were obtained: basal resources, i.e., fine and coarse particulate organic matter (FPOM and CPOM), periphyton, and terrestrial vegetation (Post, 2002). FPOM was collected by filtering 20 L of water through a

68-µm-mesh sized net to be able to remove zooplankton and CPOM. Moreover, three replicates for CPOM of terrestrial origin (i.e., terrestrial vegetation detritus) were collected by hand from the river bottom in areas spread about 100m around the littoral areas sampled. Terrestrial vegetation was also obtained manually from the trees along the riverbank. Additionally, periphyton were collected scrapping hard substrates surfaces from the river bottom around the sampling area, also per triplicate.

All samples (fish and potential resources) were stored frozen at -20°C for subsequent laboratory analysis. The samples were cleaned to remove extraneous materials and prepared following standardized protocols (Levin & Currin, 2012). Once cleaned, the material was oven-dried for 48 hours at 60°C, weighed, and encapsulated in tin capsules (0.5–1.5 mg for animal tissues and 2.0-5.0 mg for organic matter, vegetation and algae) and sent to the Center for Stable Isotopes, University of New Mexico facilities, USA, for stable isotopes analysis. The results of stable isotopes ratios were expressed as ‰ (parts per thousand) and were calculated using the standard formula:

$$\delta X = \left[\left(\frac{R\ sample}{Rstandard}\right) - 1\right] * 1000$$

where δX represents $\delta^{15}N$ or $\delta^{13}C$, R sample is the ratio of heavy to light isotopes of element X and R standard is that isotopic ratio in a standard. The C:N ratio of animal material was cross-checked with laboratory results. In cases where the ratio exceeded 3.5, the isotopic signal of lipids was adjusted using the arithmetic equations proposed for aquatic animals by Post et al. (2007).

## *2.4. Data analysis*

### *2.4.1. Mixing models: modelling mean contribution of basal resources to fish biomass*

To determine the contribution of different pathways (allochthonous, autochthonous or coupling) to fish biomass along the entire longitudinal gradient of the Uruguay River, Bayesian mixing models were performed. These models were conducted using the "simmr" package (Parnell & Inger, 2019) in the open-source software R (R Core Team, 2023). The Bayesian mixing method is one of the most widely used tools for the estimation of the proportional composition of assimilated food sources based on stable isotope values for C and N in animal tissues and in their potential food sources (Fry, 2013; Parnell et al., 2010; Parnell & Inger, 2019), corrected by the corresponding Trophic Enrichment Factors (TEF) (Parnell & Inger, 2019). From these models, the posterior proportion contribution was calculated using the Fixed Form Variational Bayes (FFVB) method.

Initially, fishes were classified into trophic groups based on López-Rodríguez et al. (2019) as piscivores, detritivores, omnivore-invertivores (aquatic), and generalist omnivores. With this information, a Bayesian mixing model was created for each trophic group at each one of the 12 sampling sites, including species as different groups withing each model, building up to a total of 47 mixing models.

The parameters introduced in each model were as follows:

$\delta^{15}$N and $\delta^{13}$C values for each individual of each species; TEF values corresponding to each trophic group, and $\delta^{15}$N and $\delta^{13}$C mean and standard deviation values of the potential resource. We extracted from the literature TEF values according to the trophic group: for N: piscivores: 5.7 ± 1.6; detritivores: 3.9 ± 1.4; omnivore-invertivores (aq): 3.4 ± 1.1; and generalist omnivores: 4.3 ± 1.5 (Bunn et al., 2013). For C, we used the TEF proposed by Post (2002): fractionation of 1.3 ± 0.39 by trophic step, resulting in: piscivores: 3.9 ± 1.17 (three trophic steps); detritivores: 1.3 ± 0.39 (one trophic step); and omnivore inv (aq) and generalist omnivores: 2.6 ± 0.78 (two trophic steps). For basal resources, periphyton was considered an autochthonous resource, while CPOM and terrestrial vegetation were considered allochthonous resources. For allochthonous sources, the isotopic values from terrestrial vegetation and CPOM were pooled and averaged at each sampling site.

As periphyton isotopic values are known to vary in relatively short time due to water velocity changes across microhabitats and hydrological changes (Finlay et al., 1999; Rasmussen & Trudeau, 2007), the signal used for autochthonous basal resources was calculated as the average signal of periphyton values from all 12 sampling sites. Periphyton isotopic values are highly variable in the short term also due to the fast turnover rate of periphyton (few days, while the turnover of fish tissue is of weeks-months). This approach could be considered a space-for-time substitution; i.e., a potentially high isotopic variability along environmental spatial gradients may resemble the natural changes in a given site in a period of weeks-months and surrogate the lack of these values.

In previous studies, it has been suggested that FPOM is generally the result of a mixture of autochthonous and allochthonous resources, and a reliable technique to verify this is the visual inspection of samples (e.g., Hoeinghaus et al., 2007; González-Bergonzoni et al., 2019). We thus visually inspected the FPOM samples from all sampling sites, detecting a dominance of algae in FPOM only in sites 8 (tail of the Salto Grande reservoir in the lower Uruguay River) and 12 (site near the mouth of the Uruguay River in the Río de la Plata). Considering that the pelagic pathway could become relevant and provide autochthonous support to trophic networks in these, somehow more lentic, sections, we included FPOM in the mixing models of sites 8 and 12 as a source of autochthonous support. In these two sites, the mixing model was performed with the "combine sources" function, mixing the signals from periphyton and FPOM as autochthonous support and using the CPOM and terrestrial vegetation signal as allochthonous support. The decision of combining resources into either autochthonous or allochthonous also responds to best practices recommended for mixing models of grouping similar resources into fewer groups to simplify the models and avoid bias produced when using more sources than isotopic tracers (Fry, 2013; Nielsen et al., 2017).

From the models, we obtained exploratory bi-plots representing the C and N isotopic values of potential food sources (i.e., basal resources: allochthonous and autochthonous) and fish (grouped by trophic group), representing the TEF-corrected contribution of each source to the fish biomass for each trophic group, along the longitudinal gradient (Fig. S1 in supporting material [SM]).

### *2.4.2. Contribution of autochthonous and allochthonous resources to fish biomass*

The relative contribution of basal resources to fish biomass was analysed in two steps, first identifying the mean contribution to the biomass of each trophic groups and species, independently of the importance of each trophic group and species in the community. Then, we estimated the actual contribution of both types of basal resources to the total fish biomass in the Uruguay River by considering the composition and the relative biomass of each species in the community.

#### *Basal resource contribution to biomass and species richness*

Firstly, the mean contribution of each pathway to the biomass of each trophic group was determined at each sampling site. From the mixing models conducted, we obtained the probability of autochthonous pathway supporting a different fraction of biomass than the allochthonous pathway for each trophic group at each sampling site. The statistics associated with this analysis are within the Bayesian framework of probabilities. If the probability of differences between autochthonous and allochthonous support was greater than 90%, differences were considered as statistically significant (i.e., González-Bergonzoni et al., 2023).

The relative abundance of species that showed more than 60% contribution to its biomass of a given pathway at a given site was calculated as the ratio between the number of species with more than 60% and the total number of species present at the sampling site. The threshold of

60% was chosen following González-Bergonzoni et al. (2019), considering that percentages lower than 60 would imply no predominance of any particular source but the combination of both.

### *Assemblage-weighted basal resource contribution to fish biomass*

The information on the mean contribution of each pathway (autochthonous vs. allochthonous) thus obtained from the Bayesian mixing models, in which each species was identified as a group within each trophic group at each sampling site, was used together with the data of the biomass of each species at each site to calculate the assemblage weighted contribution to the total fish biomass in each sampling site, with the following equation:

$$Bm\_res\_x = Bm_a \text{ X } (Cont\_res\_x_a) + ... + Bm_n \text{ X } (Cont\_res\_x_n),$$

where Bm_res_x is the total biomass of the fish community supported by resource x (expressed in grams of fresh weight), $Bm_a$ represents the total biomass of species a, and Cont_res_x represents the mean contribution of resource x to species a. The term in the equation is repeated for the number of species present in the community studied. Finally, to calculate the total proportion of fish biomass generated by each pathway (autochthonous vs. allochthonous) for each of the 12 sampling sites, the biomass generated by a resource was divided by the total fish biomass at each site.

The assemblage-weighted isotopic approaches are rare in the literature (Jardine et al., 2013; González-Bergonzoni et al., 2019). This type of approach allows a more accurate estimation of community and ecosystem wide effects, weighting by the true biomass of each species, rather than using all species as replicates irrespective of their representation or contribution to the total biomass of the ecosystem (González-Bergonzoni et al., 2019).

### *2.4.3. Longitudinal changes and potential effect of dams in the energetic subsidy of fish food webs*

To assess potential patterns along the longitudinal gradient of the river we performed linear regression analyses. We analysed the relationship between the mean contribution of autochthonous pathway to fish species biomass (for the total and for each trophic group) at each sampling site and the distance to headwaters, and also the variations in the proportion of autochthonous-supported species along the longitudinal gradient.

The same approach was followed to evaluate potential longitudinal patterns with the biomass-weighted contribution of autochthonous pathway to total fish biomass and to biomass of each trophic group.

To determine potential effects of the presence of dams on the energetic subsidies of fish we performed General Linear Model (GLM) between sites before and after dams (i.e., Site 1 vs. Site 2; Site 2 vs. Site 3 and Site 8 vs. Site 9). For the analysis, we considered each species at each sampling site as a replicate. The explanatory variables used were the sampling site (N Site), the trophic group (TG), and the interaction between these two factors. Given that the data involves proportions, the models were fitted to a beta distribution (beta_family) using the "glmmTMB" package (Brooks et al., 2017). Model selection was conducted through Likelihood Ratio Tests (LRT), the significance of each factor was verified through ANOVA analysis for each model, and the validation of the final models was done through visual inspection of the residual distribution.

All the statistical analyses were done using the open-source Statistical Software Package R (R Development Core Team, 2023).

## 3. Results

A total of 92 fish species were obtained in the 12 sampling sites, resulting in 1097 muscle samples for stable isotope analysis and a total of 109 samples of basal resources. Furthermore, in all sampling sites the trophic groups (piscivores, detritivores, generalist omnivores, and omnivore-invertivores (aquatic)) were present, except for site 3, where piscivores were absent (Fig. 2).

### *3.1. Basal resource contribution to fish biomass and species richness: mean contribution and assemblage-weighted approach*

According to the Bayesian mixing models the energetic subsidies for fish biomass were highly variable along the river longitudinal gradient, as both allochthonous and autochthonous pathways supported fish biomass along the Uruguay River. However, autochthonous support dominated in two of the sampling sites affected by the dams, both in the regions downstream of the cascade of dams in the upper Uruguay River (i.e., between sites 2 and 3) and in site 8 (tail of the Salto Grande reservoir) (Fig. 2 and Fig. 3; Table S1 and S2 in SM). Likewise, autochthonous support was also found at site 12, a site near the mouth of the Uruguay River in the Rio de la Plata Estuary (Fig. 2; Table S2 in SM).

However, distinctive predominant energetic pathways were detected within the different trophic groups, with allochthonous subsidy being particularly clear at the top of the food web. In 8 of the 12 sampling sites, piscivores showed a significant greater contribution of the allochthonous pathway to their biomass. It is worth noting that in the remaining three sites, piscivores coupled both energetic pathways evidenced by no significantly different contributions of allochthonous and autochthonous material (Fig. 2). Contrary, detritivores showed a significant greater contribution of autochthonous pathway in 10 of the 12 sites (Fig. 2), being the remaining 2 sites subsidized by both energetic pathways (at the headwaters and in site 9, i.e., immediately downstream of Salto Grande Dam).

The analysis of the proportion of species supported by each or both contrasting energetic pathways clearly indicates that the coupling of energetic pathways decreased in the presence of dams, as will be further explored in the next section. This occurred without a consistent pattern, though. Downstream of the dam cascade (60 km downstream of Foz de Chapecó dam towards site 3), not a single species was supported by allochthonous pathway as major source. The same occurred at the tail of Salto Grande reservoir towards site 8 and site 12 near the mouth of Uruguay river in the Rio de la Plata Estuary, where all species were either supported by the autochthonous pathway or by coupling both pathways. In contrast, towards site 9 (60 km downstream of the Salto Grande Dam), all species were largely supported by the allochthonous pathway and by coupling both energetic pathways (Fig. 3a; Table S2 in SM).

The assemblage-weighted contribution of each energetic pathway to the total fish biomass in each site showed consistent results with the mean contribution approach. In absolute terms, autochthonous support of fish was observed in sites 3 and 8 (Fig. 3b y c; Table S1 and S2 in SM). Particularly in site 3, 62.0% of the total biomass of the site was generated by autochthonous resources, increasing the percentage of support determined through the mean contribution approach. In site 8, 65.9% of the fish biomass seemed subsidized by autochthonous resources. On the other hand, fish biomass in sites 5 and 11 had a predominantly allochthonous origin (64.7% and 60.0% of the biomass seemed generated by allochthonous resources in sites 5 and 11, respectively) (Table S2 in SM).

### *3.2. Longitudinal gradients and potential effect of dams in the energetic subsidy of fish food webs*

We found no evident longitudinal pattern in the importance of the energetic support to fish in the Uruguay River. We found no significant correlation between the distance of each site to the headwaters and the mean contribution of autochthonous resources to total biomass or to the biomass of each trophic group in particular (p >0.05 in all cases) (Table 2). The same occurred for the proportion of species supported by any of the resources or by the coupling of pathways (p>0.05 for autochthonous, allochthonous, or coupling both pathways) (Fig 3a; Table 2).

Similarly to what was observed with the mean contribution approach, no consistent pattern was detected in the longitudinal gradient of autochthonous support to fish biomass (i.e., assemblage-weighted contribution). We found no significant correlations between the distances to the headwaters and the percentage of fish biomass subsidized by autochthonous resources, both in the analysis with the total community and in the particular case of trophic groups (Fig. 3b y c; Table 2). However, in the free-flowing stretch between sites 5 and 8 (approximately 800 km downstream), the fish biomass sustained by autochthonous pathway appeared to increase, until the Salto Grande Dam disrupted the observed pattern (Fig. 3b).

We found potential effects of the dams on the energetic support of the food webs. GLM analyses using species as replicates between sites 1 and 2, indicated that only the trophic group (TG) factor differed significantly in autochthonous support, without showing the site as a significant factor (GLM (beta): ANOVA: Chi2 = 1.8, p>0.05 and Chi2 = 12.3, p<0.05 for SITE and TG, respectively). This indicates that, despite there was no spatial differences, the support of the autochthonous pathway varied differentially among trophic groups, with an increase in autochthonous support only in the detritivore trophic group (Fig. 2). However, an apparent shift towards autochthonous support in fish biomass was observed at site 3 after the river passes through two consecutive dams, where all trophic groups showed a significant higher probability of being more largely subsided by autochthonous resources than by allochthonous resources (i.e., probability of autochthonous contribution > allochthonous contribution = 0.967, 0.923, 0.909 for detritivores, generalist-omnivores and omnivore-invertivores (aq.), respectively) (Fig. 2). This shift towards autochthonous support was supported by GLM analyses, that showed marginally significant differences between sites and with TG as a significant factor (GLM (beta): ANOVA: Chi2 = 3.3, *p=0.07* and Chi2 = 19.4, p<0.05 for SITE and TG, respectively).

The last pair of sites affected by dams were sites 8 and 9, situated before and after the Salto Grande Dam, at the boundary between the middle and the lower Uruguay River. In this case, site 8 (tail of the reservoir) showed a significantly higher mean contribution of autochthonous resources for fish species than site 9 (GLM (beta): ANOVA: Chi2 = 78.5, p<0.001 and Chi2 = 23.6, p<0.01 for SITE and TG, respectively). At site 8, a higher probability of allochthonous support was observed in piscivores, while a higher probability of autochthonous support was found in the remaining trophic groups. However, at site 9, piscivores maintained their higher probability of allochthonous support, and the omni-invertivores (aq.) switched to a higher probability of allochthonous support. The other two groups showed a coupling of energy pathways at site 9 with no pathway being more likely than the other (Fig. 2).

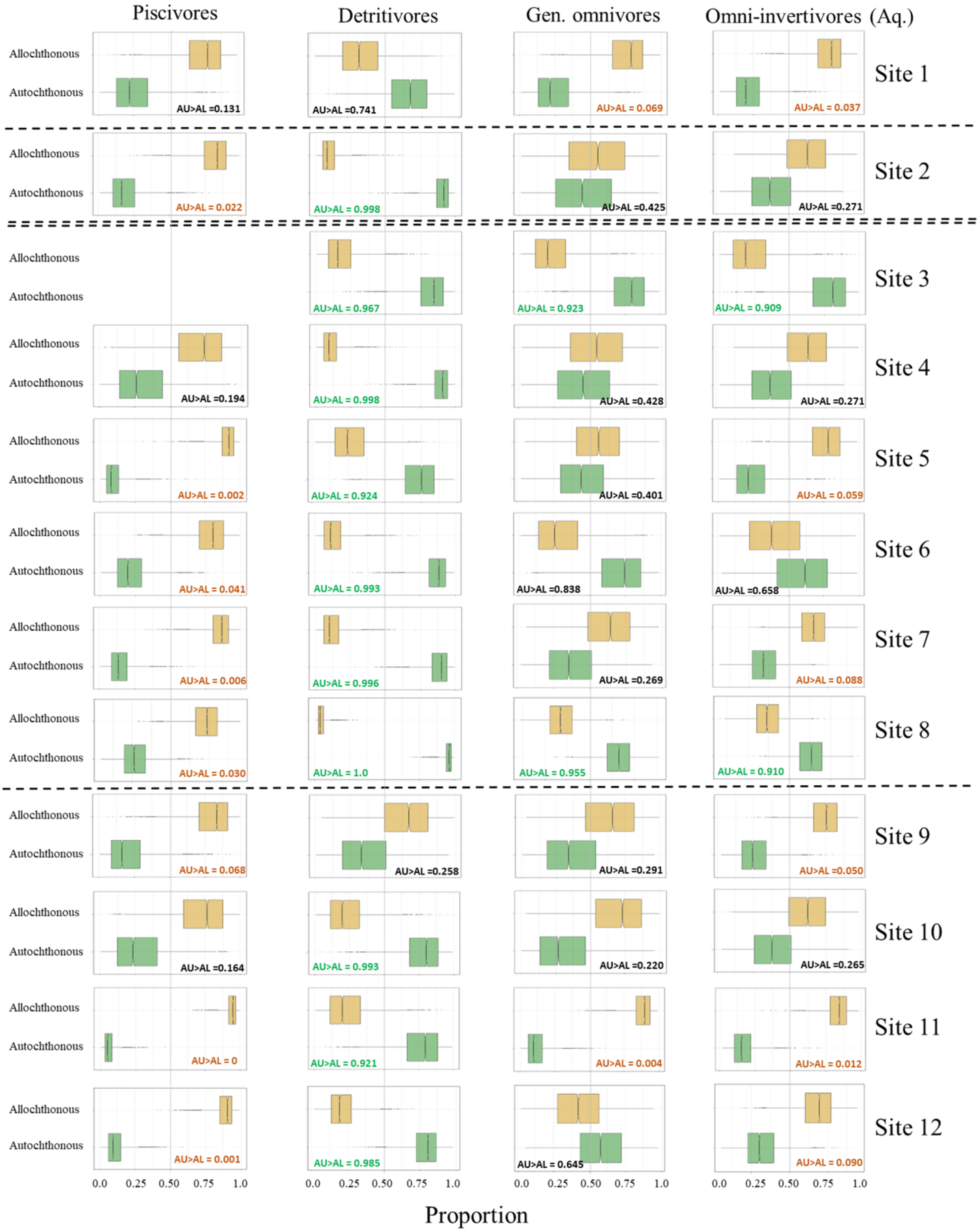


Figure 2. Estimated proportion of allochthonous (brown) and autochthonous (green) contribution to the fish biomass of the four analysed trophic groups (piscivores, detritivores, generalist omnivores and omnivore-invertivores (aq.)) at each of the 12 sampling sites along the longitudinal gradient of the Uruguay River, according to the Bayesian Mixing Models performing in “simmr”. The probabilities of the proportion of autochthonous resources (AU) being > allochthonous resources (AL) is shown for each trophic group per site. AU>AL written in brown means a significant probability (>90%) of allochthonous proportion being greater than autochthonous proportion; AU>AL in green, in contrast, represents a significant probability (>90%) of autochthonous proportion to being greater than allochthonous

proportion, while values given in black represent differences with less than 90% probability. Dashed lines indicate the presence of dams.

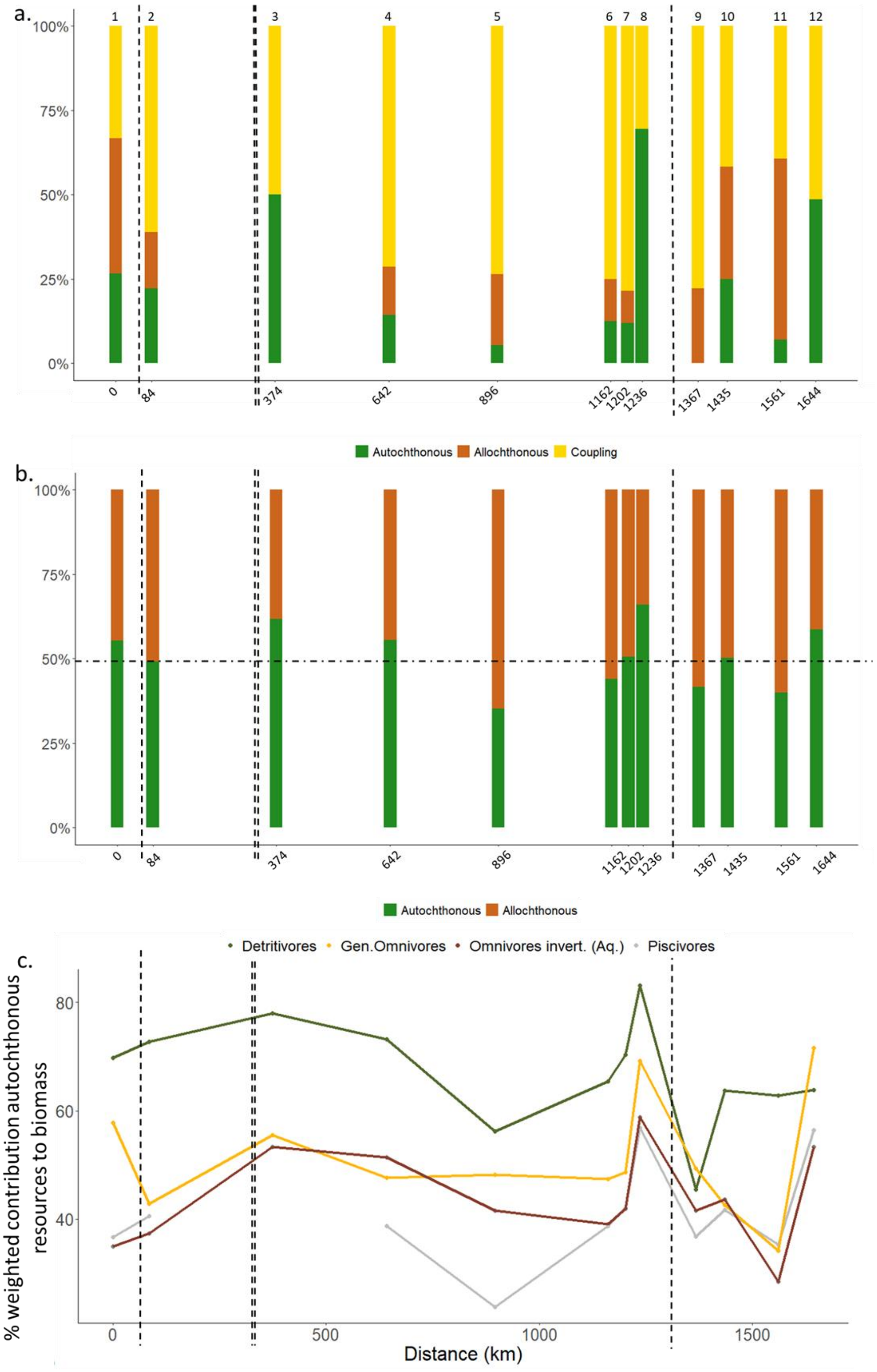


Figure 3. a. Relative contribution of resources to the fish species at each of the 12 sampling sites along the longitudinal gradient of the Uruguay River. b. Weighted contribution of resources to total fish biomass along the longitudinal gradient of Uruguay River. Dashed horizontal line indicate the 50% of

contribution. c. Mean % weighted of autochthonous contribution to the four analysed trophic groups (piscivores, detritivores, generalist omnivores and omnivore-invertivores (aq.)) at each of the 12 sampling sites along the longitudinal gradient from headwaters to mouth of the Uruguay River. The number at the top of each bar indicates the site number. Dashed vertical lines indicate the presence of dams.

Table 2. Parameters of the lineal regression models performed for: a- mean contribution; b- weighted contribution of allochthonous basal resources to fish biomass along the longitudinal gradient; c- proportion of species largely supported by the different resources (autochthonous, allochthonous and coupling pathways).

**a- Mean contribution of autochthonous resources to fish species biomass**

| | $R^2$ adjusted | F-statistics | p-value |
|---|---|---|---|
| Total | 0.1 | 0.027 | 0.874 |
| Piscivore | 0.1 | 2.067 | 1.845 |
| Detritivore | 0.09 | 0.046 | 0.832 |
| Generalist omnivore | 0.081 | 0.174 | 0.686 |
| Omnivore-inv (aq) | 0.049 | 0.491 | 0.5 |

**b- Weighted contribution of autochthonous resources to fish species biomass**

| | $R^2$ adjusted | F-statistics | p-value |
|---|---|---|---|
| Total | 0.05 | 0.477 | 0.506 |
| Piscivore | 0.001 | 0.99 | 0.346 |
| Detritivore | 0.084 | 2.014 | 0.186 |
| Generalist omnivore | 0.099 | 0.011 | 0.918 |
| Omnivore-inv (aq) | 0.049 | 0.491 | 0.5 |

**c- Proportion of resources supported species**

| | $R^2$ adjusted | F-statistics | p-value |
|---|---|---|---|
| Autochthonous | 0.1 | 0.032 | 0.862 |
| Allochthonous | 0.1 | 0.002 | 0.967 |
| Coupling | 0.09 | 0.028 | 0.87 |

## 4. Discussion

In this study, we describe for the first time the energy support of food webs along the longitudinal gradient of one of the largest rivers in South America, the Uruguay River. In contrast to expectations from several theoretical frameworks, the coupling of energy pathways seems to be the rule in this river, rather than the dominance of one pathway over the other. In this sense, we found that most fish species in the Uruguay River were supported by a combination of pathways with only a small proportion of fish species being supported by either one or the other pathway. Also, in general terms, the total biomass of the fish community along the Uruguay River seemed to be sustained by coupling both energetic pathways in a similar proportion with a slight predominance of allochthonous subsidy, but showing an increase in the relative importance of autochthonous subsidy as the river increased in width in the unregulated reach. The latter finding would be expected from the River Continuum Concept (RCC) (Vannote et al., 1980). Within the fish food web, however, distinctive predominant energetic pathways were detected for different trophic groups, with allochthonous subsidy being particularly clear at the top of the food web for the piscivorous fishes. Our results also suggest that dams may enhance one energetic pathway over the other and modify the longitudinal patterns, as one pathway, either autochthonous or allochthonous, lost relevance around the presence of a dam or a dam cascade. The direction of such changes seems to depend on local characteristics, though.

In this study, no single theory was fully supported, but rather evidence for several predictions was found in different sections of the river. For instance, we found evidence that partially supports the Flood Pulse Concept (Junk et al., 1989) in the region with the largest extent of floodplains along the Uruguay River. In site 5, approximately 65% of the fish biomass was supported by allochthonous carbon. This is also the region where fish can freely move upstream or downstream (thus assimilating resources from nearby sites, such as site 4, which has the highest riparian cover). Similar evidence supporting the importance of allochthonous support for food webs has also been found in the lower part of the Uruguay River, highlighting the key role of flood pulses and local geomorphology in determining energy subsidies (González-Bergonzoni et al., 2019).

The total fish biomass showed coupling of the two energetic pathways (allochthonous and autochthonous) along the longitudinal gradient, with most species coupling both pathways. However, in most sites piscivores exhibited a higher proportion of their biomass originating from allochthonous resources, while detritivores showed an inverse pattern, with a higher proportion of autochthonous support for their biomass. Several studies have observed that autochthonous carbon from algae is more labile and of higher nutritional quality than carbon from terrestrial plants (Thorp & Delong, 2002). However, our results suggest that this energy source may not be sufficient to sustain the higher trophic levels in this system, as has been observed in previous research in this same river (González-Bergonzoni et al., 2019), as well as in rivers with extensive floodplains in tropical areas of Australia (Jardine et al., 2017). In the latter study, it was observed that allochthonous support scales with fish biomass, with smaller fish at the base of the food web primarily supported by autochthonous resources, while larger animals occupying higher trophic positions are mainly supported by allochthonous resources (Jardine et al., 2017). Probably, this could be generalized to rivers with extensive floodplains, like the Uruguay River, where turbidity may limit the growth of local primary producers. This would result in the autochthonous energy not being sufficient to sustain the fish of the higher trophic levels (typically occupied by larger-bodied organisms).

Our results suggest that dams alter the longitudinal pattern of energy support of fishes in the Uruguay River, with variations depending on the local characteristics of each site. We observed that the presence of dams somehow led to the dominance of one pathway over another, simplifying the diversity of energetic pathways. However, the current evidence does not allow us to predict the direction of the changes. The presence of dams can have a myriad of effects on the availability of food for fish. This may result in the pauperization of some of the energy pathways, leading to changes in trophic and taxonomic diversity, based on a reduction in the available energy in the ecosystem. Other studies in the Uruguay River have shown disruptions in diversity patterns, with substantial losses in species richness, as well as decreases in the trophic and ecological diversity of fishes in regions downstream of the dams (López-Rodríguez et al., 2024). We found that the reduction in taxonomic and trophic diversity coincided in space with a change in the type of energy support and a simplification of the energy pathways.

Likewise, the loss of multiple types of diversity as a consequence of dam's presence has been documented in several studies (e.g., de Bem et al., 2021; Ganassin et al., 2021; Ribolli et al., 2021; Guo et al., 2023; López-Rodríguez et al., 2024). Specifically, dams promote the loss of genetic diversity in regions upstream of the dams (Ribolli et al., 2021), the loss of functional groups both upstream and downstream of the dams (de Bem et al., 2021), and the loss of species and alteration of beta-diversity patterns (Ganassin et al., 2021; Guo et al., 2023; López-Rodríguez et al., 2024).

Our findings in the dam-affected areas regarding changes in the energy support of food webs align particularly with the propositions by the River Ecosystem Synthesis (RES) (Thorp et al., 2008). This theory complements the Riverine Productivity Model (RPM) (Thorp & Delong, 2002), which sustains that that autochthonous or allochthonous support depends on local characteristics, strongly influenced by natural changes such as climate or geology and changes generated by anthropogenic regulation of ecosystems (Thorp et al., 2008). In this context, the presence of dams increases water residence time in the reservoir and often upstream and decreases the transport of allochthonous material, leading to greater autochthonous production in dam-affected sites (Guo et al., 2023). Other studies have found higher allochthonous subsidies in environments with riparian vegetation and increased turbidity (e.g., Hoeinghaus et al., 2007; Roach & Winemiller, 2015; Sabo et al., 2018), while predominantly autochthonous support was observed in dammed areas or downstream of dams (e.g., Hoeinghaus et al., 2007; Sabo et al. 2018; Leal et al., 2023). In this sense, Hoeinghaus et al. (2007) support to the propositions by the RPM, i.e., predominance of autochthonous support to fish biomass in dammed river stretches of the Upper Paraná Basin. Furthermore, in the free-flowing stretches, they found evidence that support the theory put forth by the FPC, with higher allochthonous subsidy to fish biomass. Our study also matches these previous findings, as the highest proportion of species supported mostly by allochthonous resources occurred in the headwaters, where the coverage of native forest in the nearby 2km was the highest. Also, we found the highest percentage of biomass being allochthonous-derived in the large floodplains area of middle river section. However, we detected that the autochthonous support to food webs increased in the tail of reservoirs or towards the mouth where planktonic autotrophic communities bloom, or downstream where allochthonous detritus was probably reduced. Likewise, the contrasting trends in the shift of energy support pathways between site 3 and site 9 (both located at the same distance downstream of dams) may result from a combination of dam effects and several local characteristics, such hydrogeomorphology, landscape, and the input of tributaries into the river. For example, at site 3, downstream of the cascade of dams in the upper part of the river, the main subsidy to fish biomass is of autochthonous origin. This may reflect the retention of detritus by dams (with a cumulative effect of several consecutive dams), significantly reducing the availability of allochthonous material downstream. The scarce riparian forest in that region and the absence of tributary inflows that could transport allochthonous resources could act on top of the direct effects of dams, enhancing the observed pattern. On the other hand, two of the largest tributaries of the Uruguay River (Daymán River and Guaviyú River) enter downstream of Salto Grande (site 9), potentially carrying resources that could largely subsidize fish biomass. Additionally, there is a large coverage of riparian forest that can contribute allochthonous material in this area.

Along river longitudinal gradients, water residence time tends to increase as current velocity decreases towards the mouth of the system, where planktonic communities become more common and frequent (Horwitz, 1978; Vannote et al., 1980). In this work, site 12 represented this scenario, where the river is close to meet the Rio de la Plata Estuary and the hydrological conditions become more lentic. In this scenario, not surprisingly, we found an average contribution of 60% from autochthonous resources to the fish biomass probably due to the more favourable conditions for the growth of planktonic algae, as confirmed by the higher presence of algae in the fine particulate organic matter (FPOM).

In general, the difference in the use of different carbon sources as subsidies for consumers may be caused by the availability of different food sources in different environments (Hoeinghaus et al., 2007). For instance, in the lacustrine regions created by dam construction there may be an increase in the relative importance of autochthonous resources, favouring the pelagic pathway through increased biomass (Doi et al., 2008). Furthermore, a global-scale meta-analysis suggested that the diet of major freshwater consumers is highly dependent on autochthonous resources in lotic systems, where water residence time and increased transparency may serve as key drivers for pelagic and benthic primary producers. (Leal et al., 2023). In contrast, a greater allochthonous support to fish biomass has been described in turbid reservoirs in the Uruguay River basin (Felden et al., 2020). Nevertheless, allochthonous contribution seemed to be slightly higher in the reservoirs with greater riparian forest canopy along the littoral zones (Felden et al., 2020).

On the other hand, the retention of particulate material in the reservoir (i.e., reducing downstream turbidity) may enhance water clarity and benthic periphyton growth, thus increasing the relative importance of autochthonous resources in subsidizing biomass in riverine regions downstream of dams (Doi et al., 2008; Wellard-Kelly et al., 2013). All these studies highlight the importance of local studies to fully understand the natural functioning of specific rivers and stretches, before the impacts of the dams disrupt the longitudinal behaviour and patterns.

Our results support the idea that stable isotope analyses are a valuable tool for detecting and quantifying changes in the energy subsidies caused by dams. However, there is a need for more studies applying a broad spatial scale, to increase the understanding of the natural patterns in dam-free areas and gather more empirical evidence that eventually permits to model and predict the direction of changes promoted by the dams.

## 5. Conclusions

We found that both autochthonous and allochthonous energetic pathways subsidized large fractions of fish biomass in a large riverine system, and that most fish species played a key role in coupling energy sources in these food webs, contrary to statements of some theories such as RPM. However, the influence zone of the dams appeared to affect this balance in the energetic support of food webs, reducing the importance of one of the energetic pathways and enhancing the other and the coupling of energetic pathways for fish biomass support. These changes in energetic pathways coincide with several observed impacts on fish trophic and taxonomic diversity observed in previously published research within this same river system and elsewhere. Whether there is a causal connection between the loss of the prevalence of one of the energetic pathways to biomass support and fish assemblage changes, or both changes occur concomitantly due to diverse environmental impacts of dams, remains to be studied in depth; however, it is clear that both fish community structure and functionality is substantially being altered by the presence of dams.

Furthermore, this work provides empirical evidence of the importance of both energy sources for maintaining food webs and, therefore, ecosystem-scale processes. Through the results of this study, the importance of maintaining riparian forests and floodplains for the exchange of matter and energy with the terrestrial region becomes evident, particularly given their relevance for higher trophic levels.

## Authors contribution

Conceptualization: AL-R, MM, IG-B; Methodology: AL-R, IG-B; Investigation: AL-R, AD, SdAS, FTM, DR-T, EZ-F, IG-B; Resources: DR-T, EZ-F, IG-B; Data curation: AL-R, SdAS, IS, IG-B; Formal analysis: AL-R; Writing-original draft: AL-R, MM, IG-B; Writing review & editing: all; Visualization: ALR; Supervision: MM, IG-B; Project administration & Funding acquisition: DR-T, EZ-F, IG-B

## Funding

This research project was partly funded by the Scientific Research Sectorial Commission (Uruguay) (Project CSIC I+D_2016_577-348, Project CSIC Groups 2022 #882442 & #883452) and the National Agency for Innovation and Research (ANII) (Project ANII-FCE_2_2016_1_126780).

## Acknowledgements

We thank the artisanal fisherman Elbio Russo for his support and collaboration with sampling and fisheries data. AL-R, MM, IGB, AD, FTM are supported by ANII and PEDECIBA. AL-R received support from CAP-UDELAR. AL-R, MM, IGB also acknowledge the funding from CSIC Groups-2022 #882442 & #883452. EZF thanks CNPq, grant 302860/2014–2, and Engie (Tractebel Energia), Consórcio Itá, and Consórcio Machadinho for financial support.

Fish sampling and handling procedures were approved by the Honorary Commission of Animal Experimentation, Uruguay (CHEA, Permit-ID 309) and the ethics committee of the Federal University of Fronteira Sul, Brazil (permit-ID 23.205.004977/2015-90).

## References

Agostinho, A.A., Marques, E.E., Agostinho, C.S., Almeida D.A., Oliveira R.J., Melo J.R., 2007. Fish ladder of Lajeado Dam: migrations on one-way routes? *Neotropical Ichthyology*, *5*, 121-130. https://doi.org/10.1590/S1679-62252007000200005

Agostinho A.A., Pelicice F.M. & Gomes L.C., 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian journal of biology*, *68*, 1119-1132. https://doi.org/10.1590/S1519-69842008000500019

Barletta M., Jaureguizar A.J., Baigun C., Fontoura N.F., Agostinho A.A., Almeida-Val V.M., Val A.L., Torres R.A., Jimenes-Segura L.F., Giarrizzo T., Fabré N.N., Batista V.S., Lasso C., Taphorn D.C., Costa M.F., Chaves P.T., Vieira J.P., Correa M.F., 2010. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. *Journal of Fish Biology*, *76*, 2118-2176. https://doi.org/10.1111/j.1095-8649.2010.02684.x

Baxter R.M., 1977. Environmental effects of dams and impoundments. *Annual Review of Ecology and Systematics*,*8*, 255-283. https://doi.org/10.1146/annurev.es.08.110177.001351

Bertaco V.A., Ferrer J., Carvalho F. R. & Malabarba L.R., 2016. Inventory of the freshwater fishes from a densely collected area in South America—a case study of the current knowledge of Neotropical fish diversity. *Zootaxa*, *4138*, 401-440. DOI: 10.11646/ZOOTAXA.4138.3.1

Brooks M.E., Kristensen K., Van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Machler M. & Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, *9*, 378-400. https://doi.org/10.3929/ethz-b-000240890

Bunn S. & Arthington A., 2002. Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. *Environmental Management*, *30*, 492–507. https://doi.org/10.1007/s00267-002-2737-0

Bunn S.E., Leigh C., & Jardine T.D., 2013. Diet-tissue fractionation of δ15N by consumers from streams and rivers. *Limnology and Oceanography*, *58*, 765-773. https://doi.org/10.4319/lo.2013.58.3.0765

Cross W.F., Baxter C.V., Donner K.C., Rosi-Marshall E.J., Kennedy T.A., Hall R.O., Holly A., Kelly W. & Rogers R.S., 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. *Ecological Application*, *21*, 2016-2033. https://doi.org/10.1890/10-1719.1

de Bem, J., Ribolli, J., Röpke, C., Winemiller, K.O., Zaniboni-Filho, E., 2021. A cascade of dams affects fish spatial distributions and functional groups of local assemblages in a subtropical river. *Neotropical Ichthyology*, *19*, e200143. https://doi.org/10.1590/1982-0224-2020-0133

Doi H., Chang K. H., Ando T., Imai H., Nakano S.I., Kajimoto A. & Katano I., 2008. Drifting plankton from a reservoir subsidize downstream food webs and alter community structure. *Oecologia*, *156*, 363-371. https://doi.org/10.1007/s00442-008-0988-z

Dudgeon D., 2000. Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity: the construction of large dams will have an impact on the biodiversity of tropical Asian rivers and their associated wetlands. *BioScience*, *50*, 793-806.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.I., Knowler D.J., Lévêque C., Naiman R.J., Prieur-Richard A-H., Soto D.; Stiassny L.J. & Sullivan C.A., 2005. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews*, *81*, 163-182. https://doi.org/10.1017/S1464793105006950

Felden, J., González-Bergonzoni I., Rauber A.M., da Luz Soares M., Massaro, M.V., Bastian R., & Reynalte-Tataje D.A., 2021. Riparian forest subsidises the biomass of fish in a recently formed subtropical reservoir. *Ecology of Freshwater Fish*, *30*, 197-210. DOI:10.1111/eff.12575

Finlay J.C., Power M.E. & Cabana G. 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. *Limnology & Oceanography*, *44*, 1198–1203, https://doi.org/10.4319/lo.1999.44.5.1198.

Flecker, A.S., Shi, Q., Almeida, R.M., Angarita, H., Gomes-Selman, J.M., García-Villacorta, R., Sethi, S.A., Thomas, S.A., Poof, N.L., Forsberger, B.R., Heilpern, S.A., Hamilton, S.K., Abad, J.D., Anderson, E.P., Barros, N., Bernal, I.C., Bernstein, R., Cañas, C.M., Dangles, O., Encalada, A.C., Fleischmann, A.S., Goulding, M., Higgins, J., Jézéquel, C., Larson, E.I., McIntyre, P.B., Melack, J.M., Montoya, M., Oberdorff, T., Paiva, R., Perez, G., Rappazzo, B.H., Steinschneider, S., Torres, S., Varese, M., Walter, M.T., Wu, X., Xue, Y., Zapata-Ríos, X. & Gomes, C.P., 2022. Reducing adverse impacts of Amazon hydropower expansion. *Science*, *375*, 753-760. DOI: 10.1126/science.abj4017

Fry B., 2013. Alternative approaches for solving underdetermined isotope mixing problems. *Marine Ecology Progress Series*, 472:1–13. DOI: https://doi.org/10.3354/meps10168

Ganassin M.J.M., Muñoz-Mas R., Oliveira F.J.M., Muniz C.M., Santos N.C.L., García-Berthou E., Gomes L.C., 2021. Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins. *Science of the Total Environment*, *778*, 146246. https://doi.org/10.1016/j.scitotenv.2021.146246

González-Bergonzoni I., D'Anatro A., Vidal N., Stebniki S., Tesitore G., Silva I. & Teixeira de Mello F., 2019. Origin of fish biomass in a diverse subtropical river: An allochthonic-supported biomass increases following flood pulses. *Ecosystems*, *22*, 1736-1753.

González-Bergonzoni I., Vidal N., D'Anatro A., Teixeira de Mello F., Silva I., & Naya D.E., 2023. Historical analysis reveals ecological shifts in two omnivorous fish after the invasion of *Limnoperna fortunei* in the Uruguay river. *Biological Invasions*, *25*, 1935-1954.

Guo F., Ebm N., Fry B., Bunn S.E., Brett M.T., Ouyang X., Hager H., Kainz M.J., 2022. Basal resources of river food webs largely affect the fatty acid composition of freshwater fish. *Science of the Total Environment*, *812*, 152450. https://doi.org/10.1016/J.SCITOTENV.2021.152450.

Guo F., Fry B., Yan K., Huang J., Zhao Q., O'Mara K., Li F., Gao W., Kainz M.J., Brett M.T., Bunn S.E., Zhang Y., 2023. Assessment of the impact of dams on aquatic food webs using stable isotopes: Current progress and future challenges. *Science of the Total Environment*, *904*, 167097. https://doi.org/10.1016/j.scitotenv.2023.167097

Hoeinghaus D.J., Winemiller K.O. & Agostinho A.A., 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. *Ecosystems*, *10*, 1019-1033. https://doi.org/10.1007/s10021-007-9075-2

Horwitz R.J., 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs*, *48*, 307–321. https://doi.org/10.2307/2937233

Humphries P., Keckeis H. & Finlayson B., 2014. The river wave concept: integrating river ecosystem models. *BioScience*, *64*, 870-882. https://doi.org/10.1093/biosci/biu130

Jardine T.D., Hunt R.J., Faggotter S.J., Valdez D., Burford M.A. & Bunn S.E., 2013. Carbon from periphyton supports fish biomass in waterholes of a wet–dry tropical river. *River Research and Applications*, *29*, 560–73.

Jardine T.D., Rayner T.S., Pettit N.E., Valdez D., Ward D.P., Lindner, G., Douglas M.M. & Bunn S.E., 2017. Body size drives allochthony in food webs of tropical rivers. *Oecologia*, *183*, 505-517. https://doi.org/10.1007/s00442-016-3786-z

Junk W.J., Bayley P.B. & Sparks R.E., 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, *106*, 110-127.

Kaymak N., Winemiller K.O., Akin S., Altuner Z., Polat F. & Dal T., 2015. Stable isotope analysis reveals relative influences of seasonal hydrologic variation and impoundment on assimilation of primary production sources by fish in the Upper Yesilırmak River, Turkey. *Hydrobiologia*, *753*, 131-147. https://doi.org/10.1007/s10750-015-2201-9

Leal J.S., González A.L., Soares B.E., Casa Nova C., Marino N.A. & Farjalla V. F., 2023. Global and local drivers of the relative importance of allochthonous and autochthonous energy sources to freshwater food webs. *Ecography*, *2023*, e06612. https://doi.org/10.1111/ecog.06612

Levêque C., Oberdorff T., Paugy D., Stiassny M.L.J. & Tedesco P.A. 2008. Global diversity of fish (Pisces) in freshwater. *Hydrobiologia*, *595*, 545-567. https://doi.org/10.1007/978-1-4020-8259-7_53

Levin L.A. & Currin C., 2012. Stable isotope protocols: sampling and sample processing. En: Scripps Institution of Oceanography Technical Report. *University of California*.

López-Rodríguez A., Silva I., de Ávila-Simas S., Stebniki S., Bastian R., Massaro M.V., Pais J., Tesitore G., Teixeirade Mello F., D'Anatro A., Vidal N., Meerhoff M., Reynalte-Tataje D.A., Zaniboni-Filho E. & González-Bergonzoni I., 2019. Diets and trophic structure of fish assemblages in a large and unexplored subtropical river: The Uruguay River. *Water*, *11*: 1374. https://doi.org/10.3390/w11071374

López-Rodríguez A., Meerhof M., D'Anatro A., Silva I., de Ávila-Simas S., Silva I., Pais J., Teixeira de Mello F., Reynalte-Tataje D.A., Zaniboni-Filho E. & González-Bergonzoni I., 2024. Longitudinal changes on ecological diversity of Neotropical fish along a 1700 km river gradient show declines induced by dams. *Perspectives in Ecology and Conservation, in press.* https://doi.org/10.1016/j.pecon.2024.03.003.

Menni R.C., 2004. Peces y ambientes en la Argentina continental (Vol. 5). Buenos Aires, Argentina: Museo Argentino de Ciencias Naturales. p. 316.

Nielsen J.M., Clare E.L., Hayden B., Brett M.T. & Kratina P., 2017. Diet tracing in ecology: Method comparison and selection. *Methods in Ecology and Evolution*, *9*, 278-291. https://doi.org/10.1111/2041-210X.12869

Nilsson C., Reidy C.A., Dynesius M. & Revenga C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science*, *308*, 405-408.

Ormerod S.J., Dobson M., Hildrew A.G. & Townsend C., 2010. Multiple stressors in freshwater ecosystems. *Freshwater Biology*, *55*, 1-4. https://doi.org/10.1111/j.1365-2427.2009.02395.x

Pachla L.A., Hartmann P.B., Massaro M.V., Pelicice F.M., Reynalte-Tataje D.A., 2022. Recruitment of migratory fish in free-flowing rivers with limited floodplain development. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 32, 1888-1900. https://doi.org/10.1002/aqc.3860

Parnell A. C. & Inger R., 2019. Stable isotope mixing models in R with SIMMR: a stable isotope mixing model. Version 0.4. 1.

Parnell A.C., Inger R., Bearhop S. & Jackson A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. *PloS one*, *5*, e9672.

Pease A.A., Capps K.A., Rodiles-Hernández R., Castillo M.M., Mendoza-Carranza M., Soria-Barreto M. & González-Díaz A.A., 2019. Trophic structure of fish assemblages varies across a Mesoamerican River network with contrasting climate and flow conditions. *Food Webs*, *18*, e00113.

Pelicice F.M. & Castello L., 2021. A political tsunami hits Amazon conservation. *Aquatic Conservation: Marine and Freshwater Ecosystem*, *31*, 1221-1229. https://doi.org/10.1002/aqc.3565

Post D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, *83*, 703-718.

Post D.M., Layman C.A., Arrington D.A., Takimoto G., Quattrochi J. & Montaña C.G., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*,*152*, 179-189. https://doi.org/10.1007/s00442-006-0630-x

Rasmussen J.B. & Trudeau V., 2007. Influence of velocity and chlorophyll standing stock on periphyton $\delta^{13}$C and $\delta^{15}$N in the Ste. Marguerite River system, Quebec. *Canandian Journal of Fish and Aquatic Science*, *64*, 1370–1381, https://doi.org/10.1139/f07-109.

Reynalte-Tataje D.A., Nuñer A.P., Nunes M.C., Garcia V., Lopes C.A. & Zaniboni-Filho E., 2012. Spawning of migratory fish species between two reservoirs of the upper Uruguay River, Brazil. *Neotropical Ichthyology*, *10*, 829-835. https://doi.org/10.1590/S1679-62252012000400016

Ribolli, J., Zaniboni-Filho, E., Barros Machado, C., de Souza Guerreiro, T.C., Domínguez de Freitas, P., Galetti, Jr. P.M., 2021. Anthropogenic river fragmentation reduces long-term viability of the migratory fish *Salminus brasiliensis* (Characiforme:Bryconidae) populations. *Neotropical Ichthyology*, *19*, e200123. https://doi.org/10.1590/1982-0224-2020-0123

Roach K.A., 2013. Environmental factors affecting incorporation of terrestrial material into large river food webs. *Freshwater Science*, *32*, 283-298.

Roach K.A. & Winemiller K.O., 2015. Hydrologic regime and turbidity influence entrance of terrestrial material into river food webs. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1099-1112. https://doi.org/10.1139/cjfas-2014-0459

Ruhí A., Muñoz I., Tornes E., Batalla R.J., Vericat D., Ponsatí L., Acuña V., Von Schiller D., Marcé R., Bussi G., Francés F. & Sabater S., 2016. Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. *Freshwater Biology*, *61*, 1536-1549. https://doi.org/10.1111/fwb.12794

Sabo J.L., Finlay J.C., Kennedy T. & Post D.M., 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science*, *33*, 965-967. DOI: 10.1126/science.1196005

Sabo J.L., Caron M., Doucett R., Dibble K. L., Ruhi A., Marks J. C., Bruce A.H. & Kennedy T.A., 2018. Pulsed flows, tributary inputs and food-web structure in a highly regulated river. *Journal of Applied Ecology*, *55*, 1884-1895. https://doi.org/10.1111/1365-2664.13109

Saccol-Pereira A., 2008. Variação sazonal e estrutura trófica da assembléia de peixes do delta do rio Jacuí, RS, Brasil. Doctoral thesis. Universidade Federal do Rio Grande do Sul, Brazil.

Thorp J.H. & Delong M.D., 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, *70*, 305-308. https://www.jstor.org/stable/3545642

Thorp J.H. & Delong M.D., 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos*, *96*, 543–50.

Thorp J.H., Thoms M.C. & Delong M.D., 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *RiverResearch and Applications*, *22*, 123-147. https://doi.org/10.1002/rra.901

Thorp J.H., Thoms M.C. & Delong M.D., 2008. The riverine ecosystem synthesis. Towards Conceptual Cohesiveness in River Science. Amsterdam, the Netherlands: Academic Press/Elsevier.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E., 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science*, *37*, 130-137. https://doi.org/10.1139/f80-017

Vörösmarty C.J., McIntyre P.B., Gessner M.O., Dudgeon D., Prusevich A., Green P., Glidden S., Bunn S.E., Sullivan C.A., Liermann C.R. & Davies P.M., 2010. Global threats to human water security and river biodiversity. *Nature*, *467*, 555-561. https://doi.org/10.1038/nature09440

Wang J., Gu B., Huang J., Han X., Lin G., Zheng F. & Li Y., 2014. Terrestrial contributions to the aquatic food web in the middle Yangtze River. *PLoS One*, *9*, e102473.

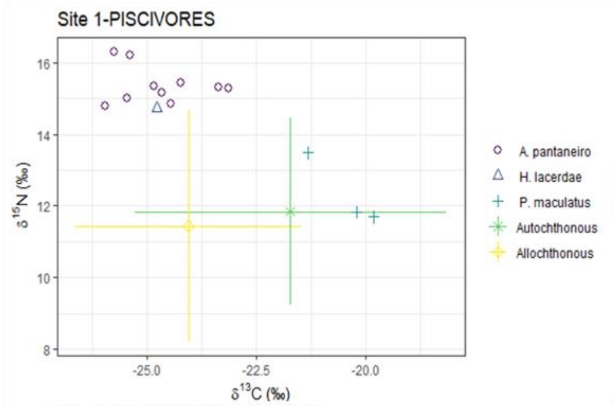
Wellard Kelly H.A., Rosi-Marshall E.J., Kennedy T.A., Hall Jr R.O., Cross W.F. & Baxter C.V., 2013. Macroinvertebrate diets reflect tributary inputs and turbidity-driven changes in food availability in the Colorado River downstream of Glen Canyon Dam. *Freshwater Science*, *32*, 397-410. https://doi.org/10.1899/12-088.1

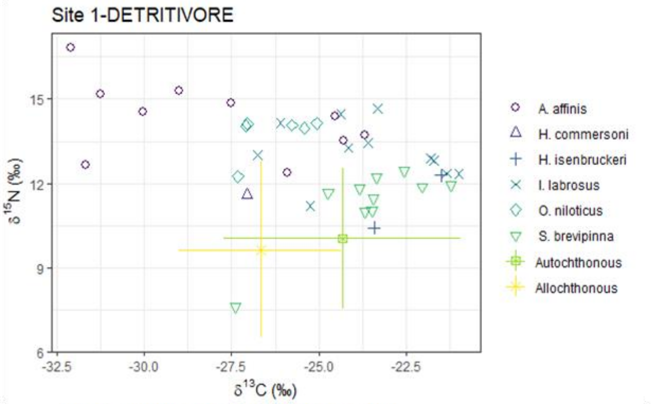
Winemiller K.O., Hoeinghaus D.J., Pease A.A., Esselman P.C., Honeycutt R.L., Gbanaador D., Carrera E. & Payne J., 2010. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. *River Research and Applications*, *27*, 791-803. https://doi.org/10.1002/rra.1396

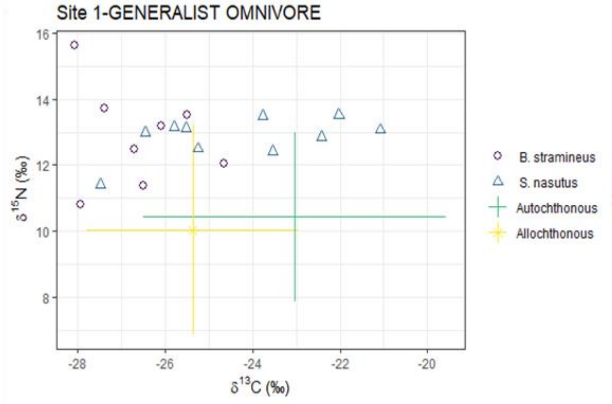
Winemiller K.O., McIntyre P.B., Castello L., Fluet-Chouinard E., Giarrizzo T., Nam S., Baird I.G., Darwan W., Lujan N.K., Harrison I., Stiassny M.L., Silvano R.A., Fitzgerald D.B., Pelicice F.M., Agostinho A.A., Gomes L.C., Albert J.S., Baran E., Petrere Jr. M.,Zarfl C., Mulligan M., Sullivan J.P., Arantes C.C., Sousa L.M., Koning A.A., Hoeignghaus D.J., Sabaj M., Lundberg J.G., Armbruster J., Thieme M.L., Petry P., Zuanon J., Torrente Vilara G., Snoeks J., Ou C., Rainboth W., Pavanelli C.S., Akama A., van Soesbergen A. & Sáenz L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, *351*, 128-129. DOI: 10.1126/science.aac7082

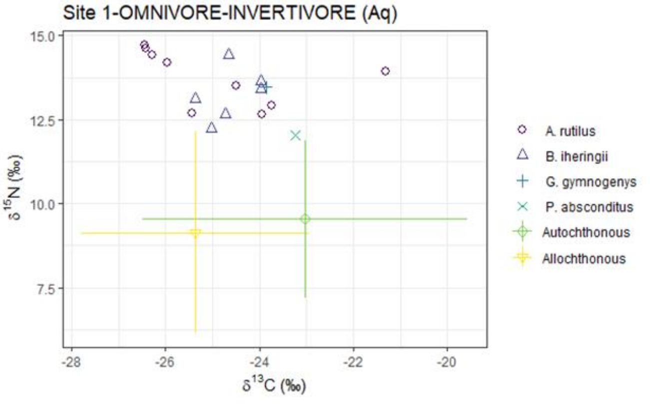
Zaniboni-Filho E. & Schulz U.H., 2003. Migratory Fishes of the Uruguay River. *In:* J. Carolsfeld, B. Harvey, C. Ross & A. Baer (Eds.). *Migratory Fish of South America. Biology, Fisheries and Conservation Status*. World Fisheries Trust/ Word Bank/ International Development Research Centre, Washington D.C., U.S.A. and Ottawa, Canada. p. 157-194.

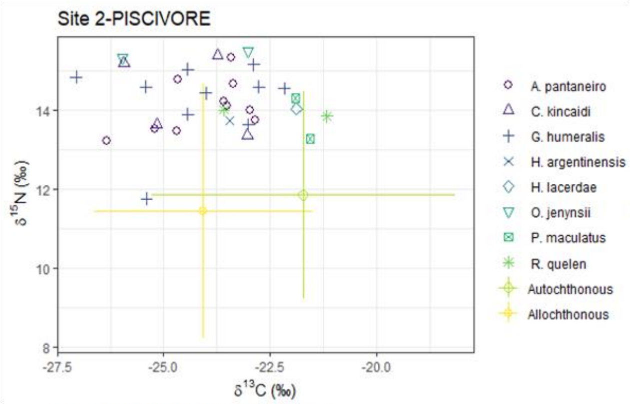
# Supporting material

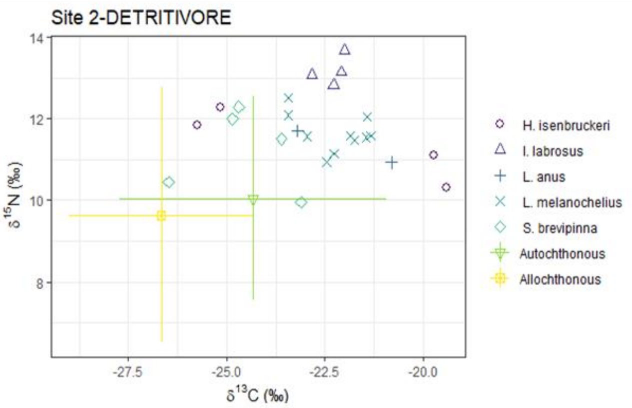

Site 1-PISCIVORES

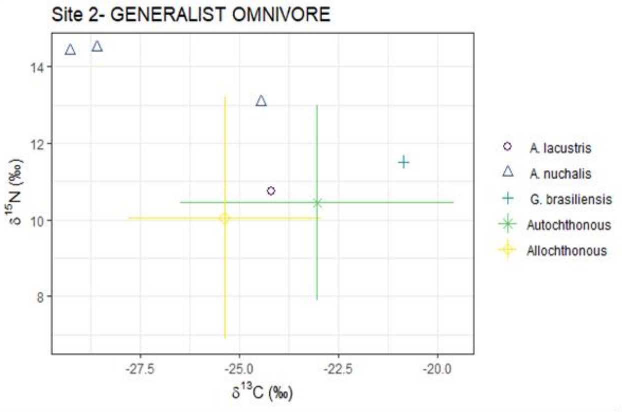

Site 1-DETRITIVORE

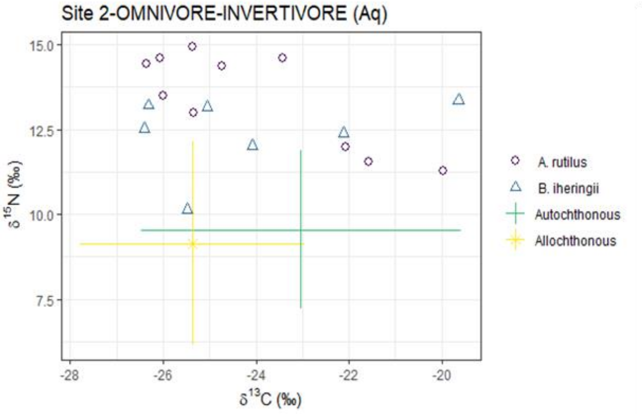

Site 1-GENERALIST OMNIVORE

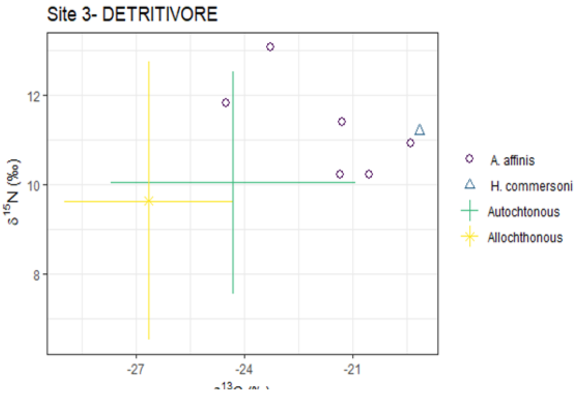

Site 1-OMNIVORE-INVERTIVORE (Aq)

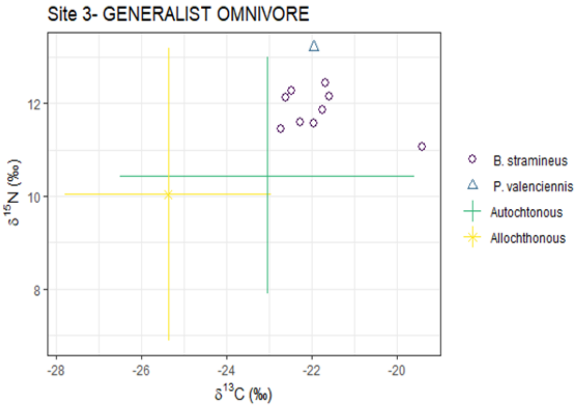

Site 2-PISCIVORE

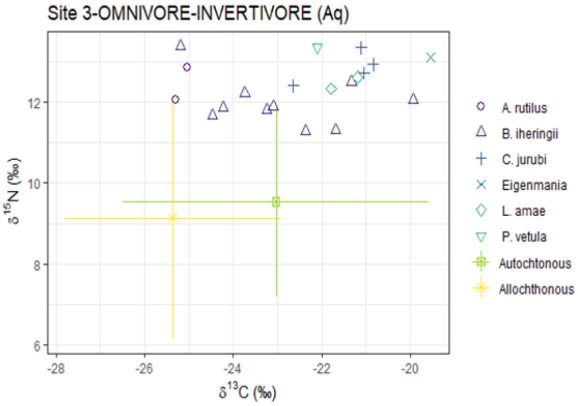

Site 2-DETRITIVORE

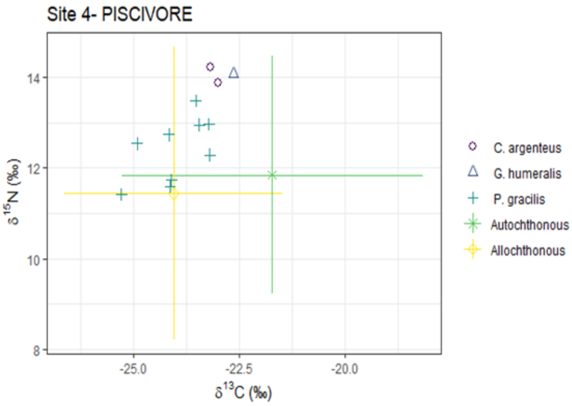

Site 2- GENERALIST OMNIVORE

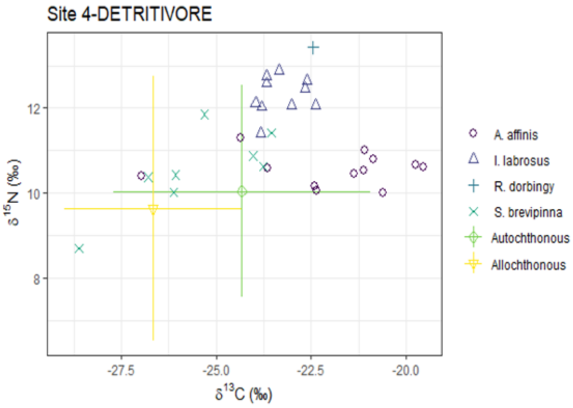

Site 2-OMNIVORE-INVERTIVORE (Aq)

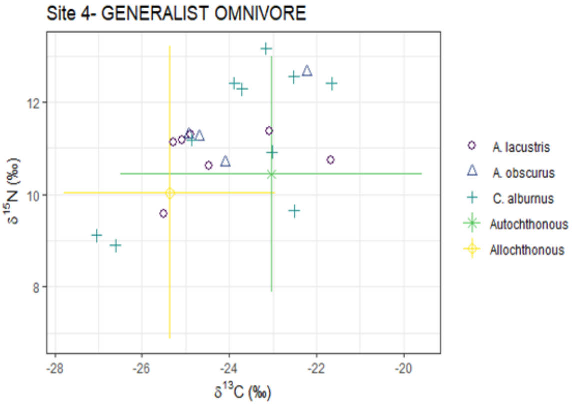

Site 3- DETRITIVORE

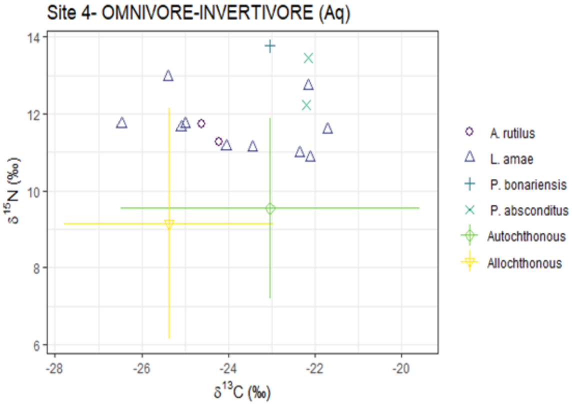

Site 3- GENERALIST OMNIVORE

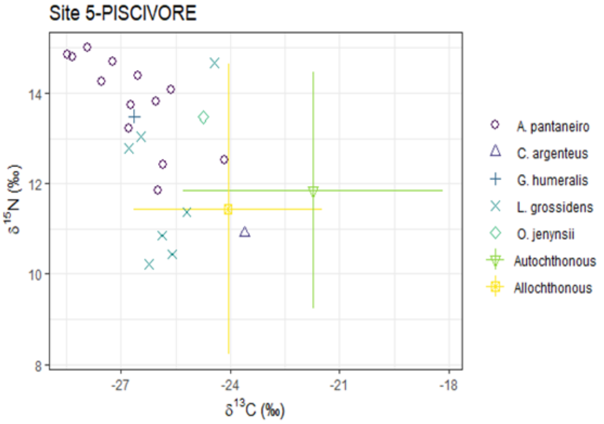

Site 3-OMNIVORE-INVERTIVORE (Aq)

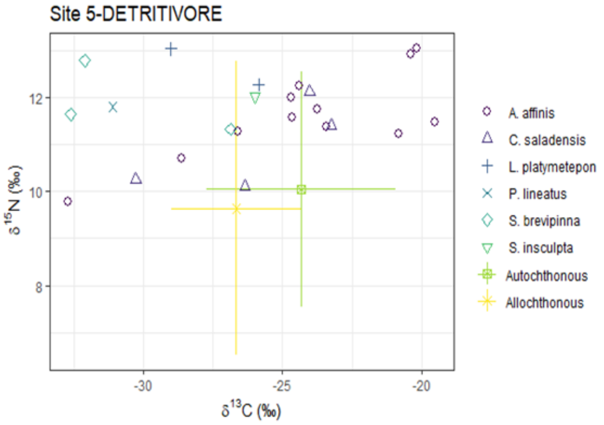

Site 4- PISCIVORE

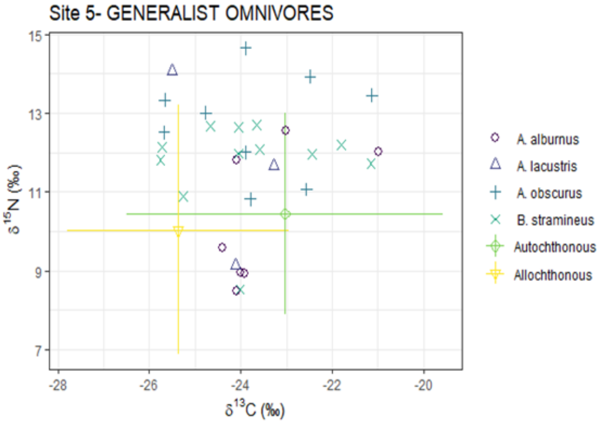

Site 4-DETRITIVORE

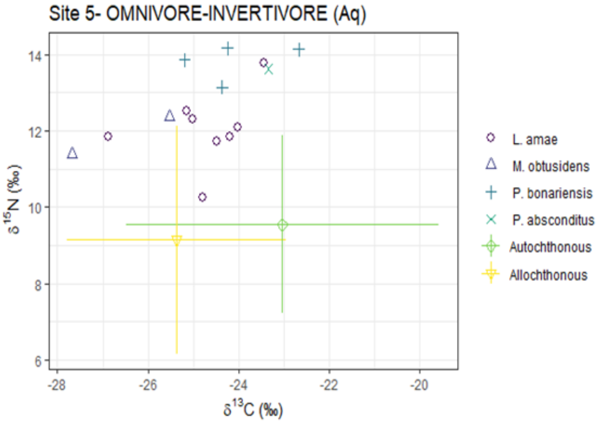

Site 4- GENERALIST OMNIVORE

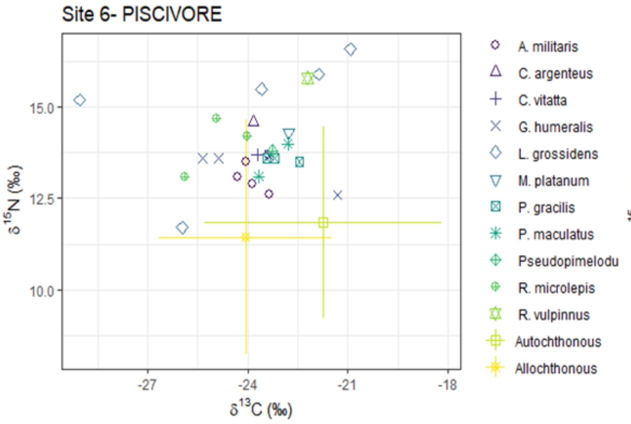

Site 4- OMNIVORE-INVERTIVORE (Aq)

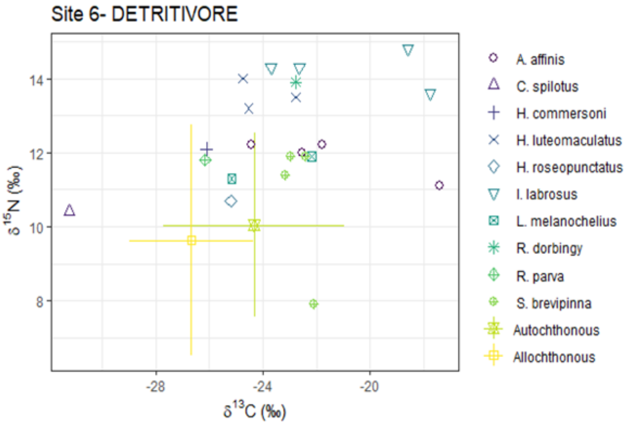

Site 5-PISCIVORE
δ 15N (‰)
14
12
10
8
-27
-24
-21
-18
δ 13C (‰)
A. pantaneiro
C. argenteus
G. humeralis
L. grossidens
O. jenynsii
Autochthonous
Allochthonous

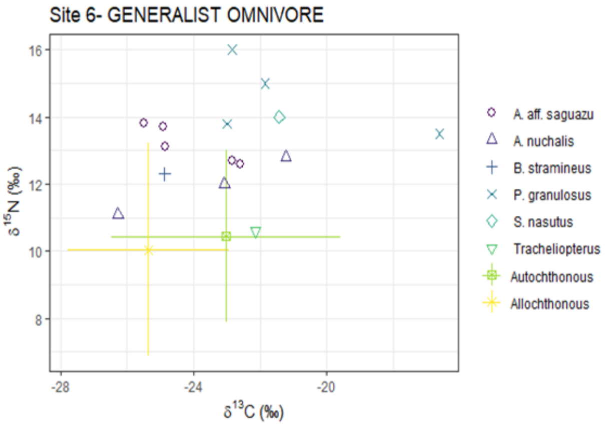

Site 5-DETRITIVORE
δ 15N (‰)
12
10
8
-30
-25
-20
δ 13C (‰)
A. affinis
C. saladensis
L. platymetepon
P. lineatus
S. brevipinna
S. insculpta
Autochthonous
Allochthonous

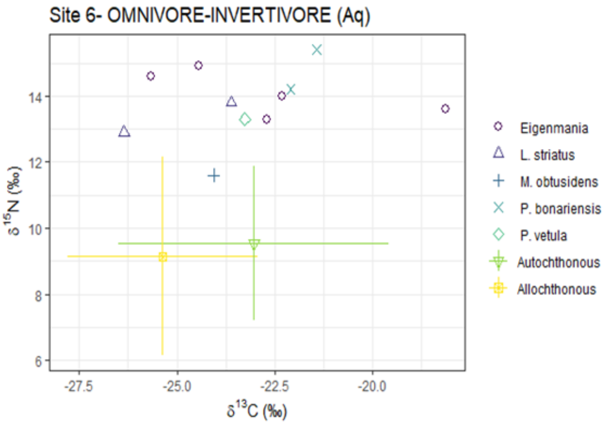

Site 5- GENERALIST OMNIVORES
δ 15N (‰)
15
13
11
9
7
-28
-26
-24
-22
-20
δ 13C (‰)
A. alburnus
A. lacustris
A. obscurus
B. stramineus
Autochthonous
Allochthonous

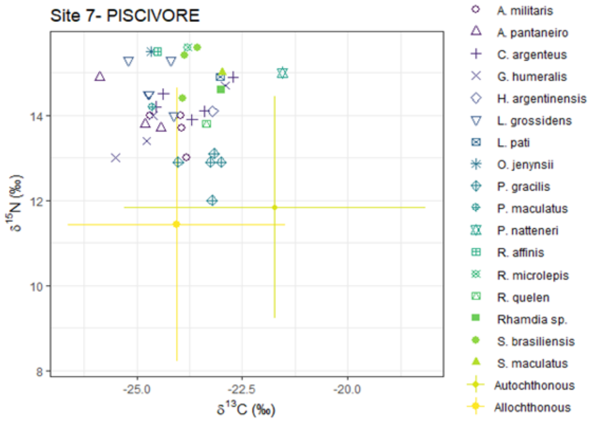

Site 5- OMNIVORE-INVERTIVORE (Aq)
δ 15N (‰)
14
12
10
8
6
-28
-26
-24
-22
-20
δ 13C (‰)
L. amae
M. obtusidens
P. bonariensis
P. absconditus
Autochthonous
Allochthonous

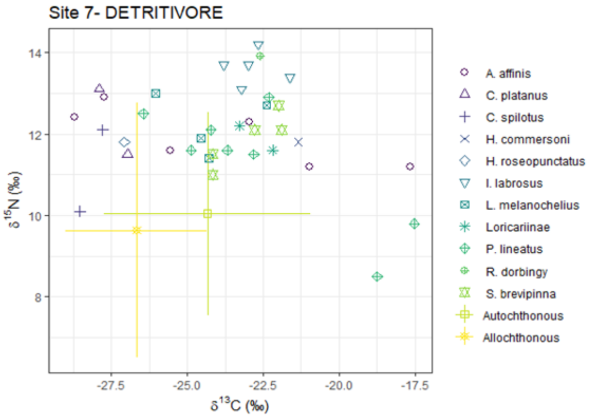

Site 6- PISCIVORE
δ 15N (‰)
15.0
12.5
10.0
-27
-24
-21
-18
δ 13C (‰)
A. militaris
C. argenteus
C. vitatta
G. humeralis
L. grossidens
M. platanum
P. gracilis
P. maculatus
Pseudopimelodu
R. microlepis
R. vulpinnus
Autochthonous
Allochthonous

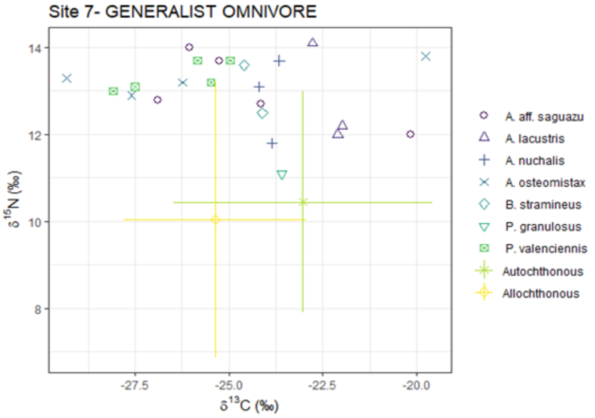

Site 6- DETRITIVORE
δ 15N (‰)
14
12
10
8
-28
-24
-20
δ 13C (‰)
A. affinis
C. spilotus
H. commersoni
H. luteomaculatus
H. roseopunctatus
I. labrosus
L. melanochelius
R. dorbingy
R. parva
S. brevipinna
Autochthonous
Allochthonous

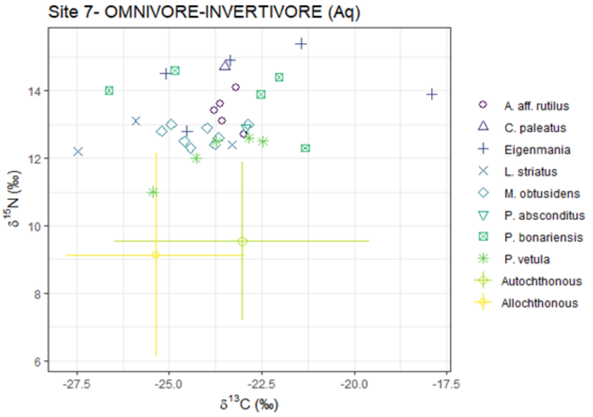

Site 6- GENERALIST OMNIVORE
δ 15N (‰)
16
14
12
10
8
-28
-24
-20
δ 13C (‰)
A. aff. saguazu
A. nuchalis
B. stramineus
P. granulosus
S. nasutus
Tracheliopterus
Autochthonous
Allochthonous

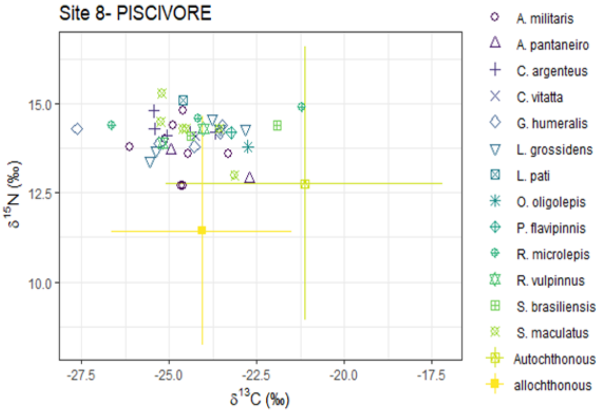

Site 6- OMNIVORE-INVERTIVORE (Aq)
δ 15N (‰)
14
12
10
8
6
-27.5
-25.0
-22.5
-20.0
δ 13C (‰)
Eigenmania
L. striatus
M. obtusidens
P. bonariensis
P. vetula
Autochthonous
Allochthonous

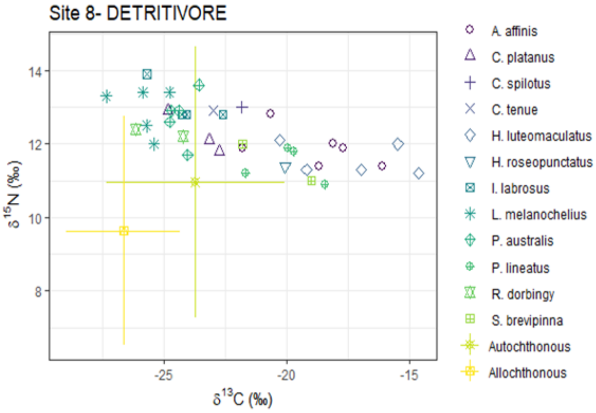

Site 7- PISCIVORE

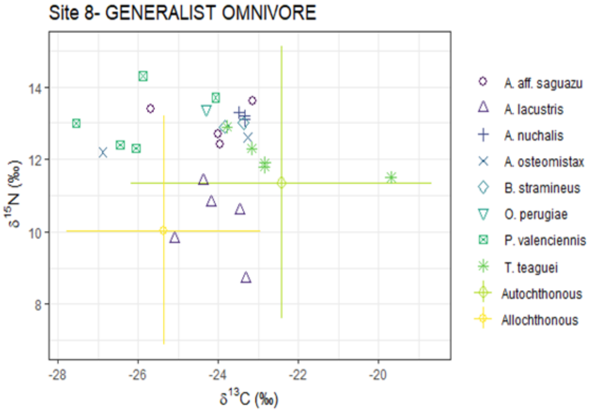

Site 7- DETRITIVORE

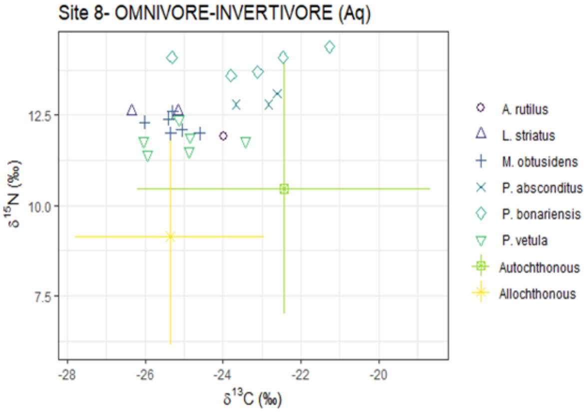

Site 7- GENERALIST OMNIVORE


Site 7- OMNIVORE-INVERTIVORE (Aq)

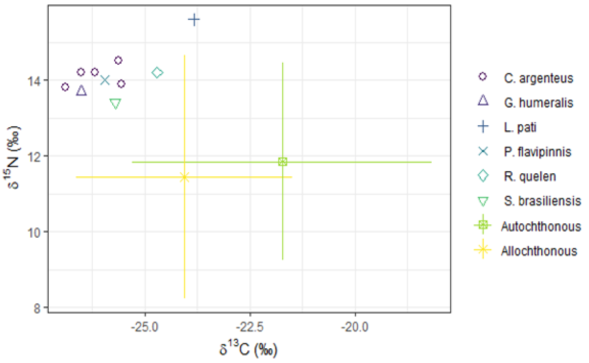

Site 8- PISCIVORE


Site 8- DETRITIVORE

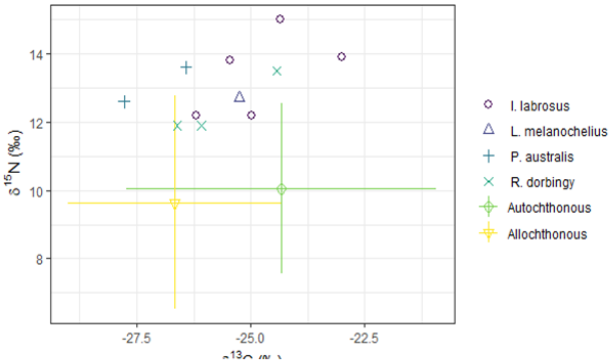

Site 8- GENERALIST OMNIVORE


Site 8- OMNIVORE-INVERTIVORE (Aq)

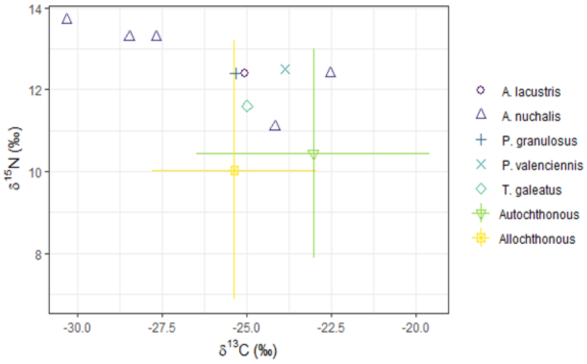
Site 9- PISCIVORE



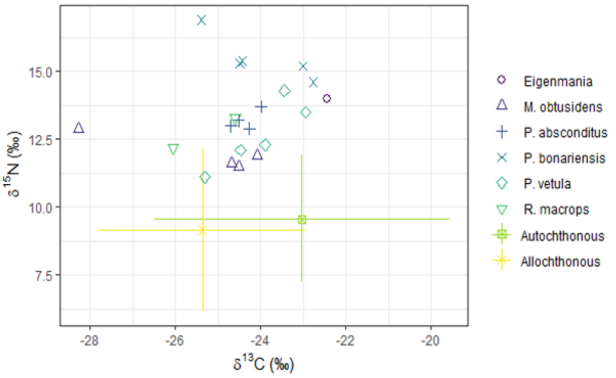
Site 9- DETRITIVORE



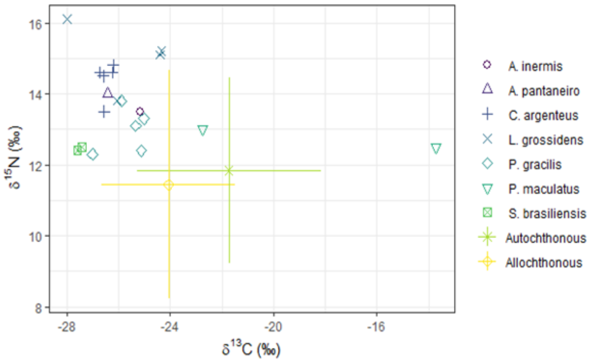
Site 9- GENERALIST OMNIVORE



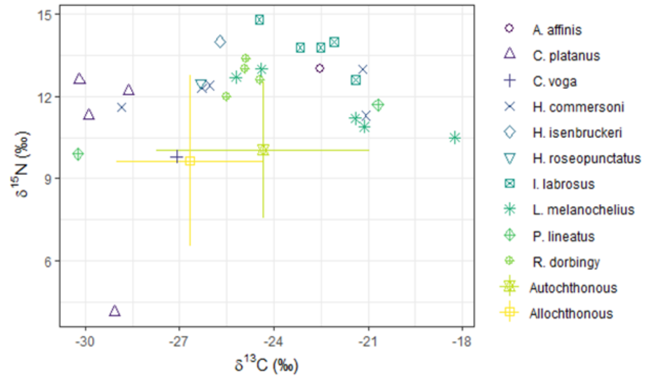
Site 9- OMNIVORE-INVERTIVORE (Aq)



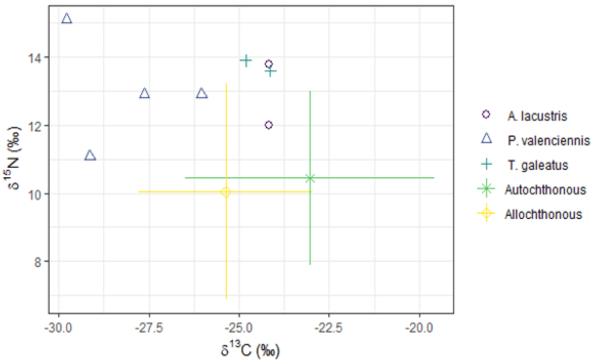
Site 10- PISCIVORE



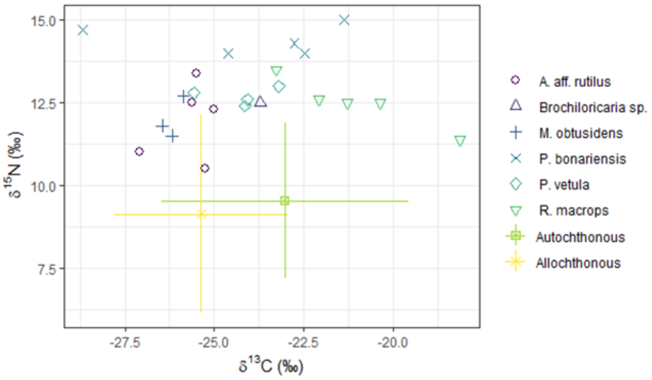
Site 10- DETRITIVORE



Site 10- GENERALIST OMNIVORE



Site 10- OMNIVORE-INVERTIVORE (Aq)



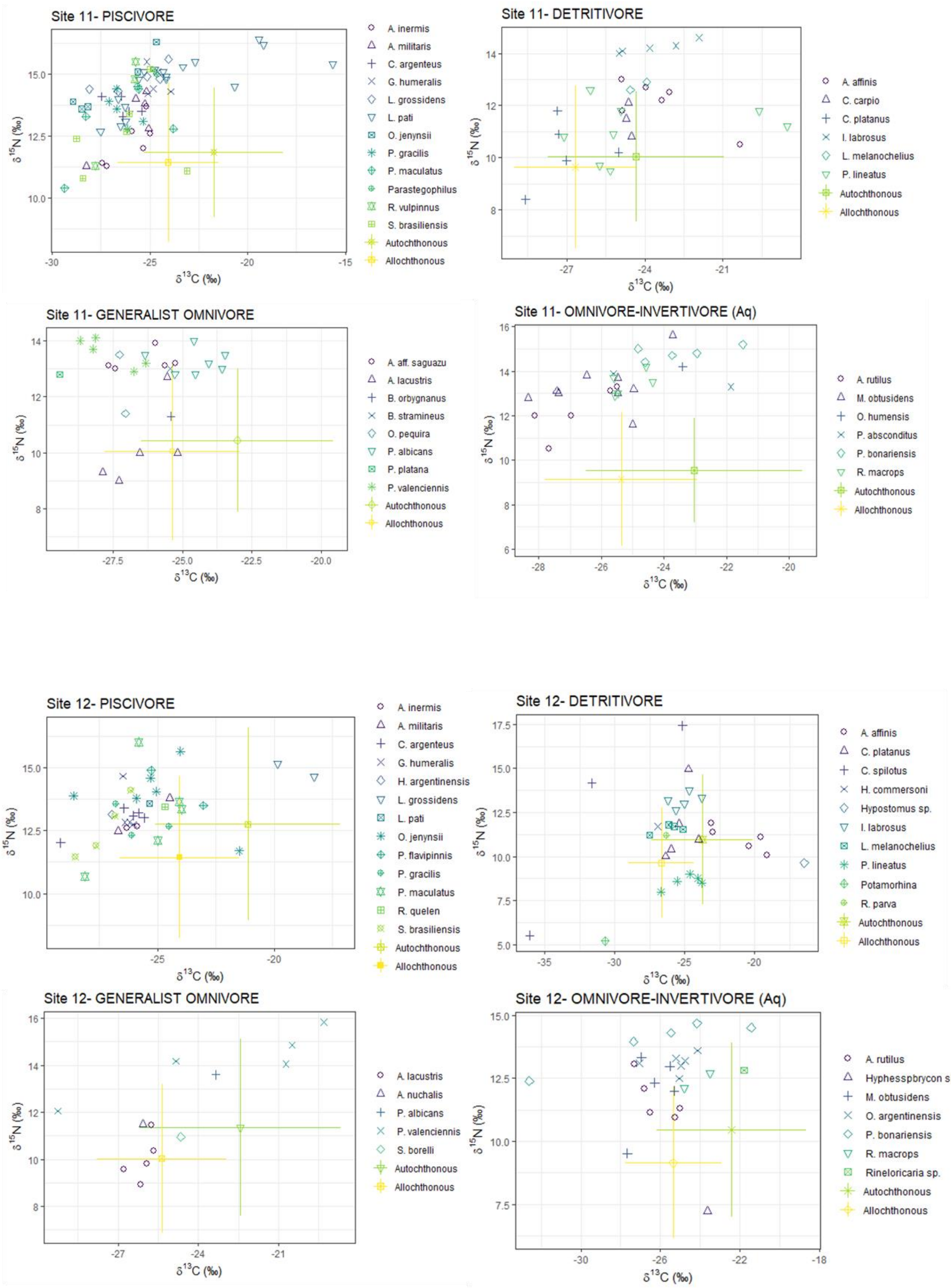


Fig. S1. Exploratory bi-plots obtained from the Bayesian, representing the C and N isotopic values of potential food sources (i.e., basal resources: allochthonous and autochthonous) and fish (grouped by trophic group), representing the contribution of each source to the fish biomass for each trophic group, corrected by the corresponding TEF, along the longitudinal gradient.

Table S1. Mean contribution and weighted contribution of basal resources to the support of fish biomass in the 4 trophic groups at 12 sampling sites along the longitudinal gradient of the Uruguay River (PIS=piscivore; DET= detritivore; GO= generalist omnivore; OI= omnivore-invertivore (Aq). Mean contribution of resource (min 95% CI- max 95% CI). Probability autoch>alloch = Probability result of Bayesian mixing models. Brown values represent a higher probability of allochthonous basal resources to fuelling fish biomass and weighted contribution to fish biomass higher than 60% fuelling by allochthonous resources; green values represent significant higher probability of autochthonous basal resources fuelling fish biomass and weighted contribution to fish biomass higher than 60% fuelling by autochtonous resources. Lines separate sampling sites; light dashed lines represent the presence of one dam; bold dashed line represent the presence of two dams.

| **N sitio** | **Grupo trófico** | **Proportional contribution** | | **Probability autoch>alloch** | **Assamblege-weighted contribution of resources to fish species biomass** | |
|---|---|---|---|---|---|---|
| | | **Allochthonous** | **Autochthonous** | | **Allochthonous** | **Autochthonous** |
| 1 | PIS | 72.5 (31.1-95.7) | 27.5 (4.3-68.9) | 0.131 | **63.3** | 36.7 |
| 1 | DET | 39.5 (13.1-71.5) | 60.5 (28.5-86.9) | 0.745 | 30.25 | **69.75** |
| 1 | GO | 74 (38.2-94.8) | 26 (5.2-61.8) | 0.069 | 42.21 | 57.8 |
| 1 | OI | 77.6 (47.1-94.7) | 22.4 (5.3-52.9) | 0.037 | **65.02** | 34.98 |
| 2 | PIS | 81.5 (56.3-95.2) | 18.5 (4.8-43.7) | 0.022 | 59.43 | 40.56 |
| 2 | DET | 11.8 (2.3-33.3) | 88.2 (66.7-97.7) | 0.998 | 27.22 | **72.78** |
| 2 | GO | 53.9 (8.0-95.1) | 46.1 (4.9-92.0) | 0.425 | 57.14 | 42.856 |
| 2 | OI | 61.1 (19.9-92.5) | 38.9 (7.5-80.1) | 0.271 | **62.63** | 37.37 |
| 3 | DET | 18.5 (3.1-50.7) | 81.5 (49.3-96.9) | 0.967 | 22.03 | **77.97** |
| 3 | GO | 22.6 (2.7-64.3) | 77.4 (35.7-97.3) | 0.923 | 44.51 | 55.49 |
| 3 | OI | 22.5 (2.4-64.7) | 77.5 (35.3-97.6) | 0.909 | 46.7 | 53.3 |
| 4 | PIS | 69.4 (20.9-96.7) | 30.6 (3.3-79.1) | 0.194 | 61.22 | 38.78 |
| 4 | DET | 11.9 (2.4-33.2) | 88.1 (66.8-97.6) | 0.998 | 26.83 | 73.17 |
| 4 | GO | 52.4 (13.1-89.9) | 47.6 (10.1-86.9) | 0.428 | 52.38 | 47.62 |
| 4 | OI | 46.3 (7.0-90.3) | 53.7 (9.7-93.0) | 0.271 | 48.64 | 51.36 |
| 5 | PIS | 89.4 (68.9-98.2) | 10.6 (1.8-31.1) | 0.002 | **76.21** | 23.79 |
| 5 | DET | 26.2 (43.2-93.2) | 73.8 (6.8-56.8) | 0.924 | 43.81 | 56.19 |
| 5 | GO | 55.0 (19.5-87.4) | 45.0 (12.6-80.5) | 0.401 | 51.8 | 48.2 |
| 5 | OI | 76.0 (40.1-95.0 | 24.0 (5.0-59.9) | 0.059 | 58.47 | 41.53 |
| 6 | PIS | 79.4 (49.5-95.5) | 20.6 (4.5-50.5) | 0.041 | **61.3** | 38.7 |
| 6 | DET | 14.1 (1.9-42.4) | 85.9 (57.6-98.1) | 0.993 | 34.6 | 65.4 |
| 6 | GO | 31.7 (5.5-72.0) | 69.3 (28-94.5) | 0.838 | 52.55 | 47.45 |
| 6 | OI | 48.0 (7.4-90.8) | 52.0 (9.1-92.6) | 0.658 | **60.95** | 39.05 |
| 7 | PIS | 85.2 (62.2-96.1) | 14.8 (3.9-37.8) | 0.006 | 57.98 | 42.02 |
| 7 | DET | 11.6 (1.9-34.9) | 88.4 (65.1-98.1) | 0.996 | 29.66 | 70.34 |
| 7 | GO | 64.0 (21.2-93.7) | 36.0 (6.3-78.8) | 0.269 | 51.39 | 48.61 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 7 | OI | 66.1 (41.0-85.3) | 33.9 (14.7-59.0) | 0.088 | 58.07 | 41.93 |
| 8 | PIS | 74.2 (52.4-89.4) | 25.8 (10.6-47.6) | 0.030 | 43.18 | 56.82 |
| 8 | DET | 4.7 (1.2-12.1) | 95.3 (87.9-98.8) | 1.0 | 16.89 | **83.11** |
| 8 | GO | 35.5 (19.1-54.3) | 64.5 (45.7-80.9) | 0.955 | 30.82 | **69.18** |
| 8 | OI | 37.1 (19.6-56.4) | 62.9 (43.6-80.4) | 0.910 | 41.19 | 58.81 |
| 9 | PIS | 77.1 (35.2-97.6) | 22.9 (2.4-64.8) | 0.068 | **63.23** | 36.77 |
| 9 | DET | 66.4 (24.3-94.0) | 33.6 (6.0-75.7) | 0.258 | 54.51 | 45.49 |
| 9 | GO | 61.9 (13.1-96.1) | 38.1 (3.9-86.9) | 0.291 | 50.66 | 49.34 |
| 9 | OI | 75.0 (44.9-93.2) | 25.0 (6.8-55.1) | 0.050 | 58.36 | 41.64 |
| 10 | PIS | 71.7 (24.4-97.4) | 23.8 (2.6-75.6) | 0.164 | 58.26 | 41.74 |
| 10 | DET | 22.4 (4.1-55.6) | 77.6 (44.4-95.9) | 0.993 | 36.27 | **63.73** |
| 10 | GO | 69.8 (21.3-97.1) | 30.2 (2.9-78.8) | 0.220 | 57.37 | 42.63 |
| 10 | OI | 59.3 (23.5-89.0) | 40.7 (11.0-76.5) | 0.265 | 56.33 | 43.67 |
| 11 | PIS | 93.5 (80.4-98.7) | 6.5 (1.3-19.6) | 0 | **64.7** | 35.3 |
| 11 | DET | 23.7 (4.8-59.9) | 76.3 (40.1-95.2) | 0.921 | 37.14 | **62.86** |
| 11 | GO | 87.4 (62.6-98.1) | 12.6 (1.9-37.4) | 0.004 | 65.8 | 34.2 |
| 11 | OI | 80.6 (51.5-95.4) | 19.4 (4.6-48.5) | 0.012 | **71.57** | 28.43 |
| 12 | PIS | 88.4 (68.7-97.2) | 11.6 (2.8-31.3) | 0.001 | 43.59 | 56.41 |
| 12 | DET | 21.4 (6.3-47.1) | 78.6 (52.9-93.7) | 0.985 | 36.12 | **63.88** |
| 12 | GO | 42.7 (9.0-80.7) | 57.3 (19.3-91.0) | 0.645 | 28.43 | **71.57** |
| 12 | OI | 67.9 (40.3-87.3) | 31.2 (12.7-59.7) | 0.090 | 46.69 | 53.31 |

Table S2. Contribution of basal resources (autochthonous vs. allochthonous) to fish biomass along the 12 sampling sites of the Uruguay River. Mean contribution represents the result of the Bayesian mixing models (mean ± sd). % species > 60% autochthonous and allochthonous subsides indicates the percentage of the total species per site that exceeds 60% contribution to the biomass by one of the resources. % species coupling pathways indicates the % of species per sampling site that do not exceed 60% contribution of any type of resources. Weighted contribution refers to the mean contribution of each pathway to the total biomass weighted by the biomass of each species in the community. Mean contributions and weighted contributions higher than 60% are shown in bold. Light dashed lines indicate the presence of one dam, and the bold dashed line indicates the presence of two dams.

| N° site | Mean contribution of resources to fish species biomass | | | | | Weighted contribution of resources to fish species biomass | |
|---|---|---|---|---|---|---|---|
| | **Autochthonous** | **Allochthonous** | **% species >60% autochthonous subside** | **% species >60% Allochthonous subside** | **% species coupling pathways** | **Autochthonous** | **Allochthonous** |
| 1 | 46.9 ± 17.3 | 53.1 ± 17.3 | 26.7 | 40 | 33.3 | 55.4 | 44.6 |
| 2 | 50.9 ± 14.1 | 49.1.1 ± 14.2 | 22.2 | 16.7 | 61.1 | 49.2 | 50.8 |
| 3 | 57.9 ± 12.6 | 42.1 ± 12.6 | 50 | 0 | 50 | **61.8** | **38.2** |
| 4 | 49.4 ± 15.9 | 50.6 ± 15.9 | 14.3 | 14.3 | 71.4 | 55.5 | 44.5 |
| 5 | 48.4 ± 10.5 | 51.6 ± 10.5 | 5.3 | 21.1 | 73.6 | **35.3** | **64.7** |
| 6 | 49.3 ± 11.8 | 50.7 ± 11.8 | 12.5 | 12.5 | 75 | 44.0 | 56.0 |
| 7 | 50.1 ± 10.1 | 49.9 ± 10.1 | 11.9 | 9.5 | 78.6 | 50.6 | 49.4 |
| 8 | **66.7 ± 11.1** | **33.2 ± 11.1** | 69.4 | 0 | 30.6 | **65.9** | **34.1** |
| 9 | 44.3 ± 5.3 | 55.7 ± 5.3 | 0 | 22.2 | 77.8 | 41.6 | 58.4 |
| 10 | 49.0 ± 13.1 | 51.0 ± 13.1 | 25 | 33.3 | 41.7 | 50.2 | 49.8 |
| 11 | 42.6 ± 12.3 | 57.5 ± 12.3 | 7.1 | 53.6 | 39.3 | **40.0** | **60.0** |
| 12 | **60.6 ± 10.0** | **39.4 ± 10.0** | 48.5 | 0 | 51.5 | 58.7 | 41.3 |

# 7. Discusión

En este trabajo se lograron avances significativos en la comprensión del funcionamiento del Río Uruguay, haciendo foco en la comunidad de peces por su enorme importancia ecológica, cultural, social y económica. Asimismo, se logró constatar empíricamente y visibilizar varios de los posibles impactos de las represas sobre el Río Uruguay. En particular, se realizó la primera descripción de la fauna íctica del Río Uruguay en la totalidad de su extensión de *ca.* 1800 km, desde las nacientes a la desembocadura en el Río de la Plata. Asimismo, se realizó la clasificación en grupos tróficos de todas las especies capturadas en el Río Uruguay. Esta descripción de la dieta y hábitos tróficos de más de 100 especies de peces representa, además, la primera descripción publicada de los hábitos alimenticios para 29 de esas especies (López-Rodríguez et al., 2019). Por su parte, la clasificación trófica está siendo un insumo esencial para varias investigaciones que avanzan sobre el conocimiento de la estructura trófica de las comunidades de peces en la región (lo cual es reflejado en el creciente número de citas de dicho artículo). Con este trabajo se logró identificar cuatro grupos tróficos principales que componen la estructura trófica de los peces de este río: piscívoros, detritívoros, omnívoro-invertívoros (acuáticos) y omnívoro-generalistas. Esta clasificación se subdividió, a su vez, en 8 grupos tróficos con mayor resolución: piscívoros, piscívoro-invertívoros, detritívoros, omnívoro-detritívoros, omnívoro-invertívoros (acuáticos), omnívoro-planctívoros, omnivoro-invertívoros (terrestres) y omnívoro-herbívoros (terrestre).

La estructura trófica del ensamble de peces mostró diferencias significativas en el gradiente longitudinal únicamente en la riqueza relativa de las especies del grupo trófico de los omnívoro-invertívoros (terrestres), con mayor riqueza en el Río Uruguay medio que en el alto o bajo Río Uruguay (López-Rodríguez et al., 2019).

Por otra parte, se logró detectar y describir patrones de diversidad de peces (i.e., diversidad específica, diversidad beta, trófica y ecológica) a lo largo del gradiente longitudinal. Encontramos que el Río Uruguay presenta una gran diversidad de peces, comparable a ríos de Sudamérica con similares flujos de descarga (Capítulo 1; López-Rodríguez et al., 2019). Además, nuestros resultados muestran la existencia de patrones longitudinales de incremento en las métricas de diversidad analizadas (Capítulo 2; López-Rodríguez et al., 2024).

Finalmente, describimos por primera vez el origen del carbono (i.e., autóctono, alóctono u ocurrencia de acoplamiento de vías) que subsidia la biomasa de los peces a lo largo del gradiente fluvial del río, describiendo los potenciales impactos que las represas pueden estar generando sobre este subsidio. Los resultados indican que el subsidio energético de las tramas tróficas del Río Uruguay proviene predominantemente de un acople de las vías autóctona (productores primarios como algas bentónicas y planctónicas) y alóctona (proveniente de detrito vegetal C3 de origen terrestre, que deriva de los bosques riparios de la cuenca), más que la dominancia de una vía sobre otra. Esto último era lo que podría esperarse de acuerdo a marcos teóricos como el Concepto de Pulsos de Inundación (FPC), el Modelo de Río Productivo (RPM), la Síntesis del Ecosistema Riverino (RES) y el Concepto de Ondas de Río (RWC). Asimismo, encontramos aumentos relativos del subsidio autóctono a medida que el río incrementa su tamaño hacia aguas abajo en las zonas libre de represas (Capítulo 3; López-Rodríguez et al., in prep.).

Por otra parte, nuestros resultados suman clara evidencia empírica de que las represas promueven directa o indirectamente la pérdida de biodiversidad (i.e., riqueza de especies, diversidad trófica, diversidad ecológica y de fuentes de subsidio energético), modificando los patrones longitudinales que ocurren en ausencia de interrupciones (López-Rodríguez et al., 2024; in prep.).

## 7.1. Revisión de marcos teóricos y actualizaciones

En este trabajo encontramos evidencia que apoya lo planteado por la teoría de metacomunidades, sobre la importancia del mantenimiento de la conectividad en los ecosistemas para permitir la dispersión de los organismos como determinante de la diversidad local (Leibold et al., 2004). Nuestros resultados muestran que las diferencias de diversidad (diversidad beta) fueron menores entre los sitios con una mayor conexión, sugiriendo que ocurre un importante movimiento de las especies entre estos sitios. Asimismo, las recuperaciones de diversidad más importantes se observaron en las regiones de aguas libres. Por el contrario, aquellos sitios donde las comunidades están aisladas por efecto de las represas, fueron los que tuvieron menor riqueza de especies respecto de las comunidades inmediatamente aguas arriba. Este efecto del aislamiento sobre la riqueza de especies de peces ya ha sido detectado en metacomunidades de sistemas fluviales (Río Negro, Uruguay, Borthagary et al., 2020), lo que resalta la importancia del mantenimiento de áreas conectadas por la red fluvial.

El aumento de riqueza de especies observado en el gradiente longitudinal a medida que el río aumenta su área, podría entenderse en el contexto de teorías clásicas de ecología general como la teoría de área-diversidad (MacArthur & Wilson, 1967), que predice un aumento en la diversidad con el aumento de la superficie del ecosistema al generarse más oportunidades de colonización por nuevas especies y potencialmente contener una mayor heterogeneidad de hábitats. En este sentido, los hallazgos también pueden explicarse por la teoría de heterogeneidad de hábitats y productividad (Wrigh, 1983). A nivel mundial, se ha detectado la importancia del aumento del área (y consecuentemente del volumen de agua) a escala local para generar ambientes más heterogéneos, así como también para incrementar la entrada de energía del ambiente circundante, lo que determinaría en gran medida los patrones de diversidad de especies de peces en sistemas fluviales (Guégan et al., 1998). En este sentido se ha planteado que, a mayor energía disponible, los ríos pueden soportar un mayor número de especies. En aquellas regiones de un río con similares productividades, la heterogeneidad de hábitats es la clave para la coexistencia de más especies (Guégan et al., 1998).

Estos resultados apoyan la idea de la importancia de la inclusión de las teorías ecológicas generales en los marcos teóricos específicos de la ecología fluvial, los cuales se han centrado en otros aspectos, poniendo la mirada en otros procesos (como cambios físicos en el ambiente que determinan la disponibilidad de recursos) que se dan en el ecosistema.

En cuanto a los marcos teóricos específicos en ecología fluvial, nuestros resultados muestran apoyos parciales a las predicciones generadas por varios de ellos. Esto depende de qué característica comunitaria o proceso se esté analizando (ya que no todos los marcos generan predicciones sobre todos los procesos y parámetros). Asimismo, nuestros resultados sugieren que las características locales tuvieron gran relevancia, ya que los ajustes a las predicciones teóricas también dependieron del tramo del río considerado.

En particular, encontramos evidencia que se alinea con las predicciones planteadas en el Concepto de Río Continuo (RCC -Vannote et al., 1980). Encontramos un patrón de aumento en el gradiente longitudinal de la riqueza de especies, la beta diversidad y el componente de recambio de especies, y la diversidad trófica y de nicho ecológico (López-Rodríguez et al., 2024). Asimismo, observamos que en términos generales la biomasa total de los peces parece ser subsidiada por una combinación de las vías energéticas alóctona y autóctona a lo largo de todo el gradiente del Río Uruguay, pero con pequeños incrementos en la importancia relativa del subsidio autóctono a medida que el río aumenta de tamaño hacia aguas abajo en las secciones sin disturbios hidrológicos (López-Rodríguez et al., in prep.). Sin embargo, también encontramos evidencia clara de los impactos negativos de las represas en la diversidad ecológica de los peces, con abruptas disminuciones de la misma, aguas abajo de las represas (López-Rodríguez et al., 2024). Esto se ajusta a las predicciones del Concepto de Discontinuidad Seriada (SDC-Ward & Stanford 1983; 1995).

El SDC, sin embargo, no genera predicciones sobre los subsidios energéticos de las tramas tróficas en los sistemas fluviales con regulaciones en la hidrología. Es por eso que estos resultados complementan este marco teórico a través de evidencia sobre el efecto de las represas sobre las dinámicas de asimilación de las fuentes alimenticias que subsidian las redes tróficas en tramos represados (López-Rodríguez et al., in prep.).

Por otra parte, observamos patrones que se ajustan a las predicciones del FPC en la sección media del río, siendo la sección con mayor presencia de planicies de inundación y bosque ripario en las márgenes (Zaniboni-Filho & Schulz, 2003). En este tramo del río de casi 1000 km de aguas libres (entre los sitios 4 y 7, i.e., entre las represas Foz de Chapecó y Salto Grande) encontramos una riqueza relativa de especies pertenecientes al grupo trófico de los omnívoros consumiendo sobre macroinvertebrados terrestres (omnívoros-invertivoro-terr-), que fue significativamente más alta en comparación con el Río Uruguay alto y bajo (López-Rodríguez et al., 2019). Este resultado coincide con lo encontrado en los estudios de subsidios energéticos (López-Rodríguez et al., in prep.). En estos estudios se observó que el 65% de la biomasa de los peces en el sitio 5 es subsidiada por carbono proveniente del medio terrestre (i.e., predominancia de la vía energética alóctona). El FPC plantea que los incrementos en la conexión entre el ambiente terrestre y acuático promueven un mayor subsidio de la vía terrestre a la biomasa de los peces (Junk et al., 1989). Estos resultados son coincidentes con estudios realizados a diversas escalas, en los que se observó que la ingesta de alimentos terrestres de los peces aumenta con el aumento de la interfase tierra-agua, por ejemplo, en bosques inundados (Winemiller & Jepsen, 1998) o en arroyos con alta concentración de bosque ripario (Baxter et al., 2005). Por lo tanto, nuestros resultados sugieren la existencia de una fuerte asociación entre el sustento de las tramas tróficas por carbono de origen terrestre y la conectividad del ambiente acuático con el terrestre en zonas con planicies de inundación.

El ajuste al FPC en la sección media del río tiene sentido, ya que esta teoría fue desarrollada en sistemas fluviales tropicales y subtropicales con grandes extensiones de planicies de inundación, características que observamos en el Río Uruguay medio. Asimismo, se plantea que, al existir planicies de inundación, el aporte al río no depende tanto de los procesos y transporte de materiales desde aguas arriba. Estos procesos se encuentran interrumpidos por la presencia de la cascada de represas en la parte alta del río.

Nuestros resultados sugieren también un ajuste parcial a lo planteado por la RES (Thorp & Delong, 2006) en cuanto a la dependencia de las características y de la geomorfología local para el sustento energético, tanto en los tramos libres de represas como en las regiones más directamente afectadas por las mismas. Por ejemplo, en las regiones libres de represas, encontramos una alta proporción de especies subsidiadas por la vía alóctona en aquellas secciones con mayor proporción de área con cobertura de bosque ripario (nacientes), así como también en la sección con mayores planicies de inundación (sección media del río). Contrariamente, se observó soporte autóctono en las regiones con mayores tiempos de residencia del agua, lo que permite un mayor desarrollo de las comunidades planctónicas (e.g., desembocadura del Río Uruguay) (López-Rodríguez et al., in prep.). Este resultado también se relaciona con lo encontrado en López-Rodríguez et al. (2019), específicamente con la una mayor frecuencia del grupo trófico de los peces omnívoro-planctívoros en la parte baja del río, probablemente reflejando que en la zona de la desembocadura la velocidad del río y el flujo turbulento decrece cuando el río se ensancha, permitiendo el establecimiento y acumulación de biomasa de comunidades planctónicas (Horwitz, 1978; Vannote et al., 1980).

En las regiones afectadas por las represas encontramos efectos sobre los sustentos energéticos, pero la dirección del cambio parece depender fuertemente de las características locales de cada sitio. Un patrón claro que surge de estos resultados es que en las regiones afectadas por las represas (i.e., aguas abajo de las mismas o cola del embalse), las vías energéticas tienden a simplificarse, con menor proporción de especies que se sustentan por una u otra vía (i.e., alóctona o autóctona). Sin embargo, las diferencias en la estructura del paisaje, el ingreso de tributarios y la presencia o ausencia de monte ripario parecen ser determinantes en la dirección del cambio (López-Rodríguez et al., in prep.). Esto destaca la importancia de los distintos parches hidrogeomorfológicos y de la estructura del paisaje en la determinación de la vía de sustento para las redes tróficas.

Por lo tanto, nuestros resultados sugieren que las características locales, en conjunto con la presencia de planicies de inundación que pueden proveer de recursos alóctonos al sistema fluvial, serían determinantes en la magnitud relativa de los distintos subsidios energéticos de los peces. Estos resultados apoyan trabajos previos (e.g., Roach & Winemiller, 2015), incluidos trabajos de la parte baja del Río Uruguay (González-Bergonzoni et al., 2019).

Un resultado altamente relevante, y que pone en consideración algo que no manejan los marcos teóricos actualmente en discusión en ecología fluvial, es la importancia del acople de las vías energéticas como sustento a la biomasa de los peces. Ninguno de los marcos teóricos analizados plantea la importancia del acople de vías energéticas en las tramas tróficas, sino que plantean: 1. un soporte cambiante de forma predecible entre la vía autóctona y alóctona a lo largo del sistema fluvial (RCC-Vannote et al., 1980), 2. un soporte mayoritario de la vía alóctona (FPC-Junk et al., 1989), 3. un soporte mayoritario de la vía autóctona (RPM-Thorp & Delong, 1994; 2002), o 4. un soporte mayoritario de una u otra vía dependiendo de las características ambientales locales (RES-Thorp et al., 2008; RWC-Humpries et al., 2014).

Sin embargo, en este trabajo se encontró fuerte evidencia de la importancia del acople de ambas vías a lo largo del gradiente fluvial (López-Rodríguez et al. in prep.). Esto es coincidente con teorías ecológicas generales que plantean la importancia del acople de las vías energéticas para mantener la estabilidad de los ecosistemas (Keppeler et al., 2021). En este sentido, se ha planteado que los depredadores tope acoplan ambas vías, ejerciendo presiones diferenciales sobre las distintas vías dependiendo de la disponibilidad de los recursos (Rooney & McCann, 2012). A nivel general en ecología, se ha planteado que las interacciones de consumo débiles favorecen la estabilidad de las redes tróficas, ya que, si un consumidor es capaz de diversificar su dieta, disminuirá la presión sobre determinado recurso y evitará su reducción, favoreciendo así una mayor estabilidad del sistema (McCann, 1998; McCann, 2000).

En el caso particular de los ecosistemas fluviales que mantienen su conexión hidrológica, los peces pueden moverse por diferentes ambientes, lo que favorecería la integración de recursos de diferentes zonas, el acople de las vías (Woodward & Hildrew, 2002) y consecuentemente una mayor estabilidad de los ecosistemas (Bellmore et al., 2015; Scholl et al., 2023). Este acoplamiento de vías energéticas podría también reducir las fuerzas de interacción entre los consumidores y las presas, disminuyendo las presiones por diversificación en la dieta, lo que promovería también redes más estables en sistemas altamente dinámicos (McCann, 2000; Cross et al., 2013). Trabajos utilizando macroinvertebrados como modelo apoyan este patrón, mostrando que los consumidores tienden a diversificar su dieta como consecuencia de la variabilidad temporal en la disponibilidad de recursos, encontrándose que las interacciones débiles son las que prevalecen (Peralta-Maraver et al., 2016).

Por otra parte, la magnitud de los ingresos de material alóctono podría ser determinante en su uso como sustento a la biomasa de los consumidores, idea que se contrapone por lo planteado por el RPM (Thorp & Delong, 1994; 2002). Este marco teórico incorpora sistemas con planicies de inundación, pero plantea que el sustento de las redes tróficas es mayormente autóctono. Esto se debería a que en las planicies de inundación se produce también el crecimiento de algas bentónicas que son más lábiles que el carbono de origen alóctono (Thorp & Delong, 2002). Además, este marco plantea que las redes tróficas fluviales se basan en sustento autóctono, sin importar la disponibilidad de sustento alóctono. En este sentido, cabe destacar que los muestreos de este trabajo fueron desarrollados en un período de altas lluvias y crecidas del río principal y sus tributarios, lo que incrementó la extensión de las planicies de inundación y probablemente también la duración de la interacción entre el ambiente terrestre y el acuático. Esto podría haber incrementado el ingreso de recursos alóctonos al río, permitiendo un mayor sustento por esta vía energética a la biomasa de los peces.

Es interesante notar que las diversas teorías mencionadas en ecología fluvial no tienen en cuenta la variabilidad climática y los patrones de precipitación como factores relevantes en el funcionamiento de los ecosistemas fluviales por sus efectos directos e indirectos sobre la disponibilidad de distintos recursos. Este podría ser uno de los motivos por los cuales las teorías de funcionamiento de ecología fluvial no parecen ser generalizables y no se ajustan cabalmente a nuestro sistema de estudio en particular. Sin embargo, el marco teórico planteado en el Concepto de Ondas de Río (Humpries et al. 2014), además de tomar la variación espacial a lo largo del gradiente longitudinal, incorpora la variación temporal de los caudales, las precipitaciones y la disponibilidad de recursos. En este aspecto, esta teoría incorpora y expande los postulados del FPC, planteando que las precipitaciones serían un factor clave que influye en los pulsos de inundación y por tanto en el ingreso de material alóctono, y en la disponibilidad de fuentes alimenticias. Por lo tanto, los distintos muestreos realizados para evaluar el funcionamiento de ríos, tanto libres como represados, podrían estar capturando o no esas ondas de ingreso de material alóctono desde el medio circundante, principalmente en aquellas regiones con grandes extensiones de planicies de inundación.

Sin embargo, es posible también que nuestro hallazgo sobre la importancia del material alóctono en las redes tróficas del Río Uruguay no sea estrictamente dependiente del momento de muestreo, sino que sea un patrón generalizable para ríos tropicales y subtropicales con extensas planicies de inundación y pulsos con patrones y duración relativamente predecibles, como plantea el FPC (Junk et al., 1989). Esta hipótesis podría darle aún más sustento al FPC como marco conceptual particularmente relevante para los ríos tropicales y subtropicales. Asimismo, también contribuye al marco RWC, principalmente en sistemas sin interrupciones en su hidrología o en aquellas regiones de aguas libres, ya que como reportamos en nuestros resultados, la presencia de represas interrumpe los patrones del gradiente longitudinal. En cualquier escenario, estos resultados remarcan la importancia de contar con muestreos que permitan capturar la variabilidad estacional para testear estos marcos teóricos en otras condiciones ambientales, por ejemplo, en épocas de bajas precipitaciones, o incluso en épocas de sequías.

En resumen, nuestros resultados permitieron generar evidencia empírica que sustenta parcialmente algunos de los marcos teóricos en ecología fluvial, pero no encontramos patrones generalizables asociados a ninguno de los marcos teóricos en particular. Destacamos que las predicciones de estos marcos fueron puestas a prueba en un sistema diferente a los típicamente usados para la generación de los mismos, con la excepción del FPC, como lo son los grandes sistemas ubicados en la región subtropical. Finalmente, destacamos la importancia de la presencia de planicies de inundación y de las características locales como determinantes de los sustentos energéticos. Por otra parte, la regulación o alteración del flujo hidrológico por presiones antrópicas (en particular por represas), interpelan a prácticamente todos los marcos teóricos actualmente en discusión en ecología fluvial.

Este trabajo incorpora estas alteraciones, y completa vacíos de información en la temática, con alcance regional y probablemente también alcance general.

## 7.2. Nuevos aportes al conocimiento sobre el funcionamiento del Río Uruguay

En el primer capítulo de esta tesis se realizó la primera descripción de la estructura trófica de los peces del Río Uruguay, a partir de la identificación de las especies presentes a lo largo de todo el gradiente longitudinal, así como también la descripción de la dieta y clasificación en grupos tróficos (López-Rodríguez et al., 2019). Esta información resulta relevante y necesaria para comenzar a generar un conocimiento integral del funcionamiento del Río Uruguay. Asimismo, la información generada en el primer capítulo sirvió de base para el desarrollo de los posteriores trabajos centrados en la evaluación del efecto de las represas sobre diferentes métricas de diversidad de los peces y sobre el funcionamiento a nivel sistémico.

Los estudios sobre los efectos de las represas en el Río Uruguay son escasos, evidenciando por ejemplo cambios en algunas métricas de diversidad, como la diversidad genética (Ribolli et al., 2021) y la diversidad de grupos funcionales (de Bem et al., 2021). Por ejemplo, se ha observado que las represas de la parte alta del Río Uruguay simplifican la diversidad genética aguas arriba (Ribolli et al., 2021) y generan pérdida de grupos funcionales, tanto aguas arriba como aguas abajo (de Bem et al., 2021). Sin embargo, esos estudios se centraron en las represas ubicadas en el Río Uruguay alto y no integraron todo el gradiente longitudinal. Asimismo, los estudios enfocados en los efectos de las represas sobre la disponibilidad de recursos y en la respuesta de las comunidades de peces son inexistentes en este río.

A nivel global se ha constatado que los cambios en el ambiente que generan las represas afectan la disponibilidad de recursos alimenticios para los peces (Sabo et al., 2010; Winemiller et al., 2010; Roach & Winemiller, 2015; Ruhí et al., 2016). Nuestros resultados muestran que los efectos de las represas sobre el Río Uruguay, probablemente a través de cambios en la disponibilidad de alimento, pueden resultar en la disminución de la proporción de las especies que se subsidian por alguna de ambas vías energéticas en las regiones afectadas por las represas, disminuyendo notablemente la proporción de especies que son sustentadas por alguna de las vías (ya sea autóctona o alóctona) (López-Rodríguez et al., in prep.). Estos resultados podrían explicar las abruptas disminuciones en la riqueza taxonómica, la diversidad trófica y en la diversidad de nicho ecológico encontradas en las áreas aguas abajo de las represas (López-Rodríguez et al., 2024), sugiriendo que el mecanismo asociado a esas disminuciones podría estar relacionado con la reducción de la energía disponible en el ecosistema.

Por lo tanto, los resultados encontrados en el Capítulo 3 retoman, complementan y explican parcialmente lo observado en el Capítulo 2 de la tesis, demostrando la importancia de emplear aproximaciones complementarias para comprender el funcionamiento del Río Uruguay y otros grandes ríos.

Estos resultados representan evidencia nueva y clara sobre los efectos de las represas sobre la biodiversidad (analizada mediante diferentes métricas) a lo largo de todo el gradiente longitudinal del Río Uruguay (López-Rodríguez et al., 2024; López-Rodríguez et al. in prep.).

Otro resultado a destacar sobre el funcionamiento del Río Uruguay refiere a la importancia de la vía alóctona para el subsidio de las redes tróficas y la dependencia de las características de cada sitio, que pueden promover un mecanismo de subsidio energético sobre otro. Sin embargo, a pesar de encontrarse un mayor sustento por acople de vías a lo largo del río, los depredadores tope (i.e., grupo trófico de los piscívoros) mostraron en general un mayor subsidio de su biomasa por la vía alóctona. Como se mencionó anteriormente, esto contradice las teorías generales que plantean la integración de las vías en los depredadores tope de los ecosistemas (Rooney & McCann, 2012). La mayor importancia de la vía alóctona en estos depredadores podría deberse a que la vía autóctona no fuera suficiente para sostener la biomasa de los niveles tróficos superiores, como ya ha sido reportado en estudios en otros sistemas (e.g., Jardine et al., 2017) y en este mismo río (González-Bergonzoni et al., 2019).

Sin embargo, desconocemos si lo observado aquí es generalizable, es decir, si este patrón responde a alguna característica particular de este sistema o incluso a las condiciones de crecidas a lo largo del río al momento del muestreo, como se mencionó anteriormente. Existen estudios que apoyan lo encontrado en este trabajo, observando, por ejemplo, que en el Río Paraná los depredadores tope dependen principalmente de la vía alóctona, pero plantean que esto probablemente se deba a los efectos de los pulsos de inundación generando fluctuaciones sobre la disponibilidad de alimento (Saigo et al., 2015). Esto, tal vez, podría indicar un patrón para ríos subtropicales con importantes fluctuaciones, aunque sería necesario profundizar en este aspecto a través de estudios de subsidios energéticos en otros grandes ríos subtropicales con similares características en cuanto a las fluctuaciones en los pulsos de inundación. Asimismo, sería importante incorporar muestreos en otras épocas, incluyendo épocas de seca para verificar si el patrón encontrado se mantiene y es generalizable. Posiblemente la respuesta de los depredadores tope de nuestro sistema se deba a las condiciones al momento del muestreo, de grandes crecidas y por tanto de gran aporte potencial de material alóctono desde las planicies de inundación. Estas condiciones podrían también tener un efecto negativo sobre la producción primaria local, ya que, al aumentar la turbidez del agua, no se permite el crecimiento de estos recursos, haciendo que no sean suficientes para sustentar los niveles tróficos más altos.

La importancia de las áreas libres de represas en el mantenimiento y la recuperación de la diversidad en el Río Uruguay ha sido otro de los resultados que se reitera a lo largo de toda la tesis. En este sentido, encontramos que las comunidades de peces entre los sitios 6 y 8 presentaron una alta riqueza de especies, pero una baja diferencia en la composición de la comunidad (bajos valores de diversidad beta entre sitios) (López-Rodríguez et al., 2024). Estos sitios podrían estar actuando como centros de diversidad que permiten la recuperación de la diversidad del sistema, disminuida aguas abajo de las represas (Massaro et al., 2019). En estos sitios encontramos también un aumento del sustento autóctono a las tramas tróficas, patrón que luego se ve interrumpido con la presencia de la represa de Salto Grande (López-Rodríguez et al., in prep.). Entre los sitios 6 y 8 (sitio ubicado en la cola del embalse de Salto Grande) observamos una recuperación y estabilización del nicho ecológico, que había sido fuertemente afectado por la cascada de represas de la parte alta del río (López-Rodríguez et al., 2024). Muchos son los factores, tanto bióticos como abióticos, que pueden potencialmente afectar la diversidad de nicho ecológico (Trudeau & Rasmussen, 2003; Layman et al., 2007b; Delong et al., 2011; Turner et al., 2015). Uno de los factores bióticos es la incorporación de señales isotópicas de diversos ambientes debido a la presencia de especies que pueden moverse largas distancias permitiendo el incremento del nicho ecológico (Rasmussen et al., 2009; Wang et al., 2021). Esto es coincidente con la presencia de especies migradoras desde el sitio 5 (López-Rodríguez et al. 2019; López-Rodríguez et al., 2024), donde los peces pueden moverse libremente y asimilar recursos en un tramo de casi 1000 km.

Esta tesis aporta así información básica sobre el funcionamiento del Río Uruguay en toda su extensión, identificando y localizando áreas clave para su recuperación ecológica.

## 7.3. Posibles aportes a la gestión ambiental

El efecto que tiene la construcción de represas a diferentes niveles es innegable y está muy bien documentado a nivel mundial. Sin embargo, se ha detectado la falta de protocolos estandarizados y comunes para este tipo de construcciones, que no existe un conocimiento adecuado para poder plantear planes de mitigación, la ausencia de monitoreos con los objetivos claros o la falta de monitoreos adecuados para este tipo de problemas, entre otros (Agostinho et al., 2016; Winemiller et al., 2016). Por otra parte, algunos de los planes de mitigación que se han propuesto y ejecutado en algunas represas, tales como la construcción de pasaje para peces, han sido ineficaces, pudiendo incluso ser negativos para la biodiversidad (Agostinho et al., 2002; 2007; 2008; CTM-Salto Grande, 2009). Otro de los problemas que se ha detectado, principalmente en el Neotrópico, es la ausencia de planes de mitigación locales. Los planes existentes se basan principalmente en planes de otras regiones del mundo, y que muchas veces no se adecuan a las condiciones en el Neotrópico (Agostinho et al., 2016).

Debido en parte a todo lo anteriormente mencionado es que en los últimos años se ha planteado la necesidad de generar modelos locales basados en información ambiental previa que permitan determinar la ubicación de las represas que genera los menores impactos ambientales, simultáneamente maximizando las capacidades de generación de energía hidroeléctrica (e.g., Winemiller et al., 2016; Flecker et al., 2022).

En el caso de la cuenca del Amazonas, se ha avanzado en la construcción de modelos y se ha planteado que la información ambiental básica y necesaria para los modelos debería ser basada en cinco criterios ambientales, los cuales integran las principales afectaciones al ambiente que pueden surgir de la construcción de represas: regulación del flujo hidrológico, conectividad del río, transporte de sedimento, diversidad de peces, y emisión de gases de efecto invernadero (Flecker et al. 2022). A pesar de la buena respuesta de estos modelos, se ha observado que la falta de información de línea de base es una de las principales restricciones a la hora de generar planes de manejo o para planificar la construcción de nuevas represas (Flecker et al. 2022). Si bien esos modelos utilizan esos cinco ejes de información, se reconoce que a medida que exista más información, los modelos se pueden ir perfeccionando, generando planes y estrategias de manejo que permitan generar menores perjuicios para la naturaleza y mayores beneficios para la población (Flecker et al. 2022).

A escala global, esperamos que los resultados obtenidos en esta tesis resalten la importancia de considerar otros aspectos ecológicos fundamentales, más allá de la diversidad específica de peces de los ríos. En particular, encontramos evidencia de la importancia de las fuentes alóctonas y autóctonas en el subsidio de las tramas tróficas fluviales. Por lo tanto, se destaca la importancia del mantenimiento de las planicies de inundación y de los montes riparios que permitan el ingreso de recursos terrestres al ambiente fluvial, principalmente dada su relevancia para los niveles tróficos más altos.

Nuestros resultados mostraron que las represas afectan no solo la diversidad de especies, sino también la dinámica de asimilación de las vías energéticas que sustentan la biomasa de los peces. Identificamos que analizar ambos aspectos resulta fundamental para una mayor comprensión del funcionamiento de los ecosistemas fluviales con alteraciones en su hidrología.

Otro aspecto clave para generar planes de mitigación de los impactos producidos por las represas, resulta en la planificación o el manejo de las represas que se ubican en fronteras internacionales, ya que se identifica como punto fundamental la cooperación entre los países para generar información de calidad y disminuir los costos ambientales de la construcción de represas (Flecker et al., 2022). Asimismo, es imperiosa una planificación estratégica que integre toda la información disponible y sustente la toma de decisiones no solamente a escala local de un sistema en particular sino a escala de cuenca, para encontrar el equilibrio necesario entre la generación de energía hidroeléctrica y la sustentabilidad de los bienes y recursos naturales (Winemiller et al. 2016).

El Río Uruguay involucra tres fronteras (Uruguay, Brasil y Argentina), lo que implica que el monitoreo ecológico se lleva a cabo en diferentes momentos y en sitios específicos, lo que puede derivar en diferentes técnicas de muestreo y por tanto resultados no siempre comparables. Si bien existen monitoreos en todos los tramos del río, los mismos no son estandarizados ni comunes a todos los equipos de investigación ni organismos de contralor. En la parte alta del Río Uruguay, por ejemplo, los monitoreos son financiados por los consorcios propietarios de las represas en el contexto de su monitoreo ambiental. En la parte media no existen monitoreos institucionales, sino que los mismos surgen de esfuerzos independientes de diferentes grupos de investigación. Por su parte, en la parte baja del río sí existen monitoreos institucionales, como lo son los monitoreos bi-nacionales desarrollados por CARU (https://caru.org.uy/nuevositio/monitoreos/) y por la Comisión Técnica Mixta de Salto Grande (CTM-Salto Grande, 2009), pero éstos sólo representan un tercio de todo el río. En este contexto, a través de esta tesis identificamos la necesidad de establecer programas de monitoreo estandarizados, con el fin de generar conocimiento científico comparable y apropiado para los planes de manejo.

Finalmente, esperamos que la información generada en esta tesis sirva como insumo para las autoridades de los diferentes países involucrados en el mantenimiento de la integridad ecológica del Río Uruguay a la hora de tomar decisiones, entre ellas la construcción y eventual localización de nuevas represas. En el Río Uruguay está proyectada la construcción de dos represas hidroeléctricas en la región media del río, sección donde encontramos la mayor diversidad ecológica de los peces y las mayores recuperaciones ecológicas, así como también las mayores planicies de inundación. Por lo tanto, esperamos que la información relevada en esta tesis sirva como insumo para la planificación de la construcción de esas nuevas represas, además de brindar información básica para comprender el funcionamiento de todo el río y la identificación de efectos específicos de las represas para incluir en los planes de monitoreo de las represas que ya existen. En este sentido, cabe resaltar que las especies de peces de mayor importancia cultural, social y comercial de este río son grandes especies migradoras que tienden a desaparecer con la fragmentación del hábitat, algo ya constatado en el Río Negro (uno de los principales afluentes del Río Uruguay) (Teixeira de Mello in press).

## 8. Conclusiones

Los resultados obtenidos a lo largo de esta tesis, a través de metodologías complementarias, muestran evidencia clara del efecto de las represas sobre la comunidad de peces. Asimismo, completamos vacíos de información en cuanto a las especies presentes a lo largo de todo el gradiente longitudinal del Río Uruguay, generamos evidencia que aporta a los distintos marcos teóricos en ecología de ecosistemas fluviales y cuantificamos por primera vez el subsidio de las dos principales vías energéticas (autóctona y alóctona) de las tramas tróficas del Río Uruguay. Toda esta información resalta la necesidad de considerar diferentes dimensiones de la biodiversidad, ya que algunas de ellas pueden ser complementarias, pero otras pueden estar brindando información fragmentada sobre la dinámica de las comunidades de los ecosistemas fluviales. Se destaca asimismo la necesidad de realizar estudios a lo largo de todo el gradiente de los ecosistemas fluviales para comprender las dinámicas de los ecosistemas, sin dejar de poner foco en las características locales de cada sitio.

El gran tamaño del sistema de estudio y el trabajo en toda su extensión permitió detectar las recuperaciones de la diversidad, que se vio afectada por las represas, en aquellas zonas de aguas libres de disturbios hidrológicos. Por lo tanto, resaltamos la necesidad de mantener áreas libres de represas para impedir un mayor deterioro ecológico de los ecosistemas fluviales y eventualmente, facilitar el reingreso de las especies migradoras.

# 9. Perspectivas

Para complementar este trabajo y poder obtener nueva evidencia que ayude a la mayor comprensión del funcionamiento de los ecosistemas fluviales, sería relevante incluir otros factores potencialmente muy importantes como la variabilidad hidrológica (tanto natural como manipulada por las represas), así como determinar los mecanismos de acción por los cuales las represas estarían generando estos cambios ecológicos (e.g., disponibilidad de alimentos, etc.).

Un resultado claro y clave fue que los depredadores tope no acoplarían vías energéticas, sino que por el contrario su biomasa estaría siendo mayormente subsidiada por la vía alóctona. Por lo tanto, en futuras investigaciones sería relevante analizar si éste es un patrón generalizable a grandes ríos represados, o si es dependiente de características locales de nuestro sistema de estudio o incluso del momento en que se realizaron los muestreos. En este sentido, se destaca también la necesidad de contar con muestreos temporales en este sistema, considerando la variabilidad intra e interanual en las características ambientales, tales como los patrones de precipitaciones (que pueden variar la entrada de recursos provenientes del medio alóctono)

(Leal et al. 2013). Este aspecto adquiere especial relevancia en el contexto actual de cambio climático, ya que se prevén cambios en los patrones de precipitación, con mayores eventos de precipitación extremas y crecidas, así como también mayores períodos sin precipitaciones, ocasionando sequías (IPCC, 2021), lo que representará grandes presiones en los ecosistemas fluviales. Este tipo de variación determinará cambios en los pulsos de inundación, en las extensiones y duración de las áreas inundadas y por tanto en las tasas de ingreso de material alóctono desde las áreas inundables. Esto en última instancia tendrá efectos sobre las vías de sustento de las tramas tróficas en los ecosistemas fluviales, planteando la necesidad de incorporar explícitamente a la variabilidad climática en los marcos teóricos actuales en ecología fluvial.

Es por esto que consideramos imperioso la generación de un programa de monitoreo tri-nacional espacialmente abarcativo y de larga duración, para poder determinar si los cambios en los patrones de precipitación alteran los patrones observados. Estos datos son relevantes también para poner a prueba marcos teóricos como RWC, el cual considera la variabilidad temporal en la hidrología.

A través de esta tesis logramos generar conocimiento de relevancia en cuanto al funcionamiento de los ecosistemas fluviales represados. Sin embargo, es posible que la respuesta de las comunidades sea aún más pronunciada que la detectada en nuestro estudio.

Las diferencias en metodologías de muestreo empleadas entre los sitios de la zona alta del río y la media y baja, podrían estar subestimando las respuestas observadas. En este sentido, la parte alta del río fue sometida a los mayores esfuerzos de muestreo, sin embargo, fue la región con menores riquezas de especies. Por ello, consideramos necesario realizar muestreos a lo largo de todo el gradiente longitudinal, siguiendo métodos de muestreo estandarizados y comunes a todos los sitios. Sería sumamente enriquecedor la inclusión de más sitios en la parte media del río, para evaluar si el comportamiento del ensamble de peces se mantiene en todo ese tramo. Esto permitiría consolidar la evidencia sobre la importancia de la conservación de secciones sin fragmentar.

Los resultados aquí obtenidos sientan la base para futuros estudios que analicen el funcionamiento de los ecosistemas fluviales en toda su extensión, ya sea en ecosistemas represados como en ecosistemas sin presencia de represas, y brindan información rigurosa que puede contribuir a la toma de decisiones y gestión ambiental de estos ecosistemas. Resulta imperioso trascender la colecta de datos con fines científicos estrictamente e incorporar el conocimiento a los programas como política nacional y trasnacional, basados en conocimiento técnico fundado.

# 10. Referencias bibliográficas

Agostinho, A.A., Gomes, L.C., Fernandez, D.R. & Suzuki, H.I., 2002. Efficiency of fish ladders for neotropical ichthyofauna. Riv. Res. Appl. 18, 299-306. **https://doi.org/10.1002/rra.674**

Agostinho, A.A., Marques, E.E., Agostinho, C.S., Almeida D.A., Oliveira R.J., Melo J.R., 2007. Fish ladder of Lajeado Dam: migrations on one-way routes? Neotrop. Ichthyol. 5, 121-130. https://doi.org/10.1590/S1679-62252007000200005

Agostinho, A.A., Pelicice, F.M. & Gomes, L.C., 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz. J. Biol. 68, 1119-1132. https://doi.org/10.1590/S1519-69842008000500019

Agostinho, A.A., Gomes, L.C., Santos, N.C., Ortega, J.C., Pelicice, F.M., 2016. Fish assemblages in Neotropical reservoirs: Colonization patterns, impacts and management. Fish. Res. 173, 26-36. https://doi.org/10.1016/j.fishres.2015.04.006

Allan, J. D. & Castillo, M. M., 2007. Stream Ecology: structure and functioning of running waters. *Springer*

Barbosa, F.A.R., Padisák, J., Espíndola, E.L.G., Borics, G., Rocha, O., 1999. The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-basin, São Paulo State, Brazil. *In*: Tundisi, JG., Straskraba, M. (Eds.)., Theoretical reservoir ecology and its applications. Leiden: Backhuys Publishers. pp. 425-437.

Barletta, M., Amaral, C.S., Correa, M.F., Guebert, F., Dantas, D.V., Lorenzi, L. & Saint-Paul, U., 2008. Factors affecting seasonal variations in demersal fish assemblages at an ecocline in a tropical-subtropical estuary. J. Fish Biol. 73, 1314–1336. https://doi.org/10.1111/j.1095-8649.2008.02005.x

Barletta, M., Jaureguizar, A.J., Baigun, C., Fontoura, N.F., Agostinho, A.A., Almeida-Val, V.M., Val, A.L., Torres, R.A., Jimenes-Segura, L.F., Giarrizzo, T., Fabré, N.N., Batista, V.S., Lasso, C., Taphorn, D.C., Costa, M.F., Chaves, P.T., Vieira, J.P., Correa, M.F., 2010. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. J. Fish Biol. 76, 2118-2176. https://doi.org/10.1111/j.1095-8649.2010.02684.x

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134-143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baxter, R.M., 1977. Environmental effects of dams and impoundments. Ann. Rev. Ecol. Syst. 8, 255-283. https://doi.org/10.1146/annurev.es.08.110177.001351

Baxter, C.V., Fausch, K.D. & Saunders, W.C, 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. *50*, 201–220. https://doi.org/10.1111/j.1365-2427.2004.01328.x

Bellmore, J.R., Baxter, C.V. & Connolly, P.J., 2015. Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. Ecology. 96, 274-283. https://doi.org/10.1890/14-0733.1

Borthagaray, A.I., Teixeira-de Mello, F., Tesitore, G., Ortiz, E., Illarze, M., Pinelli, V., Urtado, L., Raftopulos, P., González-Bergonzoni, I., Abades, S., Loureiro, M. & Arim, M., 2020. Community isolation drives lower fish biomass and species richness, but higher functional evenness, in a river metacommunity. Freshw. Biol. 65, 2081-2095. https://doi.org/10.1111/fwb.13603

Bunn, S.E., Leigh, C., & Jardine, T.D., 2013. Diet-tissue fractionation of δ15N by consumers from streams and rivers. Limnol. Oceanogr. 58, 765-773. https://doi.org/10.4319/lo.2013.58.3.0765

Carpenter, S.R., Kitchell, J. & Hodgson, J.R., 1985. Cascading Trophic Interactions and Lake Productivity. BioSci. 35, 634-639. https://doi.org/10.2307/1309989

Castello, L. & Macedo, M.N., 2016. Large-scale degradation of Amazonian freshwater ecosystems. Glob. Change Biol. 22, 990-1007. https://doi.org/10.1111/gcb.13173

Cheng, F., Li, W., Castello, L., Murphy, B. R., & Xie, S., 2015. Potential effects of dam cascade on fish: lessons from the Yangtze River. Rev. Fish Biol. Fish. 25, 569-585. https://doi.org/10.1007/s11160-015-9395-9

Cross, W.F., Baxter, C.V., Donner, K.C., Rosi-Marshall, E.J., Kennedy, T.A., Hall, R.O., Holly, A., Kelly, W. & Rogers, R.S., 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. Ecol. Appl. 21: 2016-2033. https://doi.org/10.1890/10-1719.1

Cross, W.F., Baxter, C.V., Rosi-Marshall, E.J., Hall Jr, R.O., Kennedy, T.A., Donner, K.C., Wellard-Kelly, H.A., Seegert, S.E.Z., Behn, K.E. & Yard, M.D., 2013. Food-web dynamics in a large river discontinuum. Ecol. Monogr. 83, 311-337. https://doi.org/10.1890/12-1727.1

de Bem, J., Ribolli, J., Röpke, C., Winemiller, K.O., Zaniboni-Filho, E., 2021. A cascade of dams affects fish spatial distributions and functional groups of local assemblages in a subtropical river. Neotrop. Ichthyol. 19, e200143.https://doi.org/10.1590/1982-0224-2020-0133

Delong, M., Thorp, J.M., Thons, M.S. & Mcintosh, L., 2011. Trophic niche dimensions of fish communities as a function of historical hydrological conditions in a Plains river. River Syst. 19, 177–187, doi:10.1127/1868-5749/2011/019-0036.

Doi, H., Chang, K.H., Ando, T., Imai, H., Nakano, S.I., Kajimoto, A. & Katano, I., 2008. Drifting plankton from a reservoir subsidize downstream food webs and alter community structure. *Oecologia*, 156, 363-371. https://doi.org/10.1007/s00442-008-0988-z

Dudgeon, D., 2000. Large-Scale hydrological changes in tropical Asia: Prospects for riverine biodiversity The construction of large dams will have an impact on the biodiversity of tropical Asian rivers and their associated wetlands. BioSc*i.* 50, 793-806. https://doi.org/10.1641/0006-3568(2000)050[0793:LSHCIT]2.0.CO;2

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Léveque, C., Naiman, R.J., Prieur-Richard, A-H., Soto, D., Stiassny, M.L. & Sullivan, C.A., 2005. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81, 163-182. https://doi.org/10.1017/S1464793105006950

Elton C. S., 1929. Animal Ecology. Sigwick and Jackson, London.

FAO, 2014. The State of World Fisheries and Aquaculture. Opportunities and challenges. *Food and Agriculture Organization of the United Nations*, Rome, Italy.

FAO, 2016. AQUASTAT global water information system. *Food and Agriculture Organization of the United Nations* (http://www.fao.org/nr/water/aquastat/countries_regions/URY/printesp1.stm).

Flecker, A.S., Shi, Q., Almeida, R.M., Angarita, H., Gomes-Selman, J.M., García-Villacorta, R., Sethi, S.A., Thomas, S.A., Poof, N.L., Forsberger, B.R., Heilpern, S.A., Hamilton, S.K., Abad, J.D., Anderson, E.P., Barros, N., Bernal, I.C., Bernstein, R., Cañas, C.M., Dangles, O., Encalada, A.C., Fleischmann, A.S., Goulding, M., Higgins, J., Jézéquel, C., Larson, E.I., McIntyre, P.B., Melack, J.M., Montoya, M., Oberdorff, T., Paiva, R., Perez, G., Rappazzo, B.H., Steinschneider, S., Torres, S., Varese, M., Walter, M.T., Wu, X., Xue, Y., Zapata-Ríos, X. & Gomes, C.P., 2022. Reducing adverse impacts of Amazon hydropower expansion. Science. 375, 753-760. DOI: 10.1126/science.abj4017

Fry, B., 2006. Stable isotope ecology. New York: Springer. pp. 318.

Ganassin, M.J.M., Muñoz-Mas, R., Oliveira, F.J.M., Muniz, C.M., Santos, N.C.L., García-Berthou, E., Gomes, L.C., 2021. Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins. Sci. Tot. Environ. 778, 146246. https://doi.org/10.1016/j.scitotenv.2021.146246

González-Bergonzoni, I., Teixeira de Mello, F., Vidal, N., D'Anatro, A., Masdeu, M., 2010 Reappearance and diet of juvenile armado catfish (Pterodoras granulosus) in Lower Uruguay River, (Rio Negro, Uruguay). Bol. Soc. Zool. Uruguay, 19, 42-46.

González-Bergonzoni, I., Meerhoff, M., Davidson, T., Teixeira-de Mello, F., Baattrup-Pedersen, A., Jeppesen, E., 2012. Meta-analysis Shows a Consistent and Strong Latitudinal Pattern in Fish Omnivory Across Ecosystems. Ecosyst. 15, 492-503. https://doi.org/10.1007/s10021-012-9524-4

González-Bergonzoni, I., D'Anatro, A., Vidal, N., Stebniki, S., Tesitore, G., Silva, I. & Teixeira de Mello, F., 2019. Origin of fish biomass in a diverse subtropical river: An allochthonic-supported biomass increase following flood pulses. Ecosyst. 22, 1736-1753. https://doi.org/10.1007/s10021-019-00370-0

González-Bergonzoni, I., Vidal, N., D'Anatro, A., Teixeira de Mello, F., Silva, I., & Naya, D.E., 2023. Historical analysis reveals ecological shifts in two omnivorous fish after the invasion of Limnoperna fortunei in the Uruguay river. Biol. Invasions. 25, 1935-1954. https://doi.org/10.1007/s10530-023-03020-8

Granzotti, R.V., Miranda, L.E., Agostinho, A.A. & Gomes, L.C., 2018. Downstream impacts of dams: shifts in benthic invertivorous fish assemblages. Aquat. Sci. 80, 1-14. https://doi.org/10.1007/s00027-018-0579-y

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borelli, P., Cheng, L., Crochetiere, H., Macedo, H.E., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., olden, J.D., Opperman, J.J., Petry, P., Reidy Lierman, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A. & Zarfl, C., 2019. Mapping the world's free-flowing rivers. Nature. 569, 215-221. https://doi.org/10.1038/s41586-019-1111-9

Guégan, J.F., Lek, S. & Oberdorff, T., 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. Nature, 391, 382-384. https://doi.org/10.1038/34899

Guo, F., Fry, B., Yan, K., Huang, J., Zhao, Q., O'Mara, K., Li, F., Gao, W., Kainz, M.J., Brett, M.T., Bunn, S.E., Zhang, Y., 2023. Assessment of the impact of dams on aquatic food webs using stable isotopes: Current progress and future challenges. Sci. Total Envoron. 904, 167097. https://doi.org/10.1016/j.scitotenv.2023.167097

Gutiérrez-Cánovas, C., Millán, A., Velasco, J., Vaughan, I.P. & Ormerod, S.J., 2013. Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. Glob. Ecol. Biogeogr. 22, 796-805. https://doi.org/10.1111/geb.12060

Herrera-Pérez, J., Parra, J.L., Restrepo-Santamaría, D. & Jiménez-Segura, L.F., 2019. The influence of abiotic environment and connectivity on the distribution of diversity in an Andean fish fluvial network. Front. Environ. Sci. *7*, 9. https://doi.org/10.3389/fenvs.2019.00009

Hoeinghaus, D.J., Winemiller, K.O. & Agostinho, A.A., 2008. Hydrogeomorphology and river impoundment affect food-chain length of diverse Neotropical food webs. *Oikos*. 117, 84-995. https://doi.org/10.1111/j.0030-1299.2008.16459.x

Horwitz, R.J., 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecol. Monogr. 48, 307–321. https://doi.org/10.2307/2937233

Huang, Xr., Gao, Ly., Yang, Pp. Xi, Yy., 2018. Cumulative impact of dam constructions on streamflow and sediment regime in lower reaches of the Jinsha River, China. J. Mt. Sci. 15, 2752–2765. https://doi.org/10.1007/s11629-018-4924-3

Humphries, P., Keckeis, H. & Finlayson, B., 2014. The river wave concept: integrating river ecosystem models. BioSci. 64, 870-882. https://doi.org/10.1093/biosci/biu130

IPCC, 2021. 2021: Technical Summary. *In*: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 33-144

Jackson, A.L., Inger, R., Parnell, A.C. & Bearhop, S., 2011. Comparing isotopic niche widths among and withun communities: SIBER – Stable Isotope Bayesin Ellipses in R. *J. An. Ecol.* 80, 595-602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jardine, T.D., Rayner, T.S., Pettit, N.E., Valdez, D., Ward, D.P., Lindner, G., Douglas, M.M. & Bunn, S.E., 2017. Body size drives allochthony in food webs of tropical rivers. Oecologia. 183, 505-517. https://doi.org/10.1007/s00442-016-3786-z

Johnson, B.L., Richardson, W.B. & Naimo, T.J., 1996. Past, present, and future concepts in large river ecology. BioSci. 45: 134-141. https://doi.org/10.2307/1312552

Junk, W.J., Bayley, P.B. & Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. Can. J. Fish. Aquat. Sci. 106: 110-127.

Keijzer, T., Barbarossa, V., Marques, A., Carvajal-Quintero, J.D., Huijbregts, M.A. & Schipper, A.M., 2024. Threats of dams to the persistence of the world's freshwater fishes. Glob. Change Biol. 30, e17166. https://doi.org/10.1111/gcb.17166

Keppeler, F.W., Olin, J.A., López-Duarte, P.C., Polito, M.J., Hooper-Bùi, L.M., Taylor, S.S., Rabalais, N.N., Fodrie, F.J., Roberts, B.J., Turner, R.E., Martin, C.W. & Jensen, O.P., 2021. Body size, trophic position, and the coupling of different energy pathways across a saltmarsh landscape. Limnol. Oceanogr. Lett. 6, 360-368. https://doi.org/10.1002/lol2.10212

Layman, C.A., Arrington, D.A., Montaña, C.G. & Post, D.M., 2007a. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology. 88, 42-48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Layman, C.A., Quattrochi, J.P., Peyer, C.M., Allgeier, J.E., 2007b. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecol. Lett. 10, 937-944. https://doi.org/10.1111/j.1461-0248.2007.01087.x

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Resenblatt, A.E. Vaudo, J.J., Yeager, L.A., Post, D.M. & Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol. Rev. 87, 545-562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Leal, J.S., González, A.L., Soares, B.E., Casa Nova, C., Marino, N.A. & Farjalla, V.F., 2023. Global and local drivers of the relative importance of allochthonous and autochthonous energy sources to freshwater food webs. Ecography. 2023, e06612. https://doi.org/10.1111/ecog.06612

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Glob. Ecol. Biogeogr. 23,1324–1334. https://doi.org/10.1111/geb.12207

Lehner, B., 2024. Rivers and lakes. Their distribution, origins, and forms. *In*: I.D. Jones & J.P. Smol (*Eds.*). *Wetzel's Limnology. Lakes and Rivers*. Elsevier, London, UK. p. 25-54.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Tilman, R.L., Loreau, M. & Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601-613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lévêque, C., Oberdorff, T., Paugy, D., Stiassny, M.L.J., Tedesco, P.A., 2007. Global diversity of fish (Pisces) in freshwater. In *Freshwater Animal Diversity Assessment*; Bailan, E.V., Lévêque, C., Segers, H., Martens, K., Eds.; Springer: Dordrecht, Netherlands, 2007; pp. 545–567.

Likens G., 2010. River ecosystem ecology: a global perspective: a derivative of Encyclopedia of inland waters. Academic Press Elsevier, Amsterdam. 411pp.

Lopes, J.d., Pompeu, P.S., Alves, C.B.M., Peressin, A., Prado, I.G., Suzuki, F.M., Facchin, S. & Kalapothakis, E., 2019. The critical importance of an undammed river segment to the reproductive cycle of a migratory Neotropical fish. Ecol. Freshw. Fish, 28, 302-316. https://doi.org/10.1111/eff.12454

Lopes, J.d., Alves, C.B.M., Silva, F.d. & Pompeu, P.S., 2024. Beyond just a dam blockage problem: larger artificial reservoirs are additional obstacles to reproductive fish migration in the Neotropics. Environ Biol Fish. 107, 217-229. https://doi.org/10.1007/s10641-024-01526-1

López-Rodríguez, A., Silva, I., de Ávila-Simas, S., Stebniki, S., Bastian, R., Massaro, M.V., Pais, J., Tesitore, G., Teixeira de Mello, F., D'Anatro, A., Vidal, N., Meerhoff, M., Reynalte-Tataje, D.A., Zaniboni-Filho, E. & González-Bergonzoni, I., 2019. Diets and trophic structure of fish assemblages in a large and unexplored subtropical river: The Uruguay River. Water, 11, 1374. https://doi.org/10.3390/w11071374

López-Rodríguez, A., Meerhof, M., D'Anatro, A., Silva, I., de Ávila-Simas, S., Silva, I., Pais, J., Teixeira de Mello, F., Reynalte-Tataje, D.A., Zaniboni-Filho, E. & González-Bergonzoni, I., 2024. Longitudinal changes on ecological diversity of Neotropical fish along a 1700 km river gradient show declines induced by dams. PECON. In press. https://doi.org/10.1016/j.pecon.2024.03.003.

Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos. 91, 3-17. https://doi.org/10.1034/j.1600-0706.2000.910101.x

Loures, R.C. & Pompeu, P.S., 2018. Long-term study of reservoir cascade in south-eastern Brazil reveals spatio-temporal gradient in fish assemblages. Mar. Freshw. Res. 69, 1983-1994. https://doi.org/10.1071/MF18109

MacArthur, R.H. & Wilson, E.O., 1967. The theory of island biogeography. Monographs in Population Biology 1. Princeton, NJ: Princeton University Press.

Masdeu, M., Teixeira-de Mello, F., Loureiro, M., Arim, M., 2011. Feeding habits and morphometry of Iheringichthys labrosus (Lütken, 1874) in the Uruguay River (Uruguay). Neotrop. Ichthyol. 9, 657–664. https://doi.org/10.1590/S1679-62252011005000034

Massaro, V.M., Pachla, L.A., Bastian, R., Pelicice, F.M. & Reynalte-Tataje, D.A., 2019. Seasonal and longitudinal variation in fish assemblage structure along and unregulated strech of the Middle Uruguay River. Neotrop. Ichthyol. 17, e190043. https://doi.org/10.1590/1982-0224-20190043

McCann, K.S., Hasting, A. & Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. Nature. 395, 794-798. https://doi.org/10.1038/27427

McCann, K.S., 2000. The diversity-stability debate. Nature. 405, 228-233. https://doi.org/10.1038/35012234

MVOTMA, 2012. Usos del Agua. Situación de aprovechamientos. Embalses y tomas de agua: Cuencas Río Uruguay y Río Negro.

Newsome, S.D., Martínez del Río, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429-436. https://doi.org/10.1890/060150.1

Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science. 308, 405-408. DOI: 10.1126/science.1107887

Ormerod, S.J., Dobson, M., Hildrew, A.G. & Townsend, C.R., 2010. Multiple stressors in freshwater ecosystems. Freshw. Biol. 55, 1-4. https://doi.org/10.1111/j.1365-2427.2009.02395.x

Pachla, L.A., Hartmann, P.B., Massaro, M.V., Pelicice, F.M. & Reynalte-Tataje, D.A., 2022. Recruitment of migratory fish in free-flowing rivers with limited floodplain development. Aquat. Conserv.: Mar. Freshw. Ecosyst. 32, 1888-1900. https://doi.org/10.1002/aqc.3860

Paine, R.T., 1980. Food Webs: Linkage, Interactions Strength and Community Infrastructure. J. Anim. Ecol. 49, 666-685. https://www.jstor.org/stable/4220

Parnell, A.C., Phillips, D.L., Bearhop, S., Semmens, B.X., Ward, E.J., Moore, J.W., Jackson. A.L., Grey, J., Kelly, D.J. & Inger, R., 2013. Bayesian stable isotope mixing models. Environmetrics. 24, 387-399. https://doi.org/10.1002/env.2221

Pease, A.A., González-Díaz, A.A., Rodiles-Hernández, R., Winemiller, K.O., 2012. Functional diversity and trait-environment relationship of stream fish assemblages in a large tropical catchment. Freshw. Biol. 57, 1060-1075. https://doi.org/10.1111/j.1365-2427.2012.02768.x

Peláez, O. & Pavanelli, C.S., 2018. Environmental heterogeneity and dispersal limitation explain different aspects of β-diversity in Neotropical fish assemblages. Fresw. Biol. 64, 497-505. https://doi.org/10.1111/fwb.13237

Pelicice, F.M., Pompeu, P.S. & Agostinho, A.A., 2015. Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. Fish Fish. 16, 697-715. https://doi.org/10.1111/faf.12089

Pelicice, F.M., Azevedo-Santos, V.M., Esguícero, A.L.H., Agostinho, A.A. & Arcifa, M.S., 2018. Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil. Neotrop. Ichthyol. 16, e170150. https://doi.org/10.1590/1982-0224-20170150

Pelicice, F.M., Castello, L., 2021. A political tsunami hits Amazon conservation. Aquat. Conserv.: Mar. Freshw. 31, 1221-1229.https://doi.org/10.1002/aqc.3565

Peralta-Maraver, I., López-Rodríguez, M.J. & De Figueroa, J.T., 2016. Structure, dynamics and stability of a Mediterranean river food web. Mar. Freshw. Res. 68, 484-495. https://doi.org/10.1071/MF15154

Pimm, S.L., Lawton, J.H. & Cohen, J.E., 1991. Food web patterns and their consequences. Nature. 350, 669-674. https://doi.org/10.1038/350669a0

Poff, N.L., Richter, B.D., Arthington, A.H., Bunn, S.E., Naiman, R.J., Kendy, E., Acreman, M., Apse, C., Bledsoe, B.P., Freeman, M.C., Henriksen, J., Jacobson, R.B., Kennen, J.G., Merrit, D.M., O'Keeffe, J.H., Olden, J.D., Rogers, K., Tharme, R.E. & Warner, A., 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. Freshw. Biol. 55, 147-170. https://doi.org/10.1111/j.1365-2427.2009.02204.x

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology. 83, 703-718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Power, M.E., 1990. Effects of fish in river food webs. Science. 250, 811-814. DOI: 10.1126/science.250.4982.811

Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.L. & Winterbourn, M.J., 1988. Patch dynamics in lotic systems: the stream as a mosaic. J. N. Am. Benthol. Soc. 7, 503-524. https://doi.org/10.2307/1467303

Pringle, C., 2003. What is hydrologic connectivity and why is it ecologically important?. Hydrol. Process. 17, 2685-2689. DOI: 10.1002/hyp.5145

Rasmussen, J.B., Trudeau, V., Morinville, G., 2009. Estimating the scale of fish feeding movements in rivers using δ13C signature gradients. J. Anim. Ecol. 78, 674-685. https://doi.org/10.1111/j.1365-2656.2008.01511.x

Reis, R.E., Kullander, S.O., Ferraris, C.J.Jr., 2003. Check List of the Freshwater Fishes of South and Central America. Edipucrs: Porto Alegre, Brazil, ISBN 85-7430-361-5.

Reis, R.E., Albert, J.S., Di Dario, F., Mincarones, M.M., Petry, P., Rocha L.A., 2016. Fish biodiversity and conservation in South America. J. Fish Biol. 89, 12–47. https://doi.org/10.1111/jfb.13016

Reynalte-Tataje, D.A., Nuñer, A.P., Nunes, M.C., Garcia, V., Lopes, C.A. & Zaniboni-Filho, E., 2012. Spawning of migratory fish species between two reservoirs of the upper Uruguay River, Brazil. Neotrop. Ichthyol. 10, 829-835. https://doi.org/10.1590/S1679-62252012000400016

Ribolli, J., Zaniboni-Filho, E., Barros Machado, C., de Souza Guerreiro, T.C., Domínguez de Freitas, P., Galetti, Jr. P.M., 2021. Anthropogenic river fragmentation reduces long-term viability of the migratory fish *Salminus brasiliensis* (Characiforme:Bryconidae) populations. Neotrop. Ichthyol. 19, e200123. https://doi.org/10.1590/1982-0224-2020-0123

Roach, K.A. & Winemiller, K.O., 2015. Hydrological regime and turbidity influence entrance of terrestrial material into river food webs. Can. J. Fish. Aquat, Sci. 72, 1099-1112. https://doi.org/10.1139/cjfas-2014-0459

Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin, F.S., Lambin, E., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P. & Foley, J., 2009. Planetary Boundaries: Exploring the safe operating spaces for humanity. Ecol. & Soc. 14, 1-32. https://www.jstor.org/stable/26268316

Rooney, N. & McCann, K.S., 2012. Integrating food web diversity, structure and stability. TREE. 27, 40-46. ttps://doi.org/10.1016/j.tree.2011.09.001

Ruhi, A., Muñoz, I., Tornes, E., Batalla, R.J., Vericat, D., Ponsatí, L., Acuña, V., Von Schiller, D., Marcé, R., Bussi, G., Francés, F. & Sabater, S., 2016. Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. Freshw. Biol. 61, 1536-1549. https://doi.org/10.1111/fwb.12794

Sabo, J.L., Finlay, J.C., Kennedy, T. & Post, D.M., 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. Science. 330, 965-967. DOI: 10.1126/science.1196005

Saccol-Pereira, A., 2008. Variação sazonal e estrutura trófica da assembléia de peixes do delta do rio Jacuí, RS, Brasil. Doctoral thesis. Universidade Federal do Rio Grande do Sul, Brazil.

Saigo, M., Zilli, F. L., Marchese, M. R., & Demonte, D., 2015. Trophic level, food chain length and omnivory in the Paraná River: a food web model approach in a floodplain river system. Ecol. Res. 30, 843-852. https://doi.org/10.1007/s11284-015-1283-1

Santos, N.C.L., Garcia-Berthou, E., Dias, J.D., Lopes, T.M., Affonso, I.D.P., Severi, W., Gomes, L.C., Agostinho, A.A., 2018. Cumulative ecological effects of a Neotropical reservoir cascade across multiple assemblages. Hydrobiologia. 819, 77-91. https://doi.org/10.1007/s10750-018-3630-z

Santos, N.C.L., Dias, R.M., Alves, D.C., de Melo, B.A.R., Ganassin, M.J.M., Gomes, L.C., Severi, W. & Agostinho, A.A., 2020. Trophic and limnological changes in highly fragmented rivers predict the decreasing abundance of detritivorous fish. Ecol. Indic. 110, 105933. https://doi.org/10.1016/j.ecolind.2019.105933

Scholl, E.A., Cross, W.F., Guy, C.S., Dutton, A.J. & Junker, J.R., 2023. Landscape diversity promotes stable food-web architectures in large rivers. Ecol. Lett. 26, 1740-1751. https://doi.org/10.1111/ele.14289

Sidle, R.C. & Gomi, T., 2024. Hydrological system. *In*: I.D. Jones & J.P. Smol (*Eds.*). *Wetzel's Limnology. Lakes and Rivers*. Elsevier, London, UK. p. 57-71.

Socolar, J.B., Gilroy, J.J., Kunin, W.E. & Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? TREE, 31, 67-80. https://doi.org/10.1016/j.tree.2015.11.005

Stanford, J.A. & Ward, J.V., 2001. Revisiting the serial discontinuity concept. Regul. Rivers.: Res. Manage.17, 303-310. https://doi.org/10.1002/rrr.659

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., de Vries, W., de Wit, C.A., Folke, C., Gerten, D., Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Reyers, B. & Sverker, S., 2015. Planetary boundaries: Guiding human development on a changing planet. Science. 347, 1-17. DOI: 10.1126/science.1259855

Thorp, J.H. & Delong, M.D., 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos. 70, 305-308. https://www.jstor.org/stable/3545642

Thorp, J.H. & Delong, M.D., 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos. 96, 543–50. https://doi.org/10.1034/j.1600-0706.2002.960315.x

Thorp, J.H., Thoms, M.C. & Delong, M.D., 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. Riv. Res. Appl. 22, 123-147. https://doi.org/10.1002/rra.901

Thorp, J.H., Thoms, M.C. & Delong, M.D., 2008. The riverine ecosystem synthesis. Towards Conceptual Cohesiveness in River Science. Amsterdam, the Netherlands: Academic Press/Elsevier.

Thornton, J., Steel, A. & Rast, W., 1996. Reservoirs. *In:* D. Chapman *(Ed.)*. *Water Quality Assesments- A Guide to Use of Biota, Sediments and Water in Environmental Monitoring*-Second Edition. UNESCO/WHO/UNEP. p. 371-411.

Tilman, D., Isbell, F., & Cowles, J.M., 2014. Biodiversity and ecosystem functioning. Annu. Rev. Ecol. Evol. Syst. 45, 471-493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Torremorell, A., Hegoburu, C., Brandimarte, A. L., Rodrigues, E. H. C., Pompeo, M., da Silva, S. C., Moschini-Carlos, V., Caputo, L., Fierro, P., Mojica, J.I., Matta, A.L.P., Donato, J.C., Jiménez-Pardo, P., Molinero, J., Ríos-Touma, B., Goyenola, G., Iglesias, C., López-Rodríguez, A., Merrhoff, M., Pacheco, J.P., Teixeira de Mello, F., Rodríguez-Olarte, D., Barrios Gómez, M., Montoya, J.V., López-Doval, J.C., & Navarro, E., 2021. Current and future threats for ecological quality management of South American freshwater ecosystems. Inland Waters. 11, 125-140. https://doi.org/10.1080/20442041.2019.1608115

Towsend, C.R., Scarsbrook, M.R. & Dolédec, S., 1997. Quantifying disturbance in streams: Alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. J. N. Am. Benthol. Soc. 16, 531-544. https://doi.org/10.2307/1468142

Trudeau, V., Rasmussen, J.B., 2003. The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. Limnol. Oceanogr. 48, 2194-2199. https://doi.org/10.4319/lo.2003.48.6.2194

Turgeon, K., Turpin, C. & Gregory-Eaves, I., 2019. Dams have varying impacts on fish communities across latitudes: a quantitative synthesis. Ecol. Lett. 22, 1501-1516. https://doi.org/10.1111/ele.13283

Turner, T.F., Krabbenhoft, T.J., Collyer, M.L., Krabbenhoft, C.A., Edwards, M.S., Sharp, Z.D., 2015. Retrospective stable isotope analysis reveals ecosystem responses to river regulation over the last century. Ecology. 96, 3213-3226. https://doi.org/10.1890/14-1666.1

Vander Zanden, M.J. & Vadeboncoeur, Y., 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology. 83, 2152-2161. https://doi.org/10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E., 1980. The river continuum concept. Can. J. Fish. Aq. Sci. 37, 130-137. https://doi.org/10.1139/f80-017

Vidal, N., Teixeira de Mello, F., González-Bergonzoni, I., López-Rodríguez, A., Tesitore, G., Pais, J., Stebniki, S., Silva, I. & D'Anatro, A., 2020. Long-term study of the reproductive timing of the Neotropical catfish Iheringichthys labrosus (Lütken, 1874): Influence of temperature and river discharge. Ecol. Freshw. Fish. 29, 334-345.https://doi.org/10.1111/eff.12518

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M., 1997. Human Domination of Earth's Ecosystems. Science. 277: 494-499. DOI: 10.1126/science.277.5325.494

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature. 467, 555-561. https://doi.org/10.1038/nature09440

Wang, S., Luo, B.K., Qin, Y.J., Zhao, J.G., Wang, T.T., Stewart, S.D., Yang, Y., Chen, Z-B., Qiu, H.X., 2021. Fish isotopic niches associated with environmental indicators and human disturbance along a disturbed large subtropical river in China. Sci. Tot. Environ. 750, 141667. https://doi.org/10.1016/j.scitotenv.2020.141667

Ward, J.V. & Stanford, J.A., 1983. The serial discontinuity concept of lotic ecosystems. *In:* T.D. Fontaine & S.M. Bartell (Eds). *Dynamic of Lotic Ecosystems*. Ann Arbor Science: Ann Arbor, MI; 347±356.

Ward, J.V., 1989. The four-dimensional nature of lotic ecosystems. J-NABS. 8, 2-8.

Ward, J.V. & Stanford, J.A., 1995. The serial discontinuity concept: extending the model to floodplain rivers. Reg. Riv.: Res. Manag. 10, 159-168. https://doi.org/10.1002/rrr.3450100211

Wellard Kelly, H.A., Rosi-Marshall, E.J., Kennedy, T.A., Hall Jr, R.O., Cross, W.F. & Baxter, C.V., 2013. Macroinvertebrate diets reflect tributary inputs and turbidity-driven changes in food availability in the Colorado River downstream of Glen Canyon Dam. Freshw. Sci., 32, 397-410. https://doi.org/10.1899/12-088.1

Winemiller, K.O.; Jepsen, D.B., 1998. Effects of seasonality and fish movement on tropical river food webs. J. fish Biol. 53, 267–296. https://doi.org/10.1111/j.1095-8649.1998.tb01032.x

Winemiller, K.O., Hoeinghaus, D.J., Pease, A.A., Esselman, P.C., Honeycutt, R.L., Gbanaador, D., Carrera, E. & Payne, J., 2010. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a mesoamerican coastal river. River Res. Appl. 27, 791-803. https://doi.org/10.1002/rra.1396

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I.G., Darwan, W., Lujan, N.K., Harrison, I., Stiassny, M.L., Silvano, R.A., Fitzgerald, D.B., Pelicice, F.M., Agostinho, A.A., Gomes, L.C., Albert, J.S., Baran, E., Petrere Jr., M.,Zarfl, C., Mulligan, M., Sullivan, J.P., Arantes, C.C., Sousa, L.M., Koning, A.A., Hoeignghaus, D.J., Sabaj, M., Lundberg, J.G., Armbruster, J., Thieme, M.L., Petry, P., Zuanon, J., Torrente Vilara, G., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C.S., Akama, A., van Soesbergen, A. & Sáenz, L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science, 351, 128-129. DOI: 10.1126/science.aac7082

Woodward, G.U.Y. & Hildrew, A.G., 2002. Food web structure in riverine landscapes. Freshw. Biol. 47, 777-798. https://doi.org/10.1046/j.1365-2427.2002.00908.x

Woodward, G.U.Y, 2009. Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. Freshw. Biol. 54, 2174-2187. https://doi.org/10.1111/j.1365-2427.2008.02081.x

Wright, D.H. 1983. Species energy theory: an extension of species-area theory. Oikos, 41: 495-506. https://doi.org/10.2307/3544109

Wu, H., Chen, J., Xu, J., Zeng, G., Sang, L., Liu, Q., Yin, Z., Dai, J., Yin, D., Liang, J., & Ye, S., 2019. Effects of dam construction on biodiversity: A review. J. Clean. Prod. 221, 480-489. https://doi.org/10.1016/j.jclepro.2019.03.001

Yeakley, J.A., Ervin, D., Chang, H., Granek, E.F., Dujon, V., Shandas, V. & Brown, D., 2016. *In:* D.J. Gilvear, M.T. Greenwood, M.C. Thomas & P.J. Wood (*Eds.*). *River Science. Research and Management for the 21st Century.* John Wiley & Sons Ltd., Oxford, UK. p. 335-349.

Zaniboni-Filho, E. & Schulz, U.H., 2003. Migratory Fishes of the Uruguay River. *In:* J. Carolsfeld, B. Harvey, C. Ross & A. Baer (*Eds.*). *Migratory Fish of South America. Biology, Fisheries and Conservation Status*. World Fisheries Trust/ Word Bank/ International Development Research Centre, Washington D.C., U.S.A. and Ottawa, Canada. p. 157-194.

Zaniboni-Filho, E., Ribolli, J., Hermes-Silva, S., & Nuñer, A.P., 2017. Wide reproductive period of a long-distance migratory fish in a subtropical river, Brazil. Neotrop. Ichthyol. 15, e160135. https://doi.org/10.1590/1982-0224-20160135

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., & Tockner, K., 2015. A global boom in hydropower dam construction. Aquat. Sci. 77, 161-170. https://doi.org/10.1007/s00027-014-0377-0

Zarfl, C., Berlekamp, J., He, F., Jähnig, S.C., Darwall, W., & Tockner, K., 2019. Future large hydropower dams impact global freshwater megafauna. Sci. Rep. 9, 18531. https://doi.org/10.1038/s41598-019-54980-8

Zhang, A.T. & Gu, V.X., 2023. Global Dam Tracker: A database of more than 35000 dams with location, catchment, and attribute information. Nature. 10, 111. https://doi.org/10.1038/s41597-023-02008-2