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ESTUDIO DE UNA RELACIÓN SINÉRGICA ENTRE SALMÓNIDOS INVASORES EN SUDAMÉRICA: MEDIANTE APROXIMACIONES ECOLÓGICAS Y FISIOLÓGICAS

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Dedicada a mis padres Guillermo (que en paz descanse) y Marta Margarita Aurora, a mi padrastro Jaime Rubén y a mi esposa María Rosita Ester

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RESUMEN

Las invasiones biológicas forman parte de un fenómeno complejo, debido a que pueden generar tanto problemas como beneficios en los diferentes sistemas socio-ecológicos en los que ocurren. En Chile, iniciativas privadas y públicas permitieron la exitosa introducción de salmónidos para el desarrollo de actividades económicas. Algunas especies con importancia económica, como *Oncorhynchus mykiss*, *O. tshawytscha* y *Salmo trutta* se tornaron invasoras, formando poblaciones sustentables y abundantes en los ecosistemas acuáticos del sur de Chile en donde co-habitan. El estudio del proceso de invasión de los salmónidos, así como también los efectos negativos que generan sobre la biota nativa han sido bien estudiados. Sin embargo, las interacciones entre ellos, en específico las sinérgicas no han sido examinadas en profundidad. En este estudio se utilizaron aproximaciones ecológicas y fisiológicas para estudiar una relación sinérgica unidireccional (consumo de huevos no viables), entre los salmónidos invasores *O. tshawytscha* (anádromo) y *O*. *mykiss* (residente) en el río Cisnes. El objetivo fue caracterizar los efectos ecológicos y fisiológicos de dicha relación.

Se capturaron especímenes de *O. mykiss* en dos tramos del Río Cisnes previamente identificados como áreas de desove de *O. tshawytscha*, en tres períodos de tiempo: antes (febrero; n = 20 en 2020 y n = 20 en 2021), durante (marzo-abril; n = 20 en 2019, n = 20 en 2020 y n = 20 en 2021) y después (junio-julio; n = 20 en 2020 y n = 20 en 2021) de la temporada de desove de *O. tshawytscha*; también se recolectaron presas de *O. mykiss* en el último período.

Para evaluar las relaciones ecológicas como el consumo de huevos no viables de *O. tshawytscha* por parte de *O. mykiss* y la variación de su dieta en los períodos descritos, se utilizó el análisis de contenidos estomacales. En cuanto a los aspectos fisiológicos, para determinar la variación en el factor de condición y en el contenido de ácidos grasos poliinsaturados ω-3 en *O. mykiss* residentes en los períodos descritos, se utilizaron análisis morfométricos y lipídicos, respectivamente.

Los resultados obtenidos en el primer capítulo de esta tesis demuestran que *O. mykiss* consumió de manera oportunista los huevos no viables de *O. tshawytscha* durante dos temporadas de desove consecutivas (2019 y 2020), dicho consumo estuvo asociado a un aumento en el factor de condición de *O. mykiss*. Los resultados del segundo capítulo permitieron demostrar que el consumo de huevos no viables de *O. tshawytscha* transfiere ácidos grasos poliinsaturados ω-3 (EPA y DHA) a *O. mykiss* en la trama trófica del río cisnes. Se evidenció un aumento hasta de 6 veces en el contenido de EPA y DHA en el músculo de *O. mykiss* asociado al consumo de huevos no viables. Adicionalmente, se demostró que los huevos de *O. tshawytscha* constituyeron el recurso alimenticio con el mayor contenido de EPA y DHA disponible para *O. mykiss* en la trama trófica del río Cisnes.

Los resultados indican que la interacción sinérgica unidireccional entre ambos salmónidos es importante, de tal forma que los administradores de estos recursos la consideren en futuros planes de administración pesquera en las cuencas donde co-habiten.

ABSTRACT

Biological invasions are a complex phenomenon; they can generate both problems and benefits in the different socio-ecological systems in which they occur. In Chile, private and public initiatives allowed the successful introduction of salmonids to develop of economic activities. Some economically important species, such as *Oncorhynchus mykiss*, *O. tshawytscha,* and *Salmo trutta*, have become invasive, forming persistent and abundant populations in the aquatic ecosystems of southern Chile where they co-inhabit. The study of the invasion process of salmonids, as well as the negative effects they generate on native biota have been well studied. However, the interactions between them, specifically synergistic interactions, have not been examined in depth. Here, ecological and physiological approaches were used to study a one-way synergistic relationship (consumption of non-viable eggs) between the invasive salmonids *O. tshawytscha* (anadromous) and *O. mykiss* (resident) in the Cisnes River. Our objective was to characterize the ecological and physiological effects of this relationship.

We captured specimens of *O. mykiss* in two sections of the Cisnes River previously identified as spawning areas of *O. tshawytscha*, in three periods of time: before (February; n = 20 in 2020 and n = 20 in 2021), during (March-April; n = 20 in 2019, n = 20 in 2020 and n = 20 in 2021) and after (June-July; n = 20 in 2020 and n = 20 in 2021) the spawning season of *O. tshawytscha*; *O. mykiss* prey were also collected during the latter period. To evaluate the ecological interactions, including the consumption of non-viable eggs of *O. tshawytscha* by *O. mykiss* and the variation of their diet in the periods described, the analysis of stomach contents was used. Regarding the physiological aspects, to determine the variation in the condition factor and in the content of ω-3 polyunsaturated fatty acids in resident *O. mykiss* in the periods described, morphometric and lipid analyzes were used respectively.

The results obtained in the first chapter of this thesis demonstrate that *O. mykiss* opportunistically consumed the non-viable eggs of *O. tshawytscha* during two consecutive spawning seasons (2019 and 2020), and that this consumption was associated with an increase in the *O. mykiss* condition factor. The results of the second chapter demonstrate that the consumption of non-viable eggs of *O. tshawytscha* transfers ω-3 polyunsaturated fatty acids (EPA and DHA) to *O. mykiss* in the food web of the Cisnes River. An increase of up to six times the contents of EPA and DHA in the muscle of *O. mykiss* was associated with the consumption of non-viable eggs. Additionally, we found that *O. tshawytscha* eggs constituted the food resource with the highest content of EPA and DHA available for *O. mykiss* in the Cisnes River food web.

Our results indicate that the one-way synergistic interaction between both salmonids is important for administrators of these species to consider in future fisheries management plans in the basins they co-inhabit.

INTRODUCCIÓN GENERAL

Las invasiones biológicas ocurren cuando una especie extiende su rango de distribución geográfico, ocupando regiones en las que no estaba previamente presente (Elton 1958). Son consideradas a nivel mundial, junto con la pérdida y degradación de los hábitats, sobreexplotación de especies, contaminación y cambio climático, como los principales forzantes directos de la pérdida de biodiversidad en ambientes dulceacuícolas (WWF 2020; Su et al. 2021). Sin embargo, las invasiones biológicas más exitosas han sido intencionalmente promovidas (Marr et al. 2010), lo cual desde un punto de vista ecológico-conservacionista puede ser considerado como una contradicción. Empero, desde una perspectiva socio-ecológica puede ser considerado beneficioso por el alto valor que tienen, como es el caso de las especies pertenecientes a la familia Salmonidae (en adelante salmónidos) en Chile (Arismendi and Nahuelhual 2007; Núñez and Niklitschek 2010; Cid-Aguayo et al. 2020).

La introducción de salmónidos en Chile fue un proceso desarrollado por agentes privados y públicos con apoyo internacional que data desde fines del siglo XIX, cuyo objetivo principal fue contribuir al desarrollo económico del país (Golusda 1907; Dazarola 2019). Los objetivos específicos del proceso fueron variando en el tiempo, pudiendo identificarse al menos tres: desarrollo de la pesca recreativa en ambientes dulceacuícolas y acuicultura semi-comercial, desarrollo del *ocean* *ranching* y desarrollo de la acuicultura comercial (Dazarola 2019). En general, el proceso de introducción de salmónidos en Chile fue exitoso (Golusda 1907; Soto et al. 2006, 2007; Correa and Gross 2008; Arismendi et al. 2014, 2019; Dazarola 2019), ya que en los últimos años el país logró posicionarse como uno de los mayores productores de salmones a nivel mundial, así como también en destino para la pesca recreativa de dichas especies. Sin embargo, en la actualidad el éxito sólo incluye de manera diferenciada a 6 de las 12 especies introducidas, de las cuales *Salmo salar* Linnaeus 1758, *Oncorhynchus mykiss* Walbaum 1792 y *O. kisutch* Walbaum 1792 son criadas de manera comercial en la acuicultura (Soto et al. 2006; Arismendi et al. 2014). Tanto *O. mykiss*, *S. trutta* Linnaeus 1758 y más recientemente *O. tshawytscha* Walbaum 1792 lograron establecer poblaciones asilvestradas extensamente en Chile, las cuales en algunos casos sustentan las actividades de pesca recreativa y actualmente de pesca artesanal (Soto et al. 2006, 2007; Correa and Gross 2008; Arismendi et al. 2014, 2019; Cid-Aguayo et al. 2020). Por su parte *Salvelinus fontinalis* Mitchill 1814 sólo ha logrado formar poblaciones autosustentables localizadas (Arismendi et al. 2014, 2019; Maldonado-Márquez et al. 2020) y finalmente existe evidencia temprana que postula el posible asilvestramiento de *O. kisutch* (Górski et al. 2016; Maldonado-Márquez et al. 2020).

Para comprender el éxito diferenciado del proceso de invasión de las especies de salmónidos introducidas en Chile, Arismendi et al. (2014) desarrollaron un marco conceptual que identifica dimensiones centrales, de las cuales dos son relevantes para esta tesis: 1) las características o rasgos del invasor (historia de vida, plasticidad fenotípica y tolerancia ambiental); y 2) las interacciones bióticas (con la biota nativa, otros invasores y la capacidad de carga ambiental).

Para el caso de invasores exitosos que presentan un alto valor social y económico por los beneficios que proveen, como lo son *O. mykiss* y *O. tshawytscha* (Arismendi and Nahuelhual 2007; Núñez and Niklitschek 2010; Cid-Aguayo et al. 2020), los aspectos que involucra la dimensión 1 varían considerablemente. A pesar de que ambas especies pertenecen al grupo de salmones y truchas del Pacífico, presentan historias de vida diferentes, ya que desde el punto de vista reproductivo *O. mykiss* es una especie iterópara, mientras que *O. tshawytscha* es una especie semélpara (Quinn 2018). Además, ambas especies difieren en cuanto a las migraciones que realizan, debido a que *O. mykiss* presenta dos morfotipos: uno anádromo (Steelhead) y otro sedentario-potamodromo (Rainbow trout) (Pascual et al. 2001; Soto et al. 2006; Arismendi et al. 2011; Quinn 2018). En tanto *O. tshawytscha* es una especie anádroma que presenta dos ecotipos dominantes fluvial (stream-type) y oceánico (ocean-type), los cuales difieren en el tiempo de residencia en agua dulce antes de la migración al mar (Araya et al. 2014; Quinn 2018). No obstante, también pueden existir poblaciones sedentarias-potamodromas denominadas *land locked,* que habitan en cuencas endorreicas (Soto et al. 2007). La plasticidad fenótipica de *O. mykiss* ha sido una de las características principales a las que se le atribuye su éxito como invasor; dicha plasticidad en los ambientes de Chile se complementa con su plasticidad ecológica respecto a su comportamiento de alimentación (Palma et al. 2002; Figueroa et al. 2010; Arismendi et al. 2012; Fierro et al. 2016) y al uso de hábitat (Penaluna et al. 2009). Adicionalmente, otro factor que ha contribuido a su éxito como invasor es la variabilidad genética que aportan los especímenes provenientes desde los escapes de centros de acuicultura a las poblaciones asilvestradas, a través de la reproducción (Consuegra et al. 2011), debido a que generalmente dichos ejemplares presentan mayor variabilidad genética (Benavente et al. 2015). En relación con *O. tshawytscha*, una de las características que se postula que contribuyó a su éxito como invasor es la alta diversidad genética de las diferentes poblaciones donantes, las cuales a su vez presentan un origen polifilético; y debido a la presión de propágulo y a la dispersión generada por los patrones de circulación oceánica se mezclaron (Riva-Rosi et al. 2012; Correa and Moran 2017; Gomez-Uchida et al. 2018; Musleh et al. 2020). En consideración a la tolerancia ambiental, ambas especies han logrado aclimatarse (desajuste en los períodos reproductivos con respecto al rango nativo) a las condiciones ambientales de los ecosistemas de Chile, ya que estos presentan condiciones particularmente adecuadas para los salmónidos (Golusda 1907; Correa and Gross 2008; Habit et al. 2012), producto de la similitud en el régimen hidrológico, térmico y de las derivaciones direccionales de las corrientes oceánicas. Tales factores pueden contribuir a explicar el éxito del proceso de invasión de ambas especies (Arismendi et al. 2014).

En relación con la dimensión 2, la resistencia biótica en términos de depredación y competencia tanto de la ictiofauna nativa como de depredadores marinos, terrestres y aviares con respecto a la invasión de salmónidos en ecosistemas de Chile, no son consideradas como factores de resistencia importantes (Arismendi et al. 2014). Por el contrario, son las especies salmonídeas las que causan impactos negativos sobre la fauna nativa, dichos impactos han sido estudiados en los ecosistemas dulceacuícolas de Chile e incluyen: depredación de los peces nativos (Arismendi et al. 2012) lo que se traduce en la disminución de su abundancia relativa (Soto et al. 2006; Arismendi et al. 2009), superposición en el uso de recursos alimenticios (Elgueta et al. 2013), inducción de cambios en el nivel trófico (Ortiz-Sandoval et al. 2017) y segregación interactiva del hábitat (Penaluna et al. 2009; Vargas et al. 2010). En lo que respecta a las interacciones entre salmónidos invasores en ecosistemas de Chile, tal como ocurre con otros invasores, estas pueden ser neutrales, antagónicas o sinérgicas (Jackson 2015). Las interacciones antagónicas (depredación, competencia por recursos y establecimiento previo) suelen ser beneficiosas para los ecosistemas invadidos dado que podrían aliviar algunos efectos negativos sobre ellos. Dichas interacciones son las que principalmente se han reportado en Chile, en específico, la competencia interespecífica (*O. mykiss* - *S. trutta*) entre especímenes de gran tamaño por recursos alimenticios escasos en ambientes dulceacuícolas (Arismendi et al. 2012) y la depredación interespecífica de especímenes adultos sobre juveniles (*S. trutta* - *O. keta* Walbaum 1792 y *S. trutta*-

O. gorbuscha Walbaum 1792) en ecosistemas estuarinos (Zama 1987). En cambio, las interacciones sinérgicas pueden conducir a *invasional meltdown*, un proceso en el cual el establecimiento de un invasor facilita el éxito de nuevas especies invasoras, lo cual tiene el potencial de exacerbar los impactos ecológicos sobre los ecosistemas invadidos (Simberloff and Von Holle 1999; Jackson 2015). Este tipo de interacciones no han sido estudiadas en profundidad en Sudamérica y sólo se ha descrito que los cadáveres de reproductores de *O. tshawytscha* pueden transferir nutrientes de origen marino a los ríos y arroyos en donde ocurre el desove de la especie, generando un incremento en la disponibilidad de nutrientes y un aumento en la productividad de dichos ecosistemas (Muñoz et al. 2020). Esta situación puede ser beneficiosa para las truchas residentes (Arismendi et al. 2012). Además, también se han reportado observaciones de campo que describen la presencia de huevos de *O. tshawytscha* en los contenidos estomacales de *O. mykiss* (Soto et al. 2007; Arismendi and Soto 2012).

Sinergia a través del consumo de huevos entre salmónidos en el hemisferio norte.

Las interacciones entre salmónidos (residentes-residentes, anádromos-residentes y anádromos-anádromos) que implican el consumo de huevos han sido bien documentadas en su área de distribución nativa (Scheuerell et al. 2007; Moore et al. 2008; Denton et al. 2009; Armstrong et al. 2010, 2013; Armstrong and Bond 2013; Jaecks and Quinn 2014) y en sistemas invadidos del hemisferio norte (Greeley 1932; Johnson and Ringler 1979; Johnson et al. 2016; Dunlop et al. 2020). Se han descrito dos mecanismos que regulan la disponibilidad de huevos de salmónidos como recurso alimenticio para otros salmónidos: i) las hembras no entierran todos sus huevos en la grava; ii) las hembras entierran sus huevos en nidos preexistentes, liberando huevos previamente enterrados debido a las altas densidades de reproductores en los sitios de desove (denso-dependencia) (Greeley 1932; Moore et al. 2008; Quinn 2018). En ambos casos los huevos disponibles no son viables o tienen una baja probabilidad de supervivencia, por lo tanto, su consumo no afecta a la especie desovante (Quinn 2018). Más bien, se ha reportado que el consumo de huevos no viables corresponde a una relación positiva entre salmónidos, ya que los especímenes que los consumen se benefician del escaso gasto energético que supone su consumo (Quinn 2018), su alta digestibilidad, alto contenido energético (Armstrong et al. 2010) y alto contenido de ácidos grasos poliinsaturados (Ashton et al. 1993), lo cual mejora la condición (Johnson and Ringler 1979; Armstrong and Bond 2013), crecimiento (Scheuerell et al. 2007; Denton et al. 2009; Rinella et al. 2012; Armstrong et al. 2013; Armstrong and Bond 2013) y almacenamiento de energía (Rinella et al. 2012; Armstrong and Bond 2013) de dichos peces, incidiendo de manera positiva en su adecuación (*fitness*). **Sin embargo, en ambientes acuáticos colonizados de Sudamérica, como los ríos del sur de Chile en donde existen observaciones de campo acerca del consumo de**

huevos de *O. tshawytscha* **por parte de** *O. mykiss***, un problema actual es el desconocimiento de su frecuencia, magnitud y de los efectos ecológicos y fisiológicos que esto conlleva.**

Metodologías para determinar y cuantificar el consumo de huevos en salmónidos

Los enfoques metodológicos empleados para determinar y cuantificar el consumo directo de huevos tanto intra- como inter-específico en salmónidos son 2: el análisis de contenido estomacal (SCA; *stomach content analysis*) y el análisis de isótopos estables (SIA; *stable isotopes analysis*). El SCA de uso más general (Johnson and Ringler 1979; Scheuerell et al. 2007; Moore et al. 2008; Denton et al. 2009; Armstrong et al. 2013; Armstrong and Bond 2013; Jaecks and Quinn 2014; Johnson et al. 2016; Dunlop et al. 2020), permite determinar la composición de la dieta de los especímenes en una escala temporal acotada (días). Por su parte el SIA de uso más específico entre especímenes anádromos y residentes, se basa en el uso de los isótopos estables más pesados de Nitrógeno (δ15N) y Carbono (δ13C), los cuales se ha demostrado que se acumulan en los tejidos de los consumidores. La proporción del isótopo de Nitrógeno (δ15N) permite estimar la posición trófica debido a que el δ15N de un consumidor se enriquece entre un 3 - 4%o en relación con su dieta (Post 2002), mientras que la proporción del isótopo de Carbono (δ13C) que cambia poco a través de la trama trófica, permite discernir si el alimento consumido ha incluido presas con contenidos de carbono orgánico originado en el ambiente terrestre o en el ambiente marino, por lo tanto, se puede utilizar para determinar el origen marino o terrestre de las presas consumidas (Post 2002). En base a lo descrito, ambos isótopos se pueden utilizar como trazadores para evaluar la transferencia y asimilación de los nutrientes derivados de origen marino a los huevos de salmónidos anádromos y desde estos a sus consumidores en los ríos (Scheuerell et al. 2007; Rinella et al. 2012; Armstrong and Bond 2013; Jaecks an d Quinn 2014; Dunlop et al. 2020) en una escala temporal más amplia (semanas y meses dependiendo del tejido empleado). Esto se debe a que los salmónidos anádromos adultos obtienen desde el ambiente marino (mayor abundancia de isótopos pesados de carbono que en ambientes dulceacuícolas) cerca del 99% de su masa corporal (Quinn 2018), así como también todos los nutrientes, pigmentos y energía necesarios para el proceso de maduración sexual, crecimiento (vitelogénesis) y maduración final de los ovocitos en los sitios de desove en los ríos.

Otro enfoque metodológico útil para trazar el origen marino, dulceacuícola o terrestre de las presas consumidas corresponde al estudio de la composición de los ácidos grasos altamente insaturados ω-3 de cadena larga y de los ácidos grasos poliinsaturados tanto ω-3 y ω-6 de cadena corta (Sargent et al. 2003; Twining et al. 2016, 2021). Estas moléculas se caracterizan por la escasa modificación de su estructura desde la ingestión, hasta la asimilación e incorporación en los tejidos, por lo tanto, conservan su estructura original para cumplir funciones fisiológicas por sobre las energéticas, pudiendo biomagnificarse en niveles tróficos altos (Twining et al. 2016; Strandberg et al. 2015). En la naturaleza, los ácidos grasos biosintetizados y almacenados por los productores primarios difieren tanto en su composición como en su abundancia dependiendo del ecosistema (Sargent et al. 2003; Twining et al. 2016, 2021). Los productores primarios terrestres generalmente solo contienen ácidos grasos poliinsaturados ω-3 y ω-6 de cadena corta, como el ácido alfa-linolénico (C18:3 ω-3, ALA) y el ácido linoleico (C18:2 ω-6, LIN), los cuales son considerablemente más abundante que en los productores acuáticos (Twining et al. 2016, 2021). Los productores primarios acuáticos, se caracterizan por contener ácidos grasos altamente poliinsaturados ω-3, como el ácido eicosapentaenoico (C20:5 ω-3, EPA) y el ácido docosahexaenoico (C22:6 ω-3, DHA), sin embargo, se diferencian en la abundancia de ellos, siendo considerablemente más abundantes en los productores primarios marinos (Twining et al. 2016, 2021). Por lo tanto, debido al ciclo de vida y obtención de nutrientes y energía descritos para los salmónidos anádromos, sus tejidos, incluyendo sus huevos presentan un alto contenido de los ácidos grasos EPA y DHA (Ashton et al. 1993; Heintz et al. 2004). En huevos de especímenes adultos de *O. tshawytscha* silvestres los contenidos de EPA y DHA varían entre 13,7% – 15,1% y 17,1% – 17,8% respectivamente, en relación del total de ácidos grasos (Ashton et al. 1993). En consecuencia, el consumo de tejidos y huevos de salmónidos anádromos por parte de salmónidos residentes de ríos y arroyos puede verse reflejado en el aumento del contenido de ácidos grasos como EPA y DHA (Heintz et al. 2004). Adicionalmente, el estudio de la incorporación de ácidos grasos como EPA y DHA a través del consumo de huevos de salmónidos anádromos por parte de salmónidos residentes de ríos y arroyos, puede ser utilizado como un proxy fisiológico que incide de manera positiva su fitness, debido a las importantes funciones que cumplen (Twining et al. 2016, 2021). Los estudios sugieren que, en consumidores, los ácidos grasos como ALA, EPA y DHA participan una gama de funciones con importancia fisiológica, que incluyen: i) funciones estructurales, como componentes de las membranas celulares especialmente de los tejidos nerviosos y gonadales, a las cuales le aportan mayor fluidez, que a su vez mejora su tolerancia a la dinámica estructural para su correcto funcionamiento (Twining et al. 2016, 2021; Pilecky et al. 2021); ii) funciones energéticas, ya sea de almacenamiento energético en forma de triacilgliceroles o como sustrato para la generación de energía metabólica en forma de ATP, a través de la β-oxidación mitocondrial (Sangent et al. 2003); iii) funciones neurológicas, debido a que los fosfolípidos de las membranas celulares que contienen DHA tienden a enriquecerse de proteínas transmembranales de señalización rápida (canales iónicos y receptores acoplados a proteína G), por lo tanto, su actividad puede mejorar las funciones neurológicas, influyendo así en las capacidades cognitivas como la visión, el aprendizaje, la memoria e interacciones tanto intra como interespecíficas (Pilecky et al. 2021); iv) funciones reproductivas, a través de la regulación hormonal, de la disponibilidad energética para el desarrollo de caracteres sexuales secundarios y el desarrollo gonadal, en especial el proceso de vitelogénesis que permite la acumulación de vitelogenina en los huevos; así como también de su inclusión directa en los huevos. Esto permite aumentar la fecundidad de las hembras y generar huevos de mayor calidad que proveerán la energía y nutrientes necesarios para un exitoso desarrollo de la progenie (Sargent et al. 2003; Lazzarotto et al. 2015); v) funciones inmunes, siendo el EPA un precursor de la síntesis de eicosanoides, los cuales participan en la coagulación sanguínea, respuesta inflamatoria, entre otras (Tocher 2010). En *O. mykiss* se ha determinado que su morfotipo sedentario-potamodromo aun cuando tiene la capacidad de biosintetizar EPA y DHA a partir de ALA (Sargent et al. 2003), prefiere consumir dietas con altos contenidos de dichos ácidos grasos (Roy et al. 2019), debido a que su biosíntesis tiene un alto gasto energético. De manera experimental, se ha determinado que el requerimiento de dichos ácidos grasos en *O. mykiss* oscila entre 0,4% - 0,5% en peso seco de la dieta (Tocher 2010).

En función de lo documentado, el consumo de huevos de *O. tshawytscha* por parte de *O. mykiss* en ambientes invadidos de Sudamérica, como es el caso de los ríos del sur de Chile, puede ser abordado a través del SCA, así como también del uso de trazadores dietarios como los isótopos estábles (δ13C y δ15N) y ácidos grasos (EPA y DHA). Sin embargo, por motivos logísticos-operacionales forzados por el contexto de pandemia, en esta tesis sólo se utilizaron el SCA y el análisis de ácidos grasos. Dichos análisis proveen aproximaciones ecológicas y fisiológicas, en cuanto a los cambios en la dieta de *O. mykiss* y la presión de depredación que ejerce sobre la fauna nativa, además permiten evidenciar su capacidad para adquirir desde los huevos altas cantidades de energía y moléculas escasas en los ambientes dulceacuícolas que participan en una serie de funciones fisiológicas importantes. También, de acuerdo a lo reportado en el hemisferio norte, esta relación sinérgica unidireccional entre invasores, puede mejorar la capacidad de *O. mykiss* para sobrevivir y reproducirse en ambientes invadidos de Sudamérica (*fitness*; Orr 2009), en términos del posible aumento en su tasa de crecimiento, lo que significa alcanzar en un período más acotado la talla de madurez sexual; aumento en su fecundidad y producción de huevos de mayor calidad que repercute en la sobrevivencia de la progenie; aumento en sus capacidades cognitivas como la visión, el aprendizaje y la memoria, lo cual influye en su interacción depredador-presa y, por lo tanto, en su capacidad de obtención de alimento; y el fortalecimiento de su respuesta inmune, lo que incide en su sobrevivencia ante eventuales enfermedades.

Estudiar una interacción sinérgica unidireccional entre salmónidos invasores de alto valor social y económico en Chile, también es clave para proveer información de base para el desarrollo de futuros planes de manejo de la pesca recreativa. El manejo pesquero de las cuencas donde se establezcan las áreas preferenciales para la pesca recreativa (APPR) que estipula la ley de pesca recreativa de Chile, debe considerar la relación sinérgica estudiada entre las poblaciones anádromas de *O. tshawytscha* y las poblaciones sedentarias-potamodromas de *O. mykiss*. De lo contrario, desde una perspectiva socio-ecológica se pueden generar conflictos entre grupos de interés como pescadores artesanales y recreativos.

HIPÓTESIS

Debido a la disponibilidad estacional y a las características nutricionales como el alto contenido de energía y ácidos grasos poliinsaturados ω-3 de los huevos no viables del salmón anádromo *O. tshawytscha*, la trucha residente *O. mykiss* los utiliza consistentemente en el tiempo como una importante fuente alimenticia, lo cual genera efectos ecológicos y fisiológicos que benefician su adecuación (*fitness*). Se plantean las siguientes predicciones.

I) La dieta de *O. mykiss* cambia durante el período de desove de *O. tshawytscha*, evidenciándose un alto consumo de huevos cuando están disponibles (capítulo I y II).

II) Debido al consumo de huevos no viables, se produce un aumento del factor de condición (capítulo I) y del contenido de ácidos grasos poliinsaturados de origen marino en *O. mykiss* durante y después del período desove de *O. tshawytscha* (capítulo II).

OBJETIVOS

Objetivo general

Caracterizar los efectos ecológicos y fisiológicos de una relación sinérgica (consumo de huevos no viables) entre los salmónidos invasores *O. tshawytscha* y *O. mykiss* en Chile.

Objetivos específicos

1) Evaluar el consumo interanual de huevos no viables de *O. tshawytscha* por parte de *O. mykiss* residentes en diferentes temporadas de desove (capítulo I).
2) Evaluar la variación de la dieta y del factor de condición de *O. mykiss* residentes antes, durante y después de la temporada de desove de *O. tshawytscha* (capítulo I).
3) Evaluar la variación del contenido de ácidos grasos poliinsaturados de origen marino en *O. mykiss* antes, durante y después del período desove de *O. tshawytscha* (capítulo II).
4) Evaluar la concentración de ácidos grasos poliinsaturados en los recursos alimenticios disponibles para *O. mykiss* provenientes de diferentes ecosistemas (marino, dulce acuícola y terrestre; capítulo II).

CAPÍTULO I

First record of a synergistic interaction between invasive salmonids in South America

ARTÍCULO CIENTÍFICO

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First record of a synergistic interaction between invasive salmonids in South America

Invasion Note

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Abstract

Ecological interactions among multiple invaders can aggravate their effects on invaded systems. Many salmonids including rainbow trout *Oncorhynchus mykiss* and Chinook salmon *O. tshawytscha* have established naturalized populations and co-occur in rivers worldwide. Predation of eggs and juveniles has been well documented among salmonids in their native range in the Northern Hemisphere. It has been unclear to what extent these interactions exist in invaded rivers of the Patagonia. Here, we report and quantify rainbow trout predation of Chinook salmon eggs in the Cisnes River Basin, southern Chile. We used hook and line angling to sample rainbow trout (n = 80) around salmon spawning areas before, during, and after the spawning season of Chinook salmon. Stomach contents obtained during two consecutive years show consistent evidence that rainbow trout opportunistically prey on Chinook salmon eggs. Salmon eggs occurred in 75% and 50% of the trout stomachs analyzed in 2019 and 2020, respectively. The number of salmon eggs (mean ± SD) per trout stomach ranged between 17.95 ± 24.29 in 2019 and 7.45 ± 12.90 in 2020. We assumed that consumed eggs were primarily non-viable or would have had low probabilities of survival suggesting a synergistic interaction between rainbow trout and Chinook salmon. Our findings provide baseline information that contribute to demographic studies and the management of invasive salmonids in rivers of this region and elsewhere.

Keywords: Salmon, Trout, Predation, Marine-derived nutrients, River, Southern Chile

1. Introduction

Interactions among multiple invaders have the potential to exacerbate their ecological impacts on invaded systems (Simberloff and Von Holle 1999; Jackson 2015). Salmonids have been successfully introduced worldwide owing to their value for recreational fisheries (Shepard et al. 2019). Rainbow trout (*Oncorhynchus mykiss*) and Chinook salmon (*O. tshawytscha*) have established naturalized populations across the Patagonia (Soto et al. 2006, 2007; Correa and Gross 2008; Arismendi et al. 2014). Since the 1980's, these naturalized populations have been supplemented with propagules from numerous escape events from aquaculture facilities in southern Chile (Arismendi et al. 2009; Sepúlveda et al. 2013; Gomez- Uchida et al. 2018). The negative consequences of these introductions on native species are extensively documented (e.g., Penaluna et al. 2009; Arismendi et al. 2009, 2014; Fierro et al. 2016). However, there is a lack of information about interactions among multiple salmonids in these invaded systems, especially related to the most recent invasion of Chinook salmon (Soto et al. 2007; Correa and Gross 2008; Arismendi et al. 2014).

In their native range, predation of eggs and juveniles among salmonids are well recognized (e.g., Greeley 1932; Johnson and Ringler 1979; Moore et al. 2008; Armstrong et al. 2010; Johnson et al. 2016). It is unclear to what extent such interactions exist in invaded ecosystems of southern Chile. We hypothesize that as an opportunistic-generalist consumer, rainbow trout will benefit from the seasonal availability of eggs during the spawning season of Chinook salmon in the Austral fall (i.e., March-April). Our findings provide baseline information that can contribute to future population-level studies and the management of multiple invasive salmonids in rivers of the Patagonia.

2. Materials and methods

Cisnes River basin (5464 km^2) drains to Cisnes Bay (Fig. 1). The length of the river is about 160 km with an average annual discharge of 253 m^3 s^{-1}. The source of the flow regime is a mixture of rain and snowmelt owing to the oceanic climate of the region with precipitation peaks in late fall and early winter. Our study sites included two reaches (200-m each) that have been previously identified as spawning areas for Chinook salmon. We used hook and line angling to collect rainbow trout stomachs in three periods: before (February; n = 20 in 2020), during (March-April; n = 20 in 2019 and n = 20 in 2020), and after (June; n = 20 in 2020) the spawning season of Chinook salmon. For each trout captured, we measured total mass (*W*) using a scale Pesamatic Model WTB 2000 (0.01 g) and total length (*L*) with a board meter (nearest mm) prior to dissection. We estimated the Fulton's Condition Factor, *K* (Ricker 1975) as $K = (W/L^3) \times 100$, *W* in g and *L* in cm. Stomach contents of each trout were preserved in 96% ethanol and then individually separated and identified to the lowest possible taxonomic level. Prey items were separated as aquatic (A) or terrestrial (T) and grouped by taxa including Plecoptera, Ephemeroptera, Diptera, Trichoptera, Coleoptera, Hemiptera, Hymenoptera, Trombidiformes, Oligochaeta, Gastropoda, Isopoda, Nematomorpha, Odonata, Lepidoptera, Orthoptera, Araneae, Pulmonate snails, and Chinook salmon eggs.

To evaluate the contribution of each prey item to the diet of trout during each period (before, during, and after the Chinook salmon spawning season), we calculated the dietary coefficient of Hureau (Q) as $Q = \%F \times \%W$ (Hureau 1970), where $\%F$ is the frequency of occurrence of the respective prey item, and $\%W$ is the percentage of wet weight of the respective prey item. Q reduces the bias associated with the use of numerical methods based on discrete quantities (Hureau 1970). Based on the Q index, prey items were classified as main prey ($Q > 200$), secondary prey ($200 > Q > 20$), or occasional prey ($Q < 20$) following Di Prinzio and Arismendi (2018). In addition, during salmon spawning seasons of 2019 and 2020 we counted the number of consumed eggs per stomach (N_E) and estimated (1) the total mass of eggs consumed by trout (B_E), and (2) total salmon egg biomass percent ratio ($\%W_{EB}$). These two metrics were estimated as follows $B_E = N_E \times W_E$, and $\%W_{EB} = (B_E/T_W) \times 100$, where WE is the mean egg mass (based on the mass of 30 eggs randomly selected from the stomachs), and TW is the total mass of trout.

We used a one-way ANOVA to compare trout length and Fulton’s condition factor among periods. We tested normality using a Shapiro–Wilk test ($n < 50$ per group) and homoscedasticity of variance using a Levene test. When the assumption of homoscedasticity of variance failed (i.e., Fulton’s condition factor), we used a non-parametric Kruskal–Wallis Analysis of Variance on Ranks and a Tukey Test for pairwise multiple comparisons. At the population-level, we evaluated the prey community composition of trout diets among periods using Margalef’s index of species richness (*d*), Pielou’s uniformity index (*J´*) and the Shannon–Wiener diversity index, using $\log_{10}$ (*H´*) based on %W values. At the individual-level, we performed a non-metric multidimensional scaling (nMDS) ordination procedure using a Bray-Curtis distance matrix with 9,999 random starts to visualize the similarity of individual trout diets among periods. To test the similarity of diets among periods we performed an analysis of similarity (ANOSIM) with an alpha set at 0.05 and 999,999 permutations (Clarke and Gorley 2006). The ANOSIM R statistic ranges between 1 and - 1. In our study, R values > 0 suggest dissimilar diets among periods while an R value close to 0 indicates an even distribution among periods. R values < 0 suggest diet dissimilarities are greater within periods than among periods. The nMDS and ANOSIM analyses were performed using PRIMER v6.1.5 (Plymouth, UK).

3. Results

One-way ANOVA showed that trout sizes were similar among sampling periods (Fig. 2a; d.f. = 3, F = 1.787, p-value = 0.18). The mean total mass of trout was slightly higher during the salmon spawning season (359.5 ± 187.9 g in 2019; 322.3 ± 144.4 g in 2020) compared to before (241.5 ± 122.8 g) or after (298.5 ± 124.9 g in 2020) the spawning season. Fulton’s condition factor showed statistically significant differences among periods (Fig. 2b; d.f. = 3, H = 42.4, p-value < 0.001). Pairwise comparisons of Fulton’s condition factor of trout showed higher values for the spawning season in 2019 compared to the other periods. Similarly, trout condition factor was higher during the spawning season than before the spawning season in 2020.

Trout diet spanned 42 taxa (Table 1), of which the majority represented aquatic benthic macroinvertebrates (78.6%) followed by terrestrial invertebrates (19.0%). At the population-level, the composition of prey items varied across periods (Fig. 3; Tables 1 and 2). Before the Chinook salmon spawning season, main prey items included aquatic ephemeropteran (Leptophlebiidae) and terrestrial coleopteran (Table 1). Similarly, after the Chinook salmon spawning season the main prey items in trout diets included aquatic plecopteran *Klapopteryx armillata* and Gripopterygidae, as well as the aquatic ephemeropteran Leptophlebiidae (Table 1). However, during the Chinook salmon spawning season, trout shifted their diet from macroinvertebrates to feed almost exclusively on Chinook salmon eggs (Figs. 3 and 4) followed by larvae of the aquatic Plecoptera *Klapopteryx* armillata and *Diamphipnoa* sp. (Fig. 3; Table 1). Differences in the prey composition among periods at the individual-level (Fig. 5; ANOSIM R = 0.11, pseudo p-value < 0.001, all pairwise tests showed pseudo p-value < 0.01) were consistent to the population-level dietary analysis (Fig. 3; Table 1).

The frequency of occurrence (*%F*) of eggs in trout stomachs was 75% and 50% during the Chinook salmon spawning seasons of 2019 and 2020, respectively. The mean ± SD abundance of eggs in trout stomachs (N_E) was 17.95 ± 24.29 eggs/stomach ranging between 0 and 81 in 2019. In 2020, the mean ± SD abundance of eggs was 7.45 ± 12.90 eggs/stomach ranging between 0 and 43. The mean ± SD egg biomass (B_E) in trout stomachs was 7.36 ± 9.96 g in 2019 and 3.05 ± 5.29 g in 2020, whereas the mean ± SD total salmon egg biomass percent ratio (W_{EB}) was 1.85 ± 2.29% in 2019 and 1.03 ± 1.86% in 2020.

4. Discussion

Our findings support the hypothesis of a synergistic interaction between two invasive salmonids, with rainbow trout opportunistically preying on eggs of Chinook salmon. Eggs represent a main food source for rainbow trout during the Chinook salmon spawning season, but not before or after this period. Rainbow trout diets before and after the salmon spawning season are consistent with previous studies conducted across the region (Tagliaferro et al. 2015; Fierro et al. 2016) suggesting that this shift in diets during the salmon spawning season corresponds to an opportunistic tactic of rainbow trout.

Interactions among salmonids involving egg consumption have been well documented in their native range (e.g., Moore et al. 2008; Denton et al. 2009; Armstrong et al. 2010) and in invaded systems of the Northern Hemisphere (e.g., Greeley 1932; Johnson and Ringler 1979; Johnson et al. 2016). In the Great Lakes of North America, Greeley (1932) reported native brook char (*Salvelinus fontinalis*), introduced brown trout (*Salmo trutta*), and introduced rainbow trout preying on the ‘‘waste eggs’’ (not deposited into the gravel and likely non-viable) among each other during the respective spawning seasons. Similarly, Johnson and Ringler (1979) documented eggs from introduced Chinook salmon constituting up to 90% of native brook char, introduced brown trout, and introduced rainbow trout diets. Eggs of introduced coho salmon (*O. kisutch*) were also found in juvenile Pacific salmon (39–95% of their diets), and eggs of introduced brown trout were found in stomachs of introduced juvenile rainbow trout (Johnson and Ringler 1979). Recently, Johnson et al. (2016) reported eggs of introduced Pacific salmon in stomachs of native Atlantic salmon fry (*S. salar*).

In invaded systems of the Patagonia, seasonal availability of Chinook salmon eggs as a food source has potential fitness benefits for invasive rainbow trout as suggested by the higher condition of trout during the salmon spawning season than before or after. The high level of salmon eggs consumption that we document in this study is comparable to those levels previously reported in the Northern Hemisphere (Greeley 1932; Johnson and Ringler 1979; Johnson et al. 2016). Benefits of salmon egg consumption include their high digestibility, high content of polyunsaturated and essential fatty acids, and high energy content (Heinimaa and Heinimaa 2004; Armstrong et al. 2010). The caloric content of salmon eggs is considerably higher than other available prey items in high-latitude rivers of the Patagonia (Ciancio et al. 2007). Salmon egg consumption can increase the growth and condition of salmonids in invaded systems; this suggests a synergistic interaction between invasive salmonids in the Patagonia as is seen in their native range (Moore et al. 2008; Denton et al. 2009; Armstrong et al. 2010).

In several studies conducted in the Northern hemisphere (Greeley 1932; Moore et al. 2008; Armstrong et al. 2010), the availability of eggs as a food resource for other salmonids appear to be controlled by two mechanisms. First, females may fail to bury all their eggs in the gravel; second, females may bury their eggs on preexisting redds, releasing previously buried eggs. Collectively, salmon eggs available to invasive trout to consume are likely non-viable or would have low probability of survival, and thus their consumption may not affect Chinook salmon. Invasive trout may reap fitness benefits through increased survival or growth rates, in turn, augmenting their negative impacts on native species, other invasive species, and the receiving ecosystems at large. For example, there may be competition between juvenile salmon and trout, which proposes that future management of salmonids in the Patagonia should consider the interactions among multiple invaders (Arismendi et al. 2014). Our study represents baseline information that can aid future studies on the demography of invasive salmonids.

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Figures

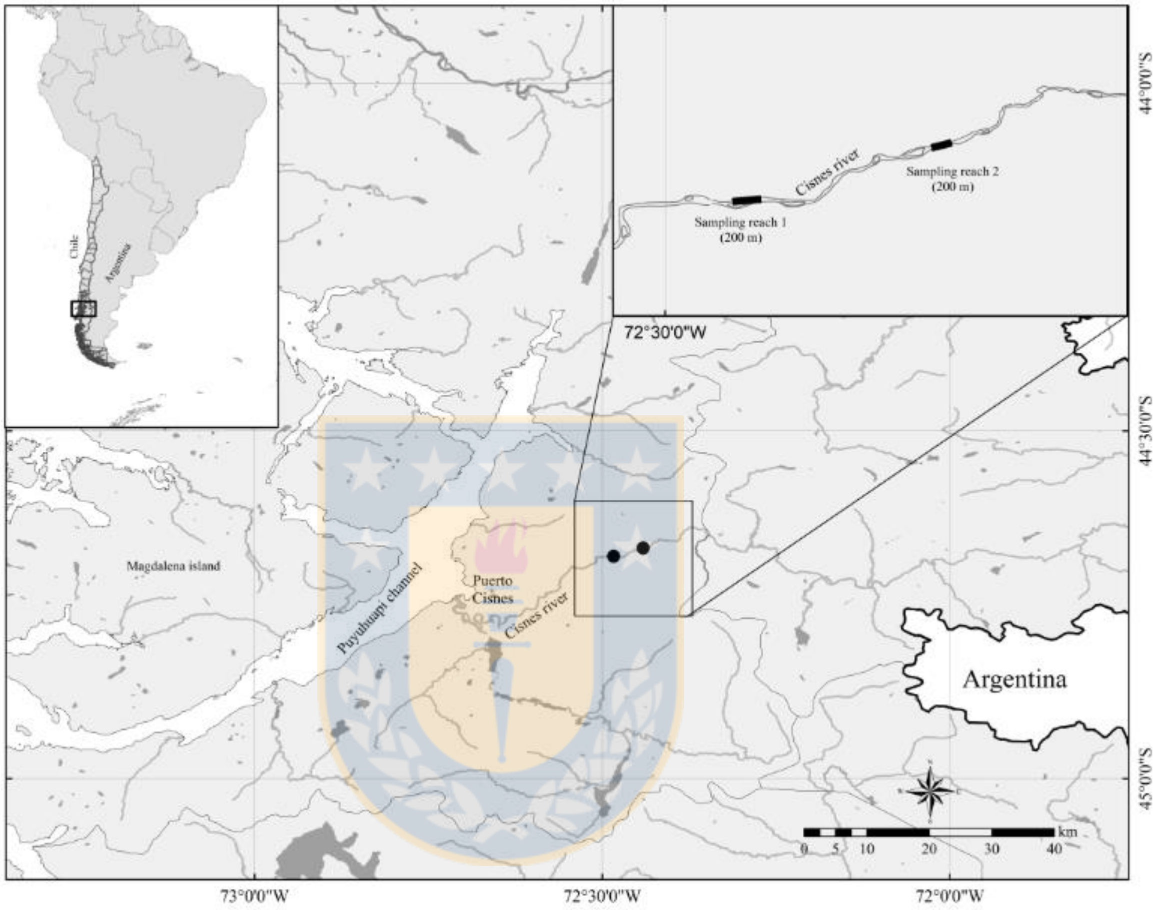

Figure 1. Map of the study sites in the Cisnes River, southern Chile, South America. Circles represent sample reaches.

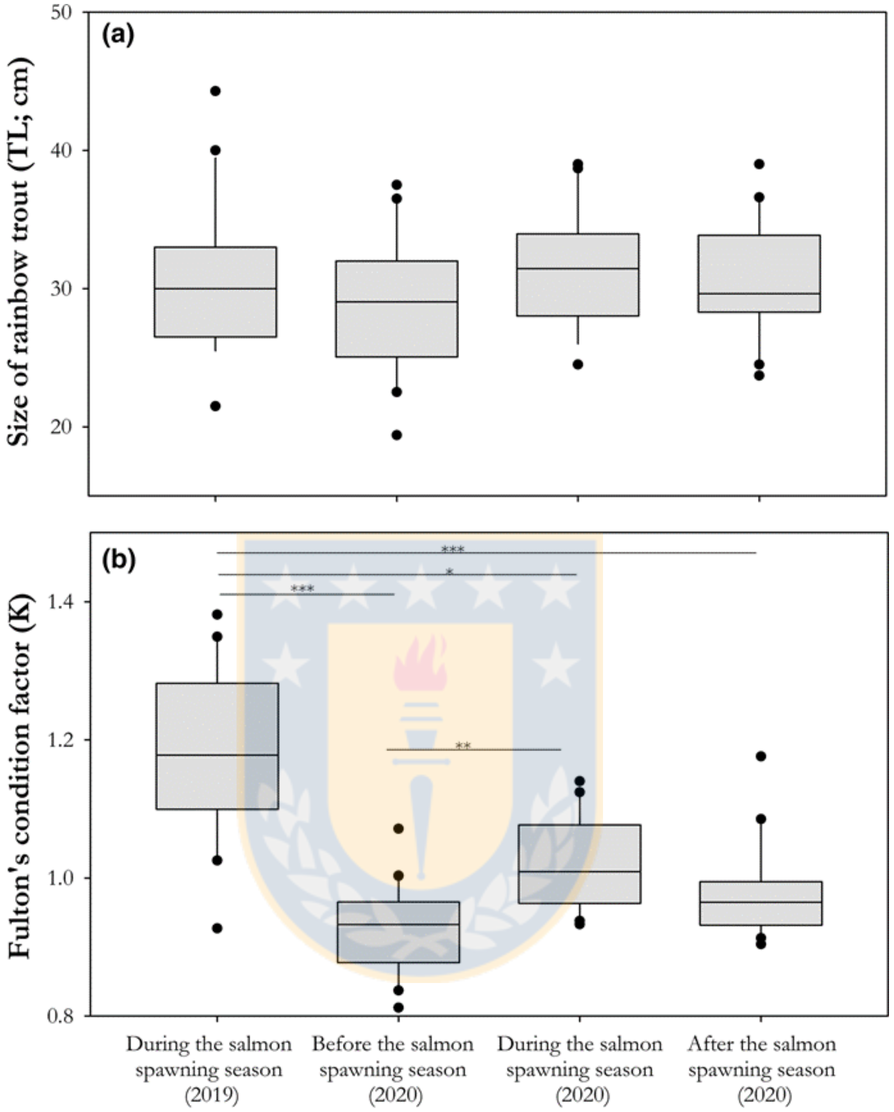

Figure 2. **a** Boxplots of total length (cm) of rainbow trout (n = 80) in the Cisnes River during each study period (2019–2020). **b** Boxplots of Fulton's condition factor of rainbow trout (n = 80) across periods. Horizontal lines represent statistically significant (***denotes p-value < 0.001; **denotes p-value < 0.01; *denotes p-value < 0.05) pairwise comparisons between periods.

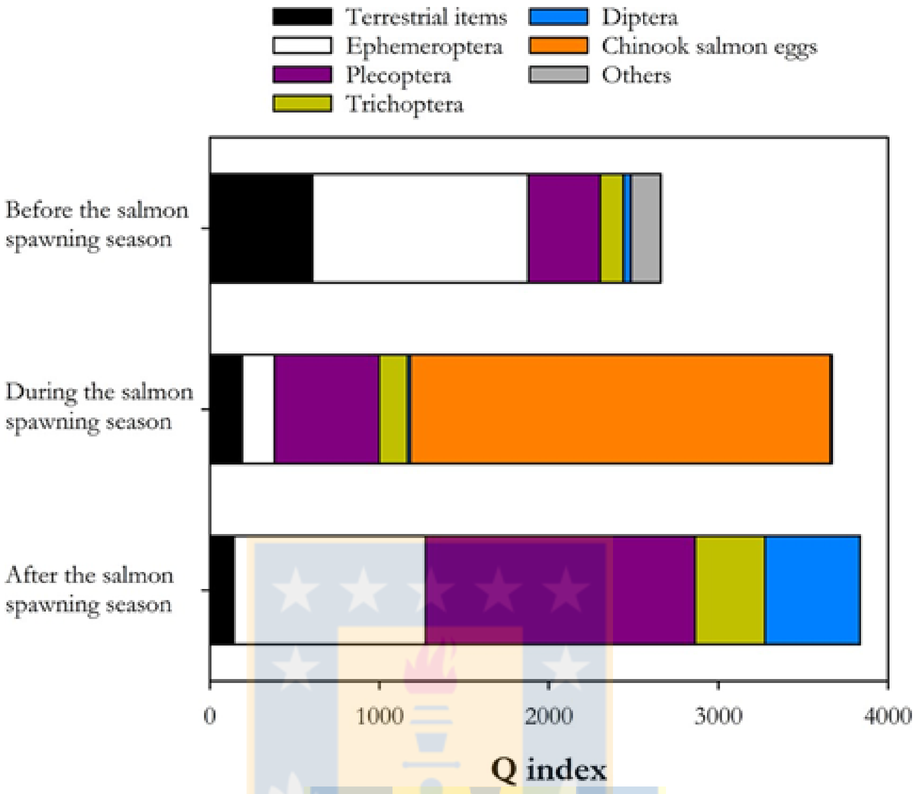

Figure 3. Diet composition of rainbow trout based on the coefficient of Hureau (*Q*) representing the main prey items for each sampling period in 2020.

Figure 4. Typical view of a stomach of rainbow trout containing Chinook Salmon eggs in the Cisnes River, southern Chile, South America.

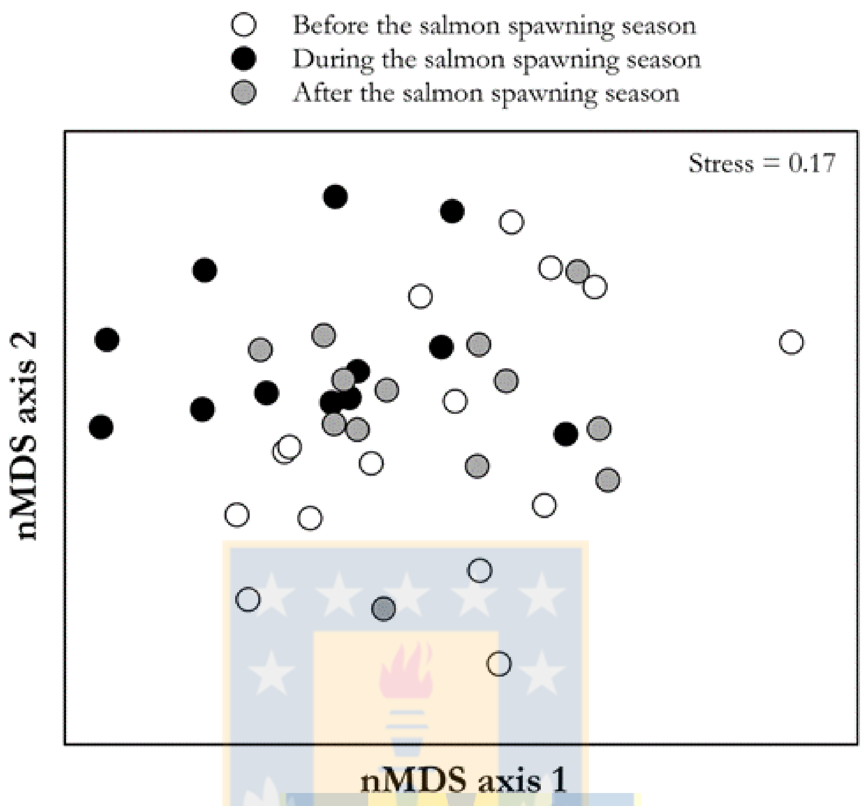

Figure 5. Non-metric multidimensional scaling (nMDS) ordination plot representing individual diets of rainbow trout among sampling periods in the Cisnes River, southern Chile, South America. The distance between circles indicates the similarity among trout diets (higher proximity of circles indicates a higher similarity, whereas trout diets that are more dissimilar are further apart).

Tables

Table 1**.** Diet composition (Q) of rainbow trout before, during, and after the spawning season of Chinook Salmon in the Cisnes River during 2020. Q > 200 represents a main food source whereas 20 < Q < 200 represents secondary food sources. Q < 20 represents occasional food sources. A = aquatic, T = Terrestrial, Ad = Adult, L = larvae.

Phylum	**Class/Order**	**Taxa**	**Before salmon spawning**	**During salmon spawning**	**After salmon spawning**
Arthropoda	Plecoptera	*Klapopteryx armillata* (A, L)	9.56	347.10	918.86
		Klapopteryx kuscheli (A, L)	0.00	21.02	0.00
		Diamphipnoa sp. (A, L)	169.32	230.14	31.21
		Perlidae (A, L)	0.00	0.00	82.85
		Gripopterygidae (A, L)	227.34	17.14	558.80
		Udamocercia sp. (A, L)	18.75	0.00	0.10
	Ephemeroptera	*Andesiops torrens* (A, L)	35.27	31.72	4.39
		Andesiops peruvianus (A, L)	0.36	0.08	12.42
		Leptophlebiidae (A, L)	1,237.50	128.16	1,112.47
		Murphyella sp. (A, L)	0.00	0.35	0.00
		Chiloporter sp. (A, L)	1.09	31.15	0.00

Diptera	Chironomidae (T, L)	37.91	0.00	0.01
	Chironomidae (A, Ad)	38.40	11.33	0.03
	Blephariceridae (A, L)	0.27	4.61	557.02
	Tipulidae (A, L)	1.76	0.00	2.73
	Limoniidae (A, L)	0.00	0.01	0.00
	Athericidae (A, L)	0.12	0.00	0.00
	Simuliidae (A, L)	3.71	0.48	0.74
Trichoptera	Leptoceridae (A, L)	7.25	14.21	218.44
	Sericostomatidae (A, L)	0.00	0.26	0.00
	Smicridea sp. (A, L)	88.47	146.75	178.82
	Limnephilidae (A, L)	0.00	2.88	5.25
	Hydrobiosidae (A, L)	41.26	3.98	7.95
	Ecnomidae (A, L)	0.16	0.00	0.00
Coleoptera	Elmidae (A, L)	0.93	0.17	0.08
	Gyrinidae (A, L)	0.79	0.02	0.00
	Coleoptera (T, Ad)	239.16	1.86	135.10
Odonata	Odonata (T, Ad)	130.89	0.00	0.00
Hemiptera	Hemiptera (A, Ad)	21.56	0.04	0.00

	Lepidoptera	Lepidoptera (T, L)	0.00	29.79	6.28
	Hymenoptera	Formicidae (T, Ad)	15.90	0.58	0.00
		Apoidea (T, Ad)	5.74	3.05	0.00
	Orthoptera	Gryllidae (T, Ad)	173.56	0.00	0.89
	Trombidiformes	Hydracarina (A, Ad)	0.01	0.00	0.00
	Araneae	Araneae (A, Ad)	4.89	0.33	1.90
Annelida	Clitellata	Oligochaeta (A, Ad)	0.00	3.20	0.00
Mollusca	Gastropoda	Planorbidae (A, Ad)	12.01	0.00	0.00
		Chilina sp. (A, Ad)	134.33	0.00	0.00
	Pulmonata	Stylommatophora (T, Ad)	0.00	142.99	0.00
Crustacea	Isopoda	*Heterias exul* (A, Ad)	0.00	2.57	0.00
Nematomorpha	Nematomorpha	Nematomorpha (A, Ad)	2.89	1.17	0.00
Chordata	Salmoniformes	*Oncorhynchus tshawytscha* (A, E)	0.00	2,480.48	0.00

Table 2**.** Diversity of prey composition for rainbow trout diets before, during, and after the spawning season of Chinook Salmon in the Cisnes River during 2020. Prey richness (*S*), Abundance (*N*), Margalef's index of species richness (*d*), Pielou´s equitability (*J'*) and Shannon-Wiener diversity (*H'*). The d, J´ and H' indices are averaged (± SD) over the 20 specimens sampling in each period.

Period	***S***	***N* (#)**	***N* (g)**	***d***	***J´***	***H´***
Before salmon spawning	31	404	5,794	0.91 ± 0.51	0.49 ± 0.23	0.37 ± 0.21
During salmon spawning	31	545	28,480	0.80 ± 0.37	0.52 ± 0.25	0.37 ± 0.19
After salmon spawning	22	508	10,385	0.83 ± 0.26	0.60 ± 0.20	0.43 ± 0.16

CAPÍTULO II

Consumption of marine-derived nutrients from invasive Chinook salmon (*Oncorhynchus tshawytscha*) transfer ω-3 highly unsaturated fatty acids to invasive resident rainbow trout (*O. mykiss*)

ARTÍCULO CIENTÍFICO

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Consumption of marine-derived nutrients from invasive Chinook salmon (*Oncorhynchus tshawytscha*) transfer ω-3 highly unsaturated fatty acids to invasive in-stream resident rainbow trout (*O. mykiss*)

Research paper

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Highlights

- Marine derived nutrients (MDN) from eggs of anadromous invasive Chinook salmon represent a resource for invasive rainbow trout (and maybe other consumers) in rivers
- During the spawning season of Chinook salmon, salmon eggs transfer ω-3 highly unsaturated fatty acids (HUFAs) from sea to rivers
- Consumption of MDN contained in Chinook salmon eggs increases HUFAs contents in rainbow trout which likely benefit their growth rate and fitness

Abstract

Marine derived nutrients (MDN) contained in gametes (mature eggs and sperm), carcasses and metabolic wastes from anadromous migratory salmon can transfer energy and materials to fresh water, thereby affecting the structure and function of stream ecosystems. This is crucial among ecosystems where humans have mediated biological invasions by propagating non-native species. Previous studies have demonstrated that consumption of MDN from salmon can benefit both native and invasive resident fishes. Yet, a more detailed understanding of the transfer of biomolecules with important physiological functions such as ω-3 highly unsaturated fatty acids (HUFAs) have received less attention among researchers. Here we demonstrate that consumption of MDN contained in invasive Chinook salmon eggs transfers ω-3 HUFAs (e.g., EPA and DHA) to resident invasive rainbow trout in a river food web. We conducted a field study in river sections previously identified as spawning areas for Chinook salmon in the Cisnes River, Patagonia. Rainbow trout were sampled around salmon spawning areas before, during, and after the salmon spawning season. Additionally, we collected tissue from different food resources and components of different origin (e.g., primary producers, aquatic and terrestrial items) from Cisnes River system. Analyses of stomach contents of trout were performed in conjunction with analyses of both lipid content and fatty acid profiles of trout tissue and food web components. Chinook salmon eggs showed higher content of ω-3 HUFAs, especially EPA (0.62 ± 0.46 mg g DW^{-1}) and DHA (0.55 ± 0.28 mg g DW^{-1}) than either freshwater or terrestrial components (0 - 0.12 mg g DW^{-1} both EPA and DHA). We measured marked shifts in the fatty acid profile (~six-fold increase in EPA and DHA) of trout following consumption of Chinook salmon eggs. Our findings suggest that MDN via consumption of salmon eggs by resident rainbow trout may positively influence the fitness and growth of resident trout and likely contribute to the long-term persistence of negative impacts of salmonid invasions on receiving ecosystems of Patagonia.

Keywords: non-native species, food webs, ocean, salmonids, anadromous, ecophysiology

1. Introduction

The movement of energy, nutrients, biomolecules, contaminants and other compounds from marine to freshwater ecosystems mediated by anadromous migratory salmon can affect the structure and function of river ecosystems, both unaltered (Elliott et al., 1997; Jaecks and Quinn, 2014; Rinella et al., 2012) and altered by human-mediated biological invasions (Arismendi and Soto, 2012; Figueroa-Muñoz et al., 2021; Gerig et al., 2019). Salmon of the genus *Oncorhynchus* obtain nearly 99% of their mass while feeding in marine environments and then return to spawn and die in streams (Quinn, 2018). During their spawning event, salmon bring marine-derived nutrients (MDN) contained in their gametes (mature eggs and sperm), carcasses, and metabolic wastes from highly productive marine systems as ephemeral resources in less-productive freshwater systems (Armstrong et al., 2010; Moore et al., 2008; Schindler et al. 2003). Transfer of MDN from invasive, anadromous migratory Chinook salmon (*O. tshawytscha* Walbaum 1792) to freshwater ecosystems, have also been reported in New Zealand (Unwin, 2006), and South America (Arismendi and Soto, 2012; Figueroa-Muñoz et al., 2021; Muñoz et al., 2022). In invaded ecosystems, consumption of MDN of anadromous migratory Chinook salmon can benefit other terrestrial and aquatic invaders (Figueroa-Muñoz et al., 2021; Muñoz et al., 2022). If one invader benefits from the presence of other invader (e.g, Arismendi et al., 2020), this has the potential to exacerbate their ecological impacts and promote ‘invasional meltdown’; here, an invaded ecosystem becomes more susceptible to new invasions (Simberloff and Von Holle, 1999).

Previous studies based on stomach contents, stable isotope and camera traps analyses have identified use and consumption of MDN from invasive, anadromous migratory Chinook salmon by primary producers and terrestrial and aquatic consumers, including invasive rainbow trout (Arismendi and Soto, 2012; Figueroa-Muñoz et al., 2021; Muñoz et al., 2021, 2022). These studies have centered on food webs of oligotrophic rivers in Patagonia, which harbor abundant populations of both anadromous migratory and non-anadromous resident salmonids (Soto et al. 2006, 2007). However, transfer and incorporation of abundant ω-3 highly unsaturated fatty acids (hereafter ω-3 HUFAs) present in marine food webs (Colombo et al., 2017), have received less attention in freshwater systems. These HUFAs accumulate in specific salmon tissues such as eggs and muscle (Ashton et al., 1993; Heintz et al., 2004), which can be subsequently consumed and incorporated into freshwater food webs.

The ω-3 HUFAs eicosapentaenoic acid (EPA; 20:5ω-3) and docosahexaenoic acid (DHA; 22:6ω-3) are scarce biomolecules that play an important role in several physiological functions in consumers. They include somatic growth in the nervous system and gonads (Pilecky et al., 2021; Sargent et al., 2002; Twining et al., 2021), structure and physical-chemical properties of cell biomembranes (Pilecky et al., 2021; Tocher, 2015), reproduction (Müller-Navarra et al., 2000; Sargent et al., 2002), cognition (Pilecky et al., 2021), and survival (Boglione et al., 2013; Sargent et al., 2002; Twining et al., 2021). In general, EPA and DHA availabilities in stream food webs depend on primary producers (Ebm et al., 2021; Guo et al., 2022) as consumers have a limited ability to biosynthesize EPA and DHA (Guo et al., 2022). Primary producers have higher DHA content in marine compared to freshwater ecosystems (Twining et al., 2016, 2021). Basal resources such as algae, macrophytes, and leaves in fresh water generally have high content of α-linolenic acid (ALA; 18:3ω-3), which together with EPA are precursors to synthesize DHA in fishes (Guo et al., 2022; Sargent et al., 2002; Twining et al., 2021). Conversely, contents of EPA and DHA varied among algae, macrophytes, and leaves. For example, leaves from vascular plants lack EPA and DHA (Ebm et al., 2021; Twinning et al., 2016). Periphytic freshwater algae can synthesize and show high contents of EPA (Ebm et al., 2021; Guo et al 2018; Sushchik et al., 2010), but very low levels of DHA (Ebm et al., 2021; Guo et al., 2018). Additionally, contents of EPA and DHA in freshwater algae can be affected by season and location (Guo et al., 2022). These variability in HUFAs contents among basal resources can be transferred to higher trophic predators as the case of salmonids (Guo et al., 2022).

MDN from anadromous migratory salmon can transfer EPA and DHA to freshwater food webs and potentially carry benefits for fitness and growth of their consumers. The ω-3 HUFAs can then be used as dietary tracers (Ebm et al., 2021; Guo et al., 2020; Happel et al., 2019) in freshwater systems by salmon – both native and non-native – as they are selectively retained and conserve their original form during tissue incorporation by consumers (Twining et al., 2016, 2021). Evidence of increased fat reserves in native resident fish consuming salmon eggs and carcasses have been reported in rivers of North America (Armstrong and Bond, 2013; Rinella et al., 2012), but the specific composition of ω-3 HUFAs has received less attention. To our knowledge, one study conducted under experimental conditions reported the ω-3 HUFAs transfer from carcasses of anadromous migratory pink salmon (O. gorbuscha Walbaum 1792) to coho salmon (O. kisutch Walbaum 1792) parr in artificial streams (Heintz et al., 2004). These authors showed that lipid content and EPA and DHA content in triacylglycerols of coho salmon exposed to pink salmon carcasses were five to six times higher than unexposed coho salmon.

Chinook salmon and rainbow trout were successfully introduced and established naturalized populations across Patagonia (Arismendi et al., 2014; Correa and Gross, 2008; Riva-Rossi et al., 2012). Both species have contributed to local economies due to their value for recreational fisheries (Arismendi and

Nahuelhual, 2007), and more recently, artisanal fisheries in the case of Chinook salmon (Sanguinetti et al., 2021). However, they have also negatively affected native species and altered native ecosystems (Arismendi et al., 2009; Fierro et al., 2016), and very little is known about interactions between these two invaders. In the Cisnes River system, non-viable eggs of Chinook salmon during its spawning season are regularly consumed by invasive stream resident rainbow trout (Figueroa-Muñoz et al., 2021).

The main objective of this study was to examine the transfer of ω-3 HUFAs (EPA and DHA) from invasive, anadromous migratory Chinook salmon to invasive resident rainbow trout through consumption of MDN contained in salmon eggs. To meet this objective, we use a combination of field surveys, diet analyses of rainbow trout, and characterization of lipid content and fatty acid profiles of rainbow trout and food web components. First, we hypothesize that consumption of anadromous migratory Chinook salmon (non-viable) eggs enriched in ω-3 HUFAs (EPA and DHA) transfer these biomolecules to non-anadromous resident rainbow trout, a high-level trophic consumer. Second, we hypothesize that resident trout have low content of EPA and DHA and high content of ALA before the salmon spawning season; however, during and after the salmon spawning season, resident trout will increase contents of EPA and DHA due to consumption of MDN contained in Chinook salmon eggs. Third, we hypothesize that ω-3

HUFAs contents in Chinook salmon eggs (i.e., EPA and DHA) are higher than in other food sources, also available to rainbow trout, but from terrestrial or freshwater origin (i.e., ALA). Our study provides insights to assess potential synergistic interactions between salmonids in invaded ecosystems, which can be relevant for mitigating and managing biological invasions.

2. Materials and methods

2.1. Study area

Cisnes River is an exorheic basin (5,464 km2) in southern Chile that drains into the Puyuhuapi channel. The length of the river is ~160 km with an average annual discharge of 253 m3/s (Dirección General de Aguas, 2021), and the flow regime is regulated by a mixture of rain and snow. The climate of the region is template type marine west coast, with temperature range 16 - 17° C (Sarricolea et al., 2017) and marked precipitation peaks in late fall and early winter with a mean of 886 mm (Centro de Información de Recursos Naturales, 2021).

The study was carried out in two river sections (200 m-each; 57 and 93 meters above sea level, respectively) and one reference tributary at the lower portion of the Cisnes River (Fig. 1). These river sections were previously identified as spawning habitat for invasive, anadromous migratory Chinook salmon (Figueroa-

Muñoz et al., 2021). A reference tributary (100 m; 55 m.a.s.l.) used as baseline for fatty acid analyses corresponded to a stream of low order close to river sections without spawning habitat for Chinook salmon (Fig. 1). Both river sections and reference tributary are dominated by native forests (Fig. 1). The dominant tree species are *Luma apiculata* and *Drimys winteri* in the first river section (include reference stream) and *Nothofagus dombeyi* in the second river section respectively. Physicochemical conditions in the two sections of the river and the reference tributary studied are described in Table 1.

2.2. Sampling procedure

2.2.1. Rainbow trout collection and tissue sampling

In 2021, adults of non-anadromous resident rainbow trout were captured using hook and line angling in three periods including before (February; n = 20), during (March-April; n = 20), and after (June; n = 20) the Chinook salmon spawning season. We sampled fish lethally without replacement. For each trout captured and prior to dissection, we measured total length (L) with a board meter (nearest mm), and total mass (W) using a scale Pesamatic Model WTB 2000 (0.01 g). Stomach of each specimen was removed, fixed in ethanol 90% and preserved separately in Falcon tubes (50 mL) for later analysis in the Benthos Laboratory of the Institute of Marine and Limnological Sciences, Universidad Austral de Chile.

Muscles from each specimen were collected and stored frozen (-20 °C) separately in cryotubes (2 mL). Prior to lipid analyses, samples were lyophilized during 36 h at -70 °C to remove any remaining water. Then, we used 20 mg dry weight (DW) of each sample for lipid analyses. We used the morphological criterion (size and color) for identifying the sampled rainbow trout as non-anadromous resident or anadromous migratory following Pascual et al. (2001).

2.2.2. Food web components collection and tissue sampling

We collected samples of food web components from two river sections and one reference tributary to Cisnes River (Fig. 1) to evaluate ω-3 HUFAs contents in the environment with and without MDN from Chinook salmon. During April 2021, from the reference tributary we sampled whole aquatic macroinvertebrates of the eight most abundant taxa, corresponding to families Eustheniidae, Diamphipnoidae, Leptophlebiidae and Tipulidae, as well as the genus *Chilina*, *Klapopteryx*, *Hyalella* and *Lumbricus*. Samples of each taxon were collected in duplicate (n = 16) using a Surber net with 500 µm mesh (0.09 m2 area) following Fierro et al. (2016). We also collected manually whole terrestrial macroinvertebrates of multiple unidentified species (Insecta) in duplicate (n = 2). We additionally collected from the reference tributary muscle tissue from 3-5 juveniles of four species of fish: brown trout (*Salmo trutta* Linnaeus 1758; n = 5), rainbow trout (n = 5), Puye (*Galaxias maculatus* Jenyns 1842; n = 5) and Chinook salmon (n = 3) using an electroshocker (Halltech, model HT 2000, 60 Hz). In addition to the reference tributary and riverbank, we collected samples of aquatic primary producers and native trees respectively. Aquatic primary producers, were constituted by macrophytes and biofilm. Leaves of the two most abundant aquatic macrophytes *Gunnera magellanica* and *Hippuris vulgaris* were collected manually in duplicate (n = 4). Samples of biofilm were collected from four rocks selected at random (n = 4) following Correa-Araneda et al. (2022) using one quadrant (1 cm^2) on the upper face of each rock and then extracting all the biofilm inside of the quadrant by scraping. The taxonomic composition of biofilm was not examined because we were primarily interested in the fatty acid composition of biofilm as a group. Regarding terrestrial primary producers, leaves from the three most abundant native trees species corresponding to *Drimys winteri*, *Amomyrtus luma* and *Nothofagus dombeyi* were collected manually in duplicate (n = 6). Lastly, we sampled white dorsal muscle tissue and eggs from five Chinook salmon spawning females (muscle n = 5 and eggs n = 5) captured by netting at river sections with MDN. All samples previously described were stored frozen (-20 °C) separately in cryotubes (2 mL). Prior to lipid analyses, samples were lyophilized during 36 h at -70 °C to remove any remaining water. Then, we used 20 mg DW of each sample for lipid analyses.

2.3. Laboratory analysis

2.3.1. Quantification of total lipid content of rainbow trout muscles and food web components

Total lipid content analysis was carried out following the gravimetric method proposed by Folch (1957) with the posterior modification of Guzmán-Rivas et al. (2021). As a first step, 20 mg DW from each collected samples were plunged in 5 mL of dichloromethane-methanol solvent (2:1 v/v), incubated in an ultrasonic bath (MRC, AC-120H) for 10 min at room temperature and then stored by 24 h. Subsequently, 1.0 mL of plunged samples were collected and mixed with 4.0 mL of 0.88% potassium chloride solution (KCl-ultra pure water) using a vortex (model SBS100-2). Samples were homogenized and centrifuged at 1,500 rpm for 5 min (FASCIO TG1650-S). Thereafter, two phases were separated, and the lower phase that contained the total lipids was transferred to a previously weighed 5.0 mL tube. The solvent was evaporated with an injection of nitrogen gas in a sample concentrator (109A YH-1, Glas-col). Finally, total lipid contents of samples were determined using a precision balance (Precisa model 120A, 0.01 mg). The mass of the tube (previously weighed) was subtracted from the mass of extracted lipids-tube to obtain the mass of the lipids. The data were collected as mg g DW^{-1}.

2.3.2. Fatty acids profiles of rainbow trout muscles and food web components

After analyzing the total lipid contents, the fatty acid profiles of each sample were quantified. Fatty acid profiles were carried out following standard methods developed by Cequier-Sánchez et al. (2008) and modified by Guzmán-Rivas et al. (2021). Fatty acid methyl esters were measured mixing 1.0 mL of the total lipid extract from the previous section with 2.0 mL of 1% sulfuric acid-methanol. The mixture was homogenized for 15 s using a vortex (model SBS100-2) and then incubated for 1.5 h at 70 °C in a thermoshaker (DBS-001, MRC). Thereafter, hexane was added three times (6.0, 3.0 and 3.0 mL) and mixture was homogenized for 15 s using a vortex each time. Two phases were separated, and the upper phase that contained the fatty acid methyl esters was transferred to an amber bottle and dried with an injection of nitrogen gas in a sample concentrator (109A YH-1, Glas-col). Subsequently, fatty acid methyl esters were collected through washes of hexane and transferred to 1.5 mL amber vial. Fatty acid methyl esters were measured on to gas chromatography - flame ionization (7890A, Agilent) mounted with a DB-225 column (J&W Scientific, 30 m long, 0.25 internal diameter, and 0.25 mm film). Finally, identification of individual fatty acids was carried out using a chromatograph software (Agilent ChemStation, USA), and values of known fatty acids of aquatic origin (certified material, Supelco 37 FAME mix 47,885-U; Guzmán-Rivas et al., 2021). An internal standard blank (23:0, trisanoic acid) was added to each sample prior to chromatography.

2.3.3. Dietary analysis of rainbow trout

Stomach content of each trout captured before, during and after Chinook salmon spawning season was analyzed followed Fierro et al. (2016). First, empty stomach contents into a Petri dish. Distinct food items were then separated, identified to the lowest possible taxonomic level (using the taxonomic key developed by Dominguez et al., 2009), and weighed (g wet weight). We evaluated contribution of each prey item to diet of trout during each period (before, during, and after Chinook salmon spawning season), calculating Hureau's (Q) dietary coefficient as follows:

$$Q = \%F \times \%W$$

Where $\%F$ is the frequency of occurrence of the respective prey item, and $\%W$ is the percentage of wet weight of the respective prey item. Q reduces the bias associated with the use of numerical methods based on discrete quantities (Di Prinzio and Arismendi, 2018; Hureau, 1970). Based on the Q index, prey items were classified as main prey ($Q > 200$), secondary prey ($200 > Q > 20$), or occasional prey ($Q < 20$) following Di Prinzio and Arismendi (2018).

2.4. Data analyses

In order to compare dietary tracer fatty acids (EPA, DHA and ALA) among our study period we used a simple one-way ANOVA with an alpha error set at 0.05.

One-way ANOVA include the time around of the Chinook salmon spawning season as factor, and levels were the before, during and after the Chinook salmon spawning season periods. We tested normality using a Shapiro–Wilk test (n < 50 per group) and homoscedasticity of variance using a Levene test. When the assumption of homoscedasticity of variance failed, we used a non-parametric Kruskal–Wallis Analysis of Variance on Ranks test. For pairwise multiple comparisons, we used a Tukey´s ranged test. We used principal component analysis (PCA) to compare fatty acid profiles of trout over the three periods (before, during and after the salmon spawning season). In addition, we used similar analysis to evaluate differences in the fatty acid profiles among stream and river food web components, using as factor the ecosystems precedence that included three levels: marine, freshwater and terrestrial. This factor includes implicitly the effect of MDN contain in the Chinook salmon tissues, as well as our nominal control (reference tributary) without influence of MDN. The food web components with nutrients precedence from the marine ecosystem includes muscle tissue and eggs of Chinook salmon spawners. The food web components with nutrients precedence from freshwater ecosystem includes aquatic macroinvertebrates, juvenile fish’s, leaves of aquatic macrophytes and composite biofilm. The food web components with nutrients precedence from terrestrial ecosystem includes terrestrial macroinvertebrates and native tree leaves. Univariate and multivariate analysis were performed using statistical R software (R Core Team, 2020).

3. Results

3.1. ω-3 HUFA contents variation in the muscle of rainbow trout among study periods

All rainbow trout specimens captured corresponded to the resident stream resident morphotype. Rainbow trout specimens showed typically pattern coloration that included green, or yellowish colors, shading to silvery white on the underside, with a horizontal pink-red stripe running from the gills to the caudal fin and black spots along their backs. The size range of trout was between 22 and 41 cm (TL) and mass between 101.85 g to 660.15 g (Table 2). One-way ANOVA showed that EPA (d.f. = 2, H = 28.187, p-value < 0.001) and DHA (d.f. = 2, H = 34.838, p-value < 0.001) contents in rainbow trout muscle showed significant differences among sampling periods; before, during, and after Chinook salmon spawning season inferred through pairwise comparisons between periods (Fig. 2). The mean (± standard deviation, SD) content of EPA showed approximately two-fold increase from before (0.004 ± 0.01 mg g DW^{-1}) to during (0.009 ± 0.01 mg g DW^{-1}) the Chinook spawning season; approximately seven-fold increase from before to after (0.026 ± 0.01 mg g DW^{-1}) the spawning season and approximately three-fold increase from during to after the spawning season. The mean (± SD) content of DHA showed approximately two-fold increase from before (0.013 ± 0.01 mg g DW^{-1}) to during (0.024 ± 0.02 mg g DW^{-1}) the spawning season, approximately six-fold increase from before to after (0.073 ± 0.03 mg g

DW^{-1}) the spawning season and approximately three-fold increased from during to after the spawning season. These were consistent with the consumption of MDN contain in Chinook salmon eggs by rainbow trout (see results below). However, ALA content on rainbow trout muscle was not statistically significantly different among periods (Fig. 2; d.f. = 2, H = 7.79, p-value = 0.06).

PCA separated fatty acid profiles of rainbow trout in the muscle before, during, and after salmon spawning season, with PC1 explaining 56% of the fatty acid variation (Fig. 3). PC1 showed moderate association with ALA (r = 0.32), EPA (r = 0.25), and DHA (r = 0.20) and clustered trout sampled during the salmon spawning season separated from before and after spawning season (Fig. 3; S1 File; Supplementary Data). PC2 explained 15.2% of the total fatty acid variation and a low association with ALA (r = -0.05), moderate association with EPA (r = -0.34), and high association with DHA (r = -0.45). Rainbow trout sampled after the salmon spawning season diverged from before and during periods (Fig. 3).

3.2. ω-3 HUFA contents of food web components from different origin

MDN contained in Chinook salmon eggs showed higher contents of EPA (0.62 ± 0.46 mg g DW^{-1}) and DHA (0.55 ± 0.28 mg g $^{DW-1}$) than in taxa of freshwater and terrestrial origin (0 - 0.12 mg g DW^{-1} both EPA and DHA) (Table 3). Conversely, components from fresh water showed higher levels of ALA than component containing MDN such as eggs and muscle of Chinook salmon spawners (Table 3). However, some components from multiple origins (i.e., juvenile Chinook salmon muscle and aquatic insect Eustheniidae) showed slightly high contents of EPA and DHA (Table 3). Freshwater and terrestrial primary producers failed to contain EPA and DHA and showed only low content of ALA (Table 3).

PCA separated components that contained MDN such as muscle and eggs of Chinook salmon from others of fresh water and terrestrial origin (Fig. 4; S2 File; Supplementary Data). The PC1 explained 31% of the total fatty acid variation of all components with a low association with ALA (correlation coefficient: $r = 0.04$), and moderate association with EPA ($r = 0.21$) and DHA ($r = 0.20$). The PC2 explained 15.7% of the total fatty acid variation of food web components and showed a high association with ALA ($r = -0.42$), and low association with EPA ($r = -0.01$) and DHA ($r = 0.04$), separating Plecoptera for the all-other food web components (Fig. 4).

3.3. Diet of rainbow trout among sampling periods

We assessed a major shift in the diet of rainbow trout before, during, and after Chinook salmon spawning season. Before salmon spawning season, main food sources included aquatic Nematomorpha, Trichopteran (Leptoceridae) and Plecopteran (*Klapopteryx kuscheli*) (Table 4). During the salmon spawning season, trout shifted their diet from macroinvertebrates to feed almost exclusively on Chinook salmon eggs, which contained MDN (Table 4), followed by Plecopteran (*Klapopteryx kuscheli*). After the salmon spawning season, the main food sources were aquatic Plecopteran (*Klapopteryx kuscheli*), Trichopteran (Leptoceridae) and terrestrial items (vegetable remains) (Table 4). Overall, trout diet spanned 55 taxa, of which the majority represented aquatic benthic macroinvertebrate larvae (52.73%) and adults (21.82%), followed by terrestrial adult invertebrates (18.18%) and larvae (3.68), and others (i.e., Chinook salmon eggs, vegetable remains).

4. Discussion

4.1. Variation of ω-3 HUFAs contents in the muscle of rainbow trout among study periods

We show that consumption of MDN contained in Chinook salmon eggs transfer ω-3 HUFAs (EPA and DHA) to rainbow trout, a higher consumer of river food webs, supporting our first hypothesis. In their native and non-native ranges, potential positive interactions between anadromous migratory salmon and non-anadromous resident species (e.g., brown trout, brook trout) have been well-studied (Gerig et al. 2018; Wipfli et al. 2003) and effects would likely be similar to what we report here. We argue that these beneficial effects, including increased growth, condition, and energy storage, could be better understood by studying transfer of ω-3 HUFAs from anadromous migratory to resident species in aquatic ecosystems at large. In particular, we know very little about how invasive Chinook salmon and rainbow trout, which were propagated in Patagonia in large numbers, interact and may ecologically benefit each other.

High contents of ω-3 HUFAs (EPA and DHA) in anadromous migratory Chinook salmon eggs supply important biomolecules to consumers in less-productive freshwater food webs. Chinook salmon eggs that contain MDN are a main food source for rainbow trout during the salmon spawning season, likely an opportunistic feeding tactic of rainbow trout (Figueroa-Muñoz et al. 2021). High consumption of salmon eggs by other salmonids is seen in both unaltered (Armstrong et al., 2010; Moore et al., 2008; Rinella et al., 2012) and altered ecosystems by biological invasions (Dunlop et al., 2021; Figueroa-Muñoz et al., 2021; Johnson et al., 2016). This suggests that increased HUFAs (EPA and DHA) contents in resident rainbow trout muscle during and after the salmon spawning season is due to consumption of MDN and selective retention of EPA and DHA, supporting our second hypothesis. This is consistent with a previous study conducted under experimental conditions using anadromous pink salmon and coho salmon parr in fresh water – the higher the density of pink salmon carcasses, the higher the transfer of EPA and DHA to coho salmon parr consuming the carcasses (Heintz et al., 2004). Low content of EPA and DHA in freshwater ecosystems means low-quality resources for higher consumers (Guo et al., 2022), which may need to biosynthesize EPA and DHA from a precursor such as ALA (Guo et al., 2022; Sargent et al., 2002; Twining et al., 2021). However, this process will have a high energetic cost considering the relatively cold condition of the Cisnes River (Table 1; Sargent et al., 2002). Stream resident fishes can then improve their condition after consuming salmon eggs (Figueroa-Muñoz et al., 2021; Johnson and Ringler, 1979). Collectively, MDN contained in Chinook salmon eggs and carcasses can affect natural food webs in rivers by providing additional resources to aquatic (Arismendi and Soto 2012; Figueroa-Muñoz et al., 2021) and terrestrial consumers (Muñoz et al., 2022).

Growth and fitness of resident fish could be influenced by the consumption of MDN contained in salmon eggs in several different ways. EPA and DHA have key roles in several physiological functions of consumers (Pilecky et al., 2021; Twining et al., 2021), likely improving individual fitness. In their native ecosystems, consumer resident fish developed different strategies for optimizing consumption of MDN from anadromous migratory salmon, including digestive flexibility or increased gut capacity (Armstrong and Bond, 2013). Resident fish also exploited thermal heterogeneity for accelerating their metabolism and increasing their assimilative capacity (Armstrong et al., 2013). These strategies together with other factors, including HUFAs transfer, may result in improved condition (Armstrong and Bond, 2013), growth (Armstrong and Bond, 2013; Denton et al., 2009; Rinella et al., 2012), and lipid storage (Armstrong and Bond, 2013; Rinella et al., 2012) of resident fish, which may improve individual fitness. Yet, we have no direct evidence of this phenomenon in ecosystems altered by biological invasions.

4.2. ω-3 HUFAs contents among food web components of different origin

We show that Chinook salmon eggs that contained MDN are the only food source with high content of EPA and DHA available to resident rainbow trout, supporting our third hypothesis. These differential abundances of ω-3 HUFAs (ALA, EPA and DHA) among food web components across terrestrial, freshwater and marine ecosystems are also consistent with previous studies (Twinning et al., 2016, 2021; Colombo et al., 2017; Table 5). Our results show that in the reference tributary without MDN from Chinook salmon, EPA and DHA contents in aquatic primary producers are scarce or absent. Aquatic primary producers from our reference tributary influence low HUFAs contents of macroinvertebrates. Guo et al. (2022) demonstrate the importance of the quality of periphyton as source of HUFAs to consumers in stream food webs. We show the relative contents of EPA and DHA (expressed in %) in macroinvertebrates are much lower than in the Ybbs River in Austria a system with high-quality primary producers (Guo et al., 2022; Table 5), but similar to results obtained from Allan River, Scotland (Bell et al., 1994; Table 5).

HUFAs (EPA and DHA) relative contents, obtained from resident rainbow trout that consumed MDN contained in Chinook salmon eggs, are higher than those obtained from specimens collected from the reference tributary. These differences stress the importance of MDN contained in Chinook salmon eggs as a source of HUFAs available to non-anadromous resident rainbow trout and other consumers. Relative contents of EPA and DHA obtained from rainbow trout influenced by MDN are similar to results obtained from brown trout inhabiting a river food web with high-quality periphyton (Guo et al., 2022; Table 5). In addition, our results were similar to results obtained from juveniles coho salmon exposed to high densities of anadromous migratory pink salmon (Heinz et al., 2004; Table 5).

4.3 Management implications

Synergistic interactions between invaders could be important to potential ‘invasional meltdown’ scenarios in Patagonia. This occurs when an invaded ecosystem becomes more susceptible to further invasions (Simberloff and Von Holle, 1999; Simberloff 2006), which can initiate population-level feedbacks that may intensify impacts on receiving ecosystems (Arismendi et al., 2020; Simberloff and Von Holle, 1999; Simberloff 2006). Muñoz et al. (2022) show Chinook salmon carcasses consumed by other invaders such as the American mink, house mice, black rat, and yellow jacket wasps. Consumption of MDN contained in Chinook salmon carcasses and eggs can also benefit native species, adding layers of complexity to the problem of managing communities composed by both native and introduced species (Murphy et al. 2021; Muñoz et al., 2022). Freshwater ecosystems are among the most threatened in the world and experiencing a high decline in biodiversity (Dudgeon et al., 2006). Ecosystems of Patagonia region with high levels of endemism are no exception, facing identical threats by invasive salmonids (Habit and Cussac, 2016). Improved condition of rainbow trout owing to consumption of MDN contained in salmon eggs could translate in additional negative effects to those already reported for native fishes (Arismendi et al. 2009; Correa and Hendry, 2012).

Single-species approaches have dominated management of invasive species. Species interactions should be integral of part of holistic, ecosystem-based solutions for the management of invasive species valued differentially by stakeholders. We proposed that policy makers consider three aspects emanated from current literature and our results: (1) Availability of MDN from anadromous migratory Chinook salmon in invaded river food web depending to their magnitude of annual return. Therefore, current initiatives shown from Patagonian region as the incipient development of artisanal fishery of Chinook salmon in the estuaries can affected MDN availability. (2) Rainbow trout benefits emanated by consumption of MDN contained in Chinook salmon eggs, can be beneficial to humans. Human benefit included possible economic benefit emanated from improved of rainbow trout recreational fishery, as well as health benefit due to the consumption of rainbow trout flesh with high contents of HUFAs (EPA and DHA).

(3) Potential conflicts between environmentalists, artisanal fisheries and recreation fisheries. Potential conflicts can be occurred, due to differential perception and interest on invasive salmonids and their interaction with the socioecological system where occur.

5. Conclusions

Our study demonstrates that consumption of MDS (i.e., eggs) from invasive, migratory Chinook salmon transfers ω-3 HUFA (EPA and DHA) to resident invasive rainbow trout in the Cisnes River food web. Chinook salmon eggs are a main food source for resident trout and contain the highest concentration of EPA and DHA in the system. As a result, fatty acid profiles of rainbow trout were higher during and after Chinook salmon spawning season. Collectively, the consumption of salmon eggs by resident trout may be a strategy to assimilate ω-3 HUFA and improve their fatty acid profile, especially EPA and DHA. This could minimize their energetic cost for reproduction and growth in low-productive ecosystems. This has ecological implications that can profoundly alter freshwater ecosystems invaded by salmonids.

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Figures

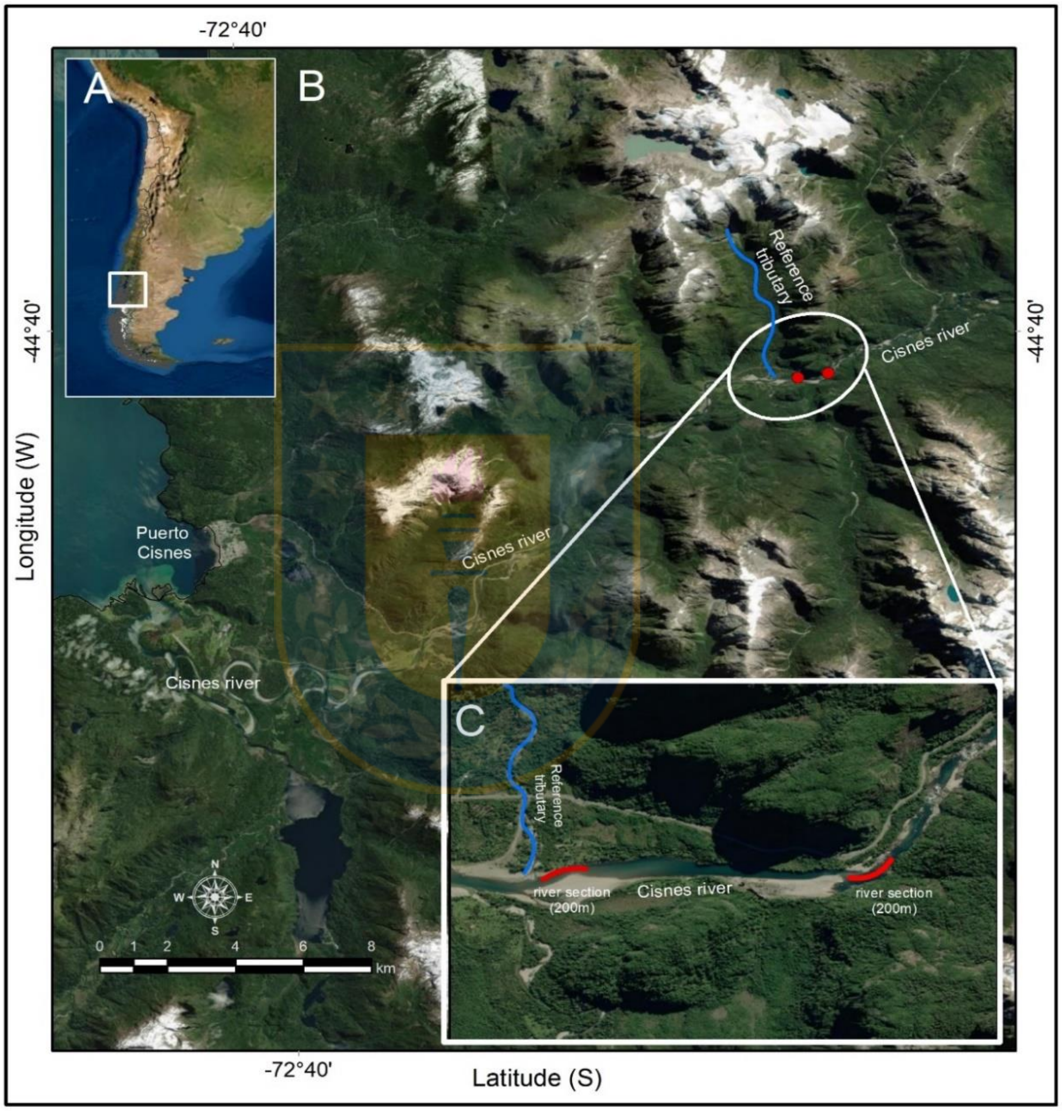

Figure 1. Study sites in Cisnes River, southern Chile, South America. Red circles and lines represent study sections with Chinook salmon spawning habitats and the blue line represents the reference tributary without Chinook salmon spawning habitats.

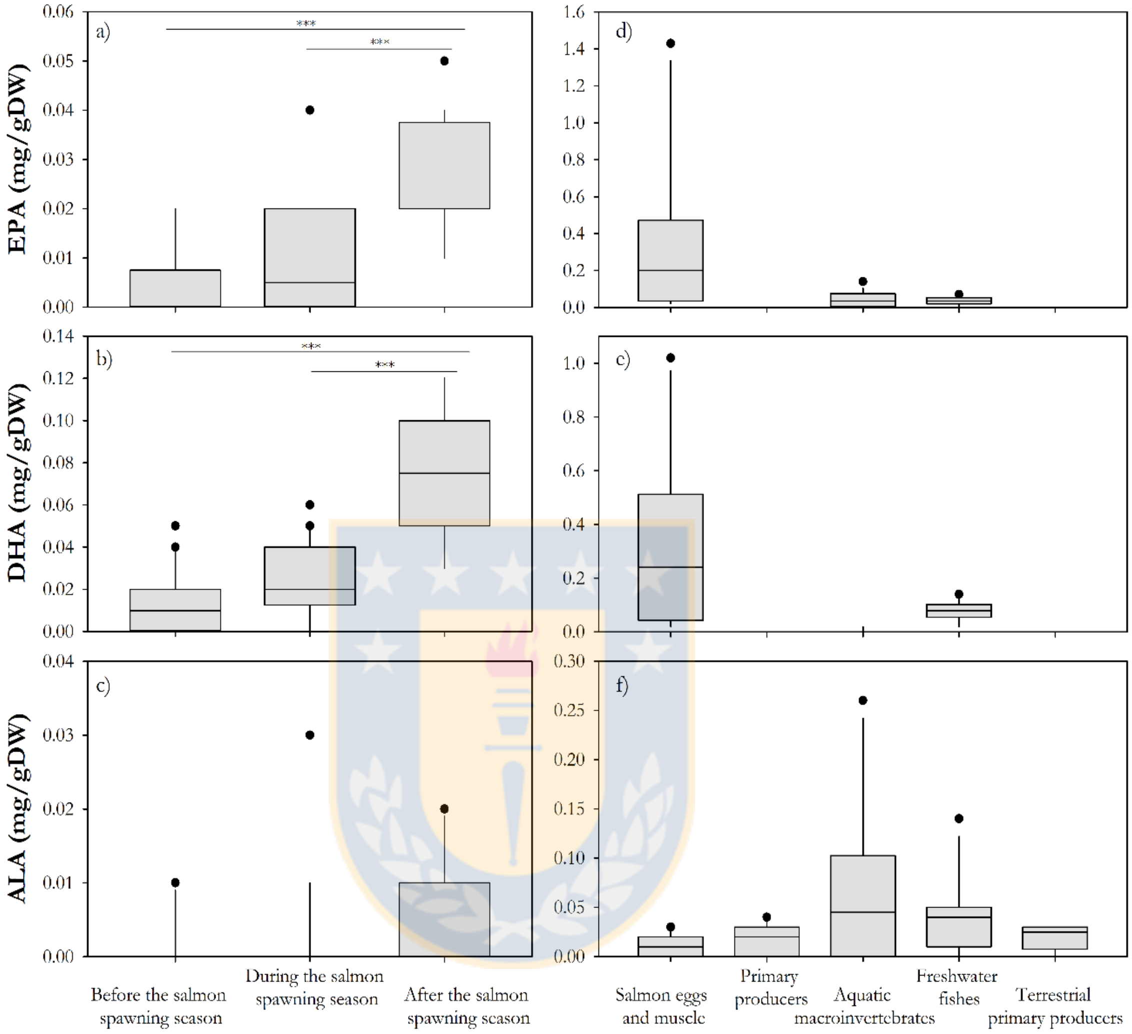

Figure 2. Boxplots of fatty acids, eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA) and α-linolenic acid (ALA) contents of the rainbow trout muscle during each period study (a-c) and food web components (d-f). Horizontal lines represent statistically significant (***denotes p-value < 0.001; and **denotes p-value < 0.01) pairwise comparisons between periods. Food web components include tissues that contain MDN as Chinook salmon eggs and muscle. Food web components from reference tributary are represent by primary producers (*Gunnera magellanica*, *Hippuris vulgaris* and unidentified species of biofilm), aquatic macroinvertebrates (Eustheniidae, Diamphipnoidae, Leptophlebiidae, Tipulidae, *Chilina* sp., *Klapopteryx* sp., *Hyalella* sp. and *Lumbricus* sp.) and juvenile's freshwater fishes (brown trout, rainbow trout, puye and Chinook salmon. Food web component from terrestrial ecosystem include primary producers (*Drimys winteri*, *Amomyrtus luma* and *Nothofagus dombeyi*).

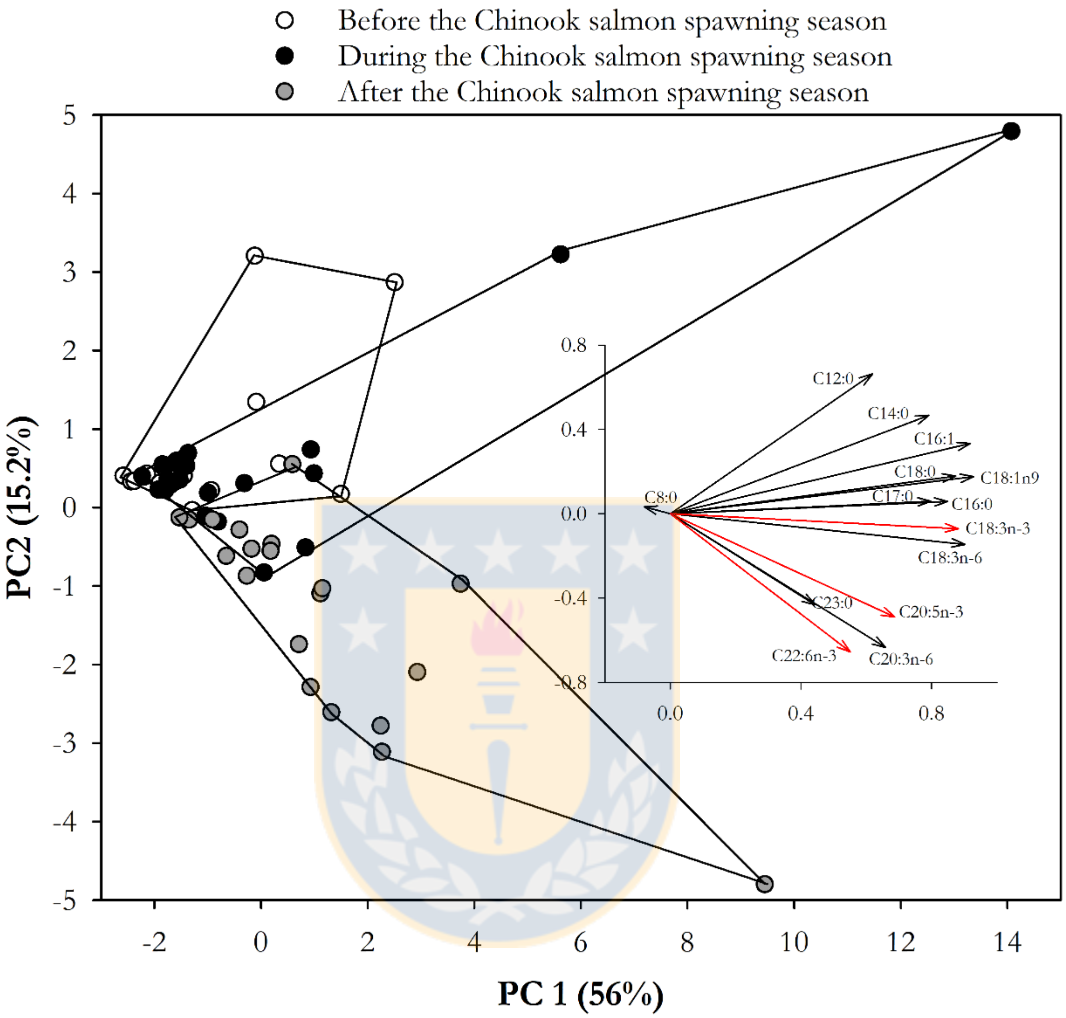

Figure 3. Principal component analysis (PCA) on all fatty acids (n = 14) of rainbow trout muscle (n = 60) during each period study. Red arrows represent eicosapentaenoic acid (20:5 n-3), docosahexaenoic acid (22:6 n-3) and α-linolenic acid (18:3 n-3).

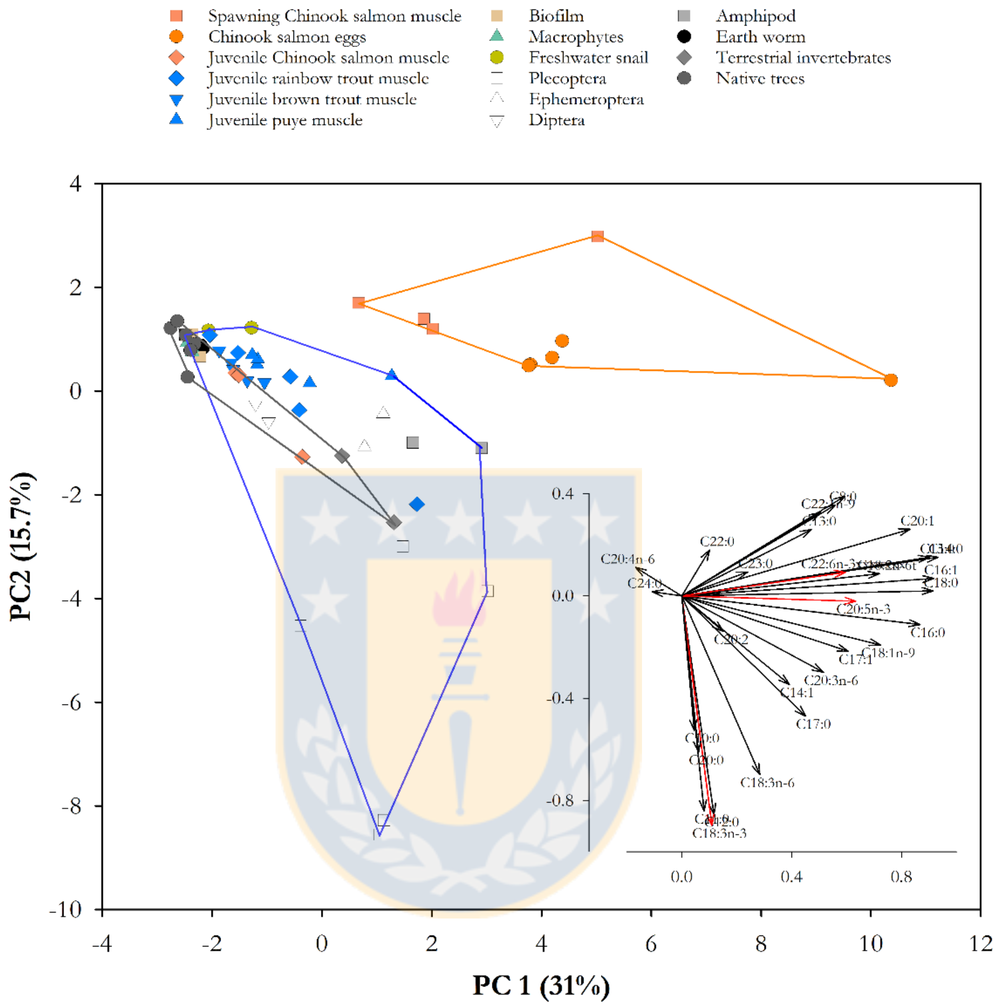

Fig. 4. Principal component analysis (PCA) on all fatty acid samples (n = 29) of food web components (n = 60) from different ecosystems origin. Food web components that contain MDN were clustering in orange. Food web components from references tributary were clustering in blue and the specific taxa that component macrophytes were *Gunnera magellanica* and *Hippuris vulgaris*; Freshwater snail was *Chilina sp*.; Plecoptera were Eustheniidae, Diamphipnoidae and *Klapopteryx* sp.; Ephemeroptera was Leptophlebiidae; Diptera was Tipulidae; Amphipod was *Hyalella* sp.; Earth worm was *Lumbricus sp*.; and Native trees were *Drimys winteri*, *Amomyrtus luma* and *Nothofagus dombeyi*. Food web components from terrestrial ecosystem were clustering in gray. Red arrows represent eicosapentaenoic acid (20:5 n-3), docosahexaenoic acid (22:6 n-3) and α-linolenic acid (18:3 n-3).

Tables

Table 1. Physicochemical characteristics (mean ± SD) of the water in the two Chinook salmon spawning study reaches and reference tributary. In each three measurements were performed in situ using a multiparameter equipment (Hanna HI9829).

	Spawning study reach 1	**Spawning study reach 2**	**Reference tributary**
Dissolved oxygen (mg/L)	11.80 ± 0.15	11.78 ± 0.06	10.34 ± 0.47
Oxygen saturation (%)	105.40 ± 1.35	105.23 ± 0.64	92.40 ± 5.07
Temperature (°C)	9.99 ± 0.07	9.69 ± 0.18	10.02 ± 0.47
pH	7.46 ± 0.09	7.35 ± 0.10	7.08 ± 0.16
Redox potential (mV)	228.13 ± 27.99	334.80 ± 12.13	166.87 ± 3.39
Conductivity (µS/cm)	36.50 ± 0.71	38.0 ± 0	27.0 ± 1.41
Total suspended solids (mg/L)	30.67 ± 21.94	19.0 ± 0	10.67 ± 4.93
Turbidity (FNU)	1.47 ± 0.31	1.17 ± 0.06	1.97 ± 3.06

Table 2. Average total mass and total length of rainbow trout before, during and after Chinook salmon spawning season captured from Chinook salmon spawning reaches. All values were presented as mean ± SD.

	Before the salmon spawning season	**During the salmon spawning season**	**After the salmon spawning season**
Total mass (g)	199.56 ± 129.0	328.95 ± 140.10	266.48 ± 94.24
Total length (cm)	26.75 ± 4.02	31.75 ± 4.23	30.27 ± 3.66

Table 3. Fatty acid and total lipid compositions (mg g DW^{-1}, mean ± sd) of marine derived subsidies, freshwater macroinvertebrates, freshwater fishes, freshwater primary producers, and terrestrial taxa.

Origin/group	**Taxa/item**	**ALA**	**EPA**	**DHA**	**Σ SAFAs**	**Σ MUFAs**	**Σ PUFAs**	**Σ HUFAs**	**Total lipids**
Marine derived subsidies	Chinook salmon eggs	0.02 ± 0.01	0.62 ± 0.46	0.55 ± 0.28	0.06 ± 0.14	0.16 ± 0.27	0.01 ± 0.01	0.03 ± 0.02	0.35 ± 0.06
	Chinook salmon muscle	0.01± 0.01	0.05 ± 0.05	0.08 ± 0.08	0.06 ± 0.16	0.13 ± 0.22	0 ± 0	0.01 ± 0.01	0.23 ± 0.10
Freshwater Macro-invertebrates	Eustheniidae	0.11 ± 0.01	0.12 ± 0.03	0 ± 0	0.04 ± 0.09	0.09 ± 0.16	0 ± 0	0.08 ± 0.10	0.19 ± 0.03
	Chilina sp.	0 ± 0	0.01 ± 0.01	0 ± 0	0.01 ± 0.01	0.01 ± 0.01	0 ± 0	0 ± 0	0.07 ± 0
	Diamphipnoidae	0.26	0.03	0 ± 0	0.05 ± 0.11	0.08 ± 0.12	0 ± 0	0.05 ± 0.07	0.19
	Klapopteryx sp.	0.22 ± 0.04	0.07 ± 0.03	0 ± 0	0.05 ± 0.09	0.06 ± 0.13	0 ± 0	0.05 ± 0.06	0.20 ± 0.02
	Leptophlebiidae	0.07 ± 0.03	0.07 ± 0.03	0 ± 0	0.04 ± 0.12	0.08 ± 0.14	0 ± 0	0.04 ± 0.05	0.15 ± 0.03
	Tipulidae	0.05 ± 0.01	0.01 ± 0.01	0 ± 0	0.02 ± 0.04	0.04 ± 0.06	0 ± 0	0.04 ± 0.05	0.10 ± 0.01
	Hyalella sp.	0.05 ± 0.01	0.06 ± 0.01	0.02 ± 0	0.02 ± 0.05	0.10 ± 0.18	0.02 ± 0	0.06 ± 0.06	0.21 ± 0.02
	Lumbricus sp.	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.01	0 ± 0	0 ± 0	0 ± 0	0.08 ± 0.01
Freshwater fishes	Muscle of juvenile rainbow trout	0.05 ± 0.05	0.03 ± 0.03	0.07 ± 0.05	0.02 ± 0.06	0.03 ± 0.07	0 ± 0	0.02 ± 0.02	0.13 ± 0.04
	Muscle of juvenile brown trout	0.03 ± 0.02	0.03 ± 0.01	0.06 ± 0.03	0.02 ± 0.04	0.02 ± 0.03	0 ± 0	0.01 ± 0.01	0.10 ± 0.03

	Muscle of juvenile whitebait	0.02 ± 0.02	0.04 ± 0.02	0.09 ± 0.03	0.02 ± 0.05	0.03 ± 0.06	0 ± 0	0.02 ± 0.02	0.11 ± 0.03
	Muscle of juvenile Chinook salmon	0.08 ± 0.05	0.05 ± 0.01	0.11 ± 0.02	0.02 ± 0.04	0.02 ± 0.04	0 ± 0	0.02 ± 0.02	0.10 ± 0.02
Freshwater primary producers	Biofilm	0.01 ± 0.01	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.01
	Macrophyte	0.03 ± 0.01	0 ± 0	0 ± 0	0 ± 0.01	0.08 ± 0	0 ± 0	0 ± 0.01	0.07 ± 0.03
Terrestrial	Macro-invertebrates	0.02 ± 0.01	0.02 ± 0.03	0 ± 0	0.06 ± 0.19	0.23 ± 0.56	0 ± 0	0.09 ± 0.13	0.29 ± 0.03
	Native trees (leaves)	0.02 ± 0.01	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.01± 0	0.10 ± 0.02

ALA, α-linolenic acid (18:3 ω-3); EPA, eicosapentaenoic acid (20:5 ω-3); DHA, docosahexaenoic acid (22:6 ω-3); Σ SAFAs, sum of saturated fatty acids (8:0, 10:0, 11:0, 12:0, 13:0, 14:0, 15:0, 16:0, 17:0, 18:0, 20:0, 22:0, 23:0 and 24:0); Σ MUFAs, sum of monounsaturated fatty acids (14:1, 16:1, 17:1, 18:1 ω-9, 20:1, 22:1 ω-9 and 24:1); Σ PUFAs, sum of polyunsaturated fatty acids (18:2 ω-6t and 20:2); Σ HUFAs, sum of highly unsaturated fatty acids (18:3 ω-6, 20:3 ω-6 and 20:4 ω-6).

Table 4. Diet composition of rainbow trout based on the coefficient of Hureau (*Q*) representing each food resources before, during and after Chinook salmon spawning season.

Phylum	Order	Taxa	Life stage	Habitat	Before the salmon spawning season	During the salmon spawning season	After the salmon spawning season
Arthropoda	Plecoptera	*Klapopteryx armillata*	Larva	Aquatic	1.05	79.32	107.85
		Klapopteryx kuscheli	Larva	Aquatic	**1142.07**	**666.09**	**4610.48**
		Diamphipnoa sp.	Larva	Aquatic	16.89	7.39	17.08
		Perlidae	Larva	Aquatic	0.00	2.16	121.63
		Gripopterygidae	Larva	Aquatic	20.64	0.00	161.42
		Udamocercia sp.	Larva	Aquatic	0.00	0.07	0.03
		Notonemoura sp.	Larva	Aquatic	0.09	0.00	0.54
	Ephemeroptera	*Andesiops torrens*	Larva	Aquatic	13.15	2.49	0.39

	Andesiops peruvianus	Larva	Aquatic	0.02	0.00	2.19
	Leptophlebiidae	Larva	Aquatic	210.63	22.31	196.94
	Murphyella sp.	Larva	Aquatic	2.25	0.00	0.04
	Chiloporter sp.	Larva	Aquatic	0.00	1.47	0.00
	Ameletopsidae	Larva	Aquatic	0.00	0.00	16.87
Diptera	Chironomidae	Larva	Terrestrial	0.63	0.01	2.42
	Chironomidae	Adult	Aquatic	1.17	0.00	0.00
	Blephabericeridae	Larva	Aquatic	0.00	0.00	16.63
	Tipulidae	Larva	Aquatic	4.35	0.00	13.65
	Limoniidae	Larva	Aquatic	1.64	0.04	1.25
	Athericidae	Larva	Aquatic	0.00	0.00	0.00
	Simuliidae	Larva	Aquatic	12.57	0.00	1.33
	Diptera	Adult	Terrestrial	0.00	0.00	9.69
Trichoptera	Leptoceridae	Larva	Aquatic	**2234.09**	0.00	**351.19**

	Sericostomatidae	Larva	Aquatic	0.16	0.16	0.70
	Smicridea sp.	Larva	Aquatic	16.97	164.41	330.66
	Limnephilidae	Larva	Aquatic	0.00	0.00	5.53
	Hydrobiosidae	Larva	Aquatic	1.03	0.05	20.41
	Ecnomidae	Larva	Aquatic	0.00	0.00	0.01
Coleoptera	Elmidae	Larva	Aquatic	0.00	0.01	0.00
	Elmidae	Adult	Aquatic	0.03	0.00	0.00
	Gyrinidae	Larva	Aquatic	0.00	0.00	0.01
	Coleoptera	Adult	Terrestrial	207.25	0.00	19.24
	Staphylinidae	Larva	Aquatic	0.02	0.00	0.25
	Hydrophilidae	Larva	Aquatic	0.00	0.01	0.00
Odonata	Odonata	Adult	Terrestrial	1.52	0.00	0.00
Hemiptera	Hemiptera	Larva	Aquatic	1.88	0.00	0.00
	Hemiptera	Adult	Aquatic	6.89	0.00	0.41
Lepidoptera	Lepidoptera	Larva	Terrestrial	0.00	0.70	0.00

	Hymenoptera	Formicidae	Adult	Terrestrial	2.08	0.00	0.00
		Apoidea	Adult	Terrestrial	67.65	15.43	0.00
		Vespidae	Adult	Terrestrial	53.30	0.00	0.00
	Ortoptera	Gryllidae	Adult	Terrestrial	6.05	0.00	0.00
		Ortoptera	Adult	Terrestrial	3.67	0.00	0.00
Entognatha	Collembola	Collembola	Adult	Aquatic	0.00	0.00	0.01
Chelicerata	Acari	Hydracarina	Adult	Aquatic	0.01	0.00	0.00
	Acari	Araneae	Adult	Aquatic	0.01	0.00	0.00
		Araneae	Adult	Terrestrial	1.21	0.17	0.00
Annelida	Oligochaeta	Oligochaeta	Adult	Aquatic	0.00	0.00	1.10
Mollusca	Gastropoda	Planorbidae	Adult	Aquatic	0.00	0.01	0.00
		Chilina sp.	Adult	Aquatic	0.00	0.00	2.65
	Pulmonata	Stylommatophora	Adult	Terrestrial	0.00	0.01	0.00
Crustacea	Isopoda	*Heterias exul*	Adult	Aquatic	0.00	0.01	0.00
	Amphipoda	*Hyalella* sp.	Adult	Aquatic	0.00	0.00	9.09

Nematomorpha	Nematomorpha	Nematomorpha	Adult	Aquatic	**2594.83**	13.43	0.01
		Vegetable remains (seeds and leaves)		Terrestrial	114.66	496.54	**516.78**
Chordata		Mouse hairs		Terrestrial	0.00	0.00	2.63
	Salmonidae	Chinook salmon eggs		Aquatic	0.00	**4286.83**	0.00

Table 5. Mean (± sd) EPA and DHA contents (% of total fatty acids) in freshwater fishes and macroinvertebrates from Cisnes River and other locations.

Taxa	Tissue	Size (mean or range length, cm)	Influence MDN	EPA	DHA	Location	Reference
Fishes							
Rainbow trout	Muscle	31.75 ± 4.23	Yes	3.67 ± 3.89	12.2 ± 7.3	Cisnes River, Chile	This study (DCSS)
		30.27 ± 3.66	Yes	9.68 ± 2.06	26.7 ± 6.4	Cisnes River, Chile	This study (ACSS)
		< 10	No	3.05 ± 2.91	9.46 ± 4.31	Cisnes River, Chile	This study (RT)
		10.9 ± 3.5	No	13 ± 3	24 ± 6	Ybbs River, Austria	Ebm et al. (2021)
Brown trout	Muscle	6.9 – 23.7	No	13.43 ± 3.16	26.17 ± 5.25	Ybbs River, Austria	Guo et al. (2022) (HQP)
		6.9 – 23.7	No	13.82 ± 2.34	25.26 ± 4.87	Ybbs River, Austria	Guo et al. (2022) (MQP)
		6.9 – 23.7	No	11.48 ± 1.46	22.26 ± 7.23	Ybbs River, Austria	Guo et al. (2022) (LQP)
Coho salmon	Muscle	4.4 – 6.7	No	1.47 ± 0.25	3.31 ± 0.61	Artificial streams	Heinz et al. (2004)
		4.4 – 6.7	Yes	6.56 ± 0.91	16.61 ± 1.94	Artificial streams	Heinz et al. (2004) (LCD)

		4.4 – 6.7	Yes	9.11 ± 0.66	20.76 ± 1.16	Artificial streams	Heinz et al. (2004) (HCD)
Macroinvertebrates							
Plecoptera	whole	-	No	4.39 ± 2.80	ND	Cisnes River, Chile	This study (RT)
Ephemeroptera	whole	-	No	4.66 ± 2.51	ND	Cisnes River, Chile	This study (RT)
Diptera	whole	-	No	0.77 ± 1.08	ND	Cisnes River, Chile	This study (RT)
Freshwater snail	whole	-	No	3.7 ± 5.23	ND	Cisnes River, Chile	This study (RT)
Amphipod	whole	-	No	4.39 ± 0.32	1.24 ± 0.04	Cisnes River, Chile	This study (RT)
Macroinvertebrates (composite)	whole	-	No	14 ± 6	ND	Ybbs River, Austria	Ebm et al. (2021)
Plecoptera	whole	-	No	15.80 ± 6.02	0.10 ± 0.11	Ybbs River, Austria	Guo et al. (2022)
Ephemeroptera	whole	-	No	16.09 ± 4.55	0.03 ± 0.03	Ybbs River, Austria	Guo et al. (2022)
Plecoptera	whole	-	Yes	15.2 ± 2.2	0.3 ± 0.1	Allan River, Scotland	Bell et al. (1994)
Ephemeroptera	whole	-	Yes	14.8 ± 1.1	ND	Allan River, Scotland	Bell et al. (1994)

Diptera	whole	-	Yes	11.6 ± 5.9	0.1 ± 0.1	Allan River, Scotland	Bell et al. (1994)
Amphipod	whole	-	Yes	12.7 ± 2.9	1.4 ± 0.6	Allan River, Scotland	Bell et al. (1994)

DCSS, during Chinook salmon spawning season; ACSS, after Chinook salmon spawning season; RT, reference tributary; HQP, fish from food web with high quality periphyton; MQP, fish from food web with middle quality periphyton; LQP, fish from food web with low quality periphyton; LCD, fish exposed to low carcass density; HCD, fish exposed to high carcass density; ND, not detected.

DISCUSIÓN GENERAL

Las invasiones biológicas forman parte de un complejo fenómeno, el cual al ser analizado desde diferentes perspectivas puede resultar tanto perjudicial, como beneficioso para los diferentes componentes de los sistemas socio-ecológicos en los que ocurren. En el caso particular de los salmónidos en Chile, su exitosa introducción ha permitido el desarrollo de actividades económicas que benefician a las personas (Arismendi and Nahuelhual 2007; Núñez and Niklitschek 2010). Sin embargo, también generan efectos negativos sobre la biota nativa, los cuales han sido estudiados en profundidad en los ambientes dulceacuícolas del sur de Chile (Penaluna et al. 2009; Arismendi et al. 2012; Ortiz-Sandoval et al. 2017). Ante esta dicotomía, es importante entender los mecanismos ecológicos que regulan la abundancia de los salmónidos en los sistemas invadidos del sur de Chile. Para ello, una dimensión clave de estudiar corresponde a las interacciones entre los salmónidos, de las cuales sólo se han estudiado las antagónicas, que incluyen depredación, competencia por recursos y establecimiento previo (Zama 1987; Arismendi et al. 2012) y se desconoce si existen relaciones del tipo sinérgicas.

Estudios previos han reportado observaciones de campo, en las cuales se describe la presencia de huevos de *O. tshawytscha* en los contenidos estomacales de *O. mykiss* en ríos invadidos del sur de Chile (Soto et al. 2007; Arismendi and Soto 2012). Para estudiar en profundidad dicha interacción, en esta tesis se utilizaron aproximaciones ecológicas y fisiológicas, que permiten postular que dicho comportamiento de alimentación constituye una interacción sinérgica unidireccional entre ambas especies, es decir, una especie se beneficia de la presencia de la otra, mientras que la otra especie no se ve influenciada en ningún sentido. Se postula ese tipo de interacción, debido a que *O. mykiss* se beneficia de la presencia de *O. tshawytscha*, consumiendo los subsidios de origen marino (huevos no viables) que produce en las tramas tróficas de los ríos, cuando retorna a desovar y luego muere (Quinn et al., 2018). Con respecto a esta interacción, *O. tshawytscha* no se ve beneficiado o perjudicado por la presencia de *O. mykiss* (Simberloff and Von Holle 1999). La disponibilidad de los huevos de *O. tshawytscha* como recurso alimenticio para *O. mykiss*, posiblemente está regulada por los mecanismos descrito para ambientes del hemisferio norte (ver introducción general; Greeley 1932; Moore et al. 2008; Quinn 2018). Por lo tanto, los huevos que son consumidos por *O. mykiss* principalmente no son viables o tienen una baja probabilidad de sobrevivencia, es por ello que su consumo no afecta a *O. tshawytscha*.

Las aproximaciones metodológicas utilizadas en esta tesis permiten sugerir que en el río Cisnes *O. mykiss* consume regularmente los huevos no viables de *O. tshawytscha* cuando están disponibles, durante la temporada de desove de la especie. Este comportamiento alimentico fue registrado durante tres temporadas de desove de *O. tshawytscha* consecutivas. En estudios realizados en el sur de

Chile, *O. mykiss* ha sido descrito como un depredador generalista y oportunista (Arismendi et al. 2012; Fierro et al. 2016), lo cual se ha evidenciado en esta tesis. Se encontraron marcados cambios en la dieta de *O. mykiss*, la cual pasa desde el consumo de macroinvertebrados acuáticos antes de la temporada de desove de *O. tshawytscha*, a casi exclusivamente huevos no viables de *O. tshawytscha*, durante su temporada de desove, para finalmente retornar a una dieta basada en macroinvertebrados acuáticos. El alto consumo de huevos no viables de *O. tshawytscha* por parte de *O. mykiss* en el río Cisnes, concuerda con los trabajos realizados sobre el consumo de huevos de salmónidos anádromos por parte de salmónidos residentes su ambiente nativo (Armstrong et al. 2010, 2013; Armstrong and Bond 2013; Jaecks and Quinn 2014). Por lo tanto, se evidencia que las interacciones existentes entre ambas especies en su ambiente nativo están resurgiendo en un ambiente invadido.

El consumo de huevos no viables de *O. tshawytscha* por parte de *O. mykiss* es beneficioso para su capacidad de sobrevivir y reproducirse (*fitness*). En esta tesis demostramos que, a partir de su consumo, se genera un aumento tanto del factor de condición de *O. mykiss*, como del contenido de los ácidos grasos poliinsaturados ω-3 eicosapentaenoico (EPA) y docosahexaenoico (DHA). El aumento en el factor de condición de *O. mykiss*, como consecuencia del consumo de los huevos de *O. tshawytscha* es consistente con estudios previos realizados en ambientes tanto nativos como invadidos del hemisferio norte (Johnson and

Ringler 1979; Armstrong and Bond 2013). Una posible explicación al aumento en el factor de condición de *O. mykiss* radica en el alto contenido energético que poseen los huevos (Armstrong et al. 2010), con respecto a las demás presas disponibles, así como también, al escaso gasto energético que supone su consumo, debido a que son principalmente derivados por la corriente (Quinn 2018).

En relación con el aumento del contenido de EPA y DHA en *O. mykiss*, en esta tesis se demuestra por primera vez que en un sistema invadido (río Cisnes) el consumo de huevos no viables de un salmónido anádromo (*O. tshawytscha*) transfiere EPA y DHA a un salmónido residente (*O. mykiss*). Este hallazgo, complementa los resultados obtenidos por Heintz et al. (2004), quienes describen dicha transferencia desde *O. gorbuscha* hacia *O. kisutch* a través del consumo de la carne de sus cadáveres en condiciones experimentales. Debido a las importantes funciones fisiológicas en las que participan el EPA y DHA, su incorporación en *O. mykiss* puede ser beneficioso para su *fitness*. Adicionalmente, se demuestra que los huevos de *O. tshawytscha* constituyen el recurso alimenticio con el mayor contenido de EPA y DHA para *O. mykiss* en la cadena trófica del río Cisnes, por lo tanto, el consumo de los huevos de *O. tshawytscha*, puede suplir la baja disponibilidad de EPA y DHA en dicha cadena trófica. Estas diferencias, posiblemente se deban a las características del ecosistema de procedencia de cada recurso alimenticio. Se ha documentado que los ácidos grasos poliinsaturados ω-3 como el EPA y el DHA, son biosintetizados principalmente por productores primarios, los cuales difieren considerablemente en su capacidad de biosíntesis de acuerdo al ecosistema de procedencia, siendo los productores primarios marinos quienes presentan los contenidos más altos de ambos ácidos grasos (Twining et al. 2016, 2021), con respecto a los productores primarios dulceacuícolas y terrestres.

Los resultados obtenidos en esta tesis proveen información de base sobre una interacción sinérgica unidireccional entre dos especies de salmónidos invasores, que co-habitan en los ecosistemas acuáticos de la zona sur de Chile. Ambas especies presentan un alto valor social, debido a los beneficios económicos generados a partir de actividades como el turismo relacionado a su pesca recreativa (Arismendi and Nahuelhual 2007; Núñez and Niklitschek 2010), y más recientemente al desarrollo de la pesquería artesanal de *O. tshawytscha*, para la cual se registró un desembarque de 61,6 toneladas en el año 2021. Es por ello, que existen varios grupos de interés en torno a ambas especies. Por lo tanto, la información proporcionada en esta tesis les brinda a las autoridades encargadas de su manejo, la posibilidad de tener un mejor entendimiento de las interacciones entre ellas. Los resultados indican que la interacción sinérgica unidireccional entre ambos salmónidos es importante para que los administradores de estas especies la consideren en futuros planes de administración pesquera en las cuencas donde co-habitan, ya que la disponibilidad de huevos de *O. tshawytscha* para *O. mykiss* podría estar controlada por una relación denso-dependiente de los reproductores en los sitios de desove (Greeley 1932; Moore et al. 2008; Quinn 2018).

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