Universidad de Concepción
Facultad de Ciencias Naturales y Oceanográficas

DIFERENCIAS TRÓFICAS ENTRE *ENGRAULIS RINGENS* (JENYNS, 1842) Y *STRANGOMERA BENTINCKI* (NORMAN, 1936), EN DOS ZONAS DE LA CORRIENTE DE HUMBOLDT

Tesis presentada a Facultad de Ciencias Naturales y Oceanográficas para
optar al grado de Magíster en Ciencias con Mención en Pesquerías

POR: BASTIÁN EDMUNDO GARRIDO ROJAS
Concepción, Chile, 2025

Profesor Guía: Leonardo Román Castro Cifuentes
Facultad de Ciencias Naturales y Oceanográficas
Universidad de Concepción

La presente tesis se realizó en el Departamento de Oceanografía de la Facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción y ha sido evaluada por la siguiente Comisión Evaluadora:

Profesor Guía

Dr. Leonardo Castro
Departamento de Oceanografía
Universidad de Concepción

Comisión evaluadora

Dr. Luis Cubillos Santander
Departamento de Oceanografía
Universidad de Concepción

Dr. Sergio Neira
Departamento de Oceanografía
Universidad de Concepción

Dr. Luis Miguel Pardo
Instituto de Ciencias Marinas y Limnológicas
Universidad Austral de Chile

Director de Programa

Dr. Billy Ernst
Departamento de Oceanografía
Universidad de Concepción

AGRADECIMIENTOS

Comenzaré agradeciendo a Dios por la vida y salud, por permitirme el desarrollo profesional.

También, agradecer a todas las personas que de una u otra forma han sido parte de este camino. Todos quienes me han sostenido y apoyado durante el periodo del Magíster, compañeros, amigos, profesores, colegas y mi familia.

Quiero dedicar un párrafo especial la familia Castillo Beltrán, quienes me abrieron las puertas de su hogar durante toda mi estadía en Concepción y transcurso del Magíster. Sin duda, ellos han sido un pilar fundamental en todo este camino, su apoyo, cariño y respeto siempre me alentaron a continuar y no decaer en el proceso.

Agradecer a mi profesor guía de tesis Leonardo Castro, por su apoyo, orientación y humildad a la hora de compartir sus conocimientos. Agradecer su compromiso, respeto y profesionalismo para conmigo, ya que siempre demostró confianza en mis capacidades, y me orientó a continuar. Finalmente, destacar su gran calidad humana a la hora de guiarme en el camino de esta tesis y los diferentes trabajos que desarrollamos en conjunto.

Agradecer al equipo LOPEL, Pamela B, Roxana L, Eduardo E, Carlos V, entre otros, que sin lugar a dudas hicieron que este camino sea mucho más ligero y confortable.

Agradecer a mi amigo, colega y compañero del Magíster, Horacio Diez, con quien comenzamos juntos este recorrido y ha sido un pilar fundamental para lograr con éxito la realización del programa. Creo que además del aprendizaje y vivencias, me llevo la amistad de bellas personas.

Finalmente, agradecer a mi familia quienes me han apoyado en todo momento, sobre todo en los tiempos más difíciles. Su contención y confianza me dieron las fuerzas necesarias para continuar día a día, aspecto fundamental para llevar a cabo un programa tan exigente como éste.

Agradecer al Magíster en Pesquerías y sus profesionales asociados por compartirme tanto conocimiento, y darme un sin número de nuevas herramientas educativas que permitirán continuar mi desarrollo profesional a futuro.

AGRADECIMIENTOS INSTITUCIONALES

Agradecer a todas las instituciones que me brindaron apoyo y sustento durante todo el desarrollo de esta tesis y mi estadía en el programa de Magíster.

Agradece al Centro COPAS Coastal por el apoyo financiero durante 1 año y medio de mi estadía, por financiar parcialmente los análisis de muestras de isótopos, mis viajes a congresos nacionales e internacionales, y por su confianza sistemática en mis cualidades estudiantiles.

Agradecer al LOPEL por proveer de apoyo financiero y con muestras para el desarrollo de esta tesis. Agradecer a INPESCA e IFOP por proveer las muestras requeridas para esta tesis, y a Gabriel Claramunt y su equipo de trabajo por proveerme las muestras y mediciones de Iquique. Agradecer a la tripulación de la embarcación Kay Kay II, por su apoyo y guía durante los embarques realizados en la zona costera del Bio Bio, donde pudimos obtener las muestras necesarias para la realización de esta tesis.

Finalmente, agradecer a la Universidad de Concepción, el Departamento de Oceanografía y todas las instituciones que fueron parte del apoyo recibido para finalizar este trabajo.

TABLA DE CONTENIDO

INDICE DE TABLAS

INDICE DE FIGURAS

Resumen

El Sistema de la Corriente de Humboldt (SCH) es uno de los ambientes marinos más productivos del mundo, que sustentado por el ascenso de aguas subsuperficiales ricas en nutrientes que ascienden hasta la capa fótica, sostiene una de las actividades pesqueras más productivas del mundo. *Engraulis ringens* y *Strangomera bentincki* representan dos especies de importancia comercial para la flota artesanal e industrial de Chile. Especies con un amplio rango de distribución latitudinal como la anchoveta, se ven expuestas a condiciones ambientales diversas, a cambios en la disponibilidad de alimento y a cambios en la estructura trófica de los ecosistemas. La Zona Sur del SCH se caracteriza por presentar una marcada estacionalidad de las condiciones ambientales y oceanográficas, con un aporte estacional variable de nutrientes a través de los ríos, lo cual contrasta con la Zona Centro del SCH, donde los efluentes de agua dulce son escasos, y las condiciones ambientales de surgencia costera son persistentes a lo largo de todo el año. Cómo estas variaciones ambientales (latitudinales y estacionales) afectan la ecología trófica de estos peces pelágicos pequeños, es todavía poco conocido.

De manera reciente los isótopos estables (IE) de carbono y nitrógeno se han aplicado para estudiar la estructura de las tramas tróficas en los ecosistemas marinos. Las señales de nitrógeno ($\delta^{15}N$) son indicadoras del nivel trófico de los organismos, mientras que señales de carbono ($\delta^{13}C$) se emplean para identificar las fuentes de carbono orgánico que sustenta los consumidores, permitiendo identificar posibles variaciones estacionales en el uso del hábitat. Ambos IE pueden proporcionar información clave sobre la estructura trófica del ecosistema, las interacciones entre especies, y la asimilación de presas.

Empleando análisis de isótopos estables de $\delta^{13}C$ y $\delta^{15}N$ se analizó la variabilidad estacional en la ecología trófica de *E. ringens* y *S. bentincki* de dos zonas latitudinalmente distantes del Sistema de la Corriente de Humboldt: (Iquique 20°S, SCH Centro) y (Talcahuano 36°S, SCH Sur). El patrón de las condiciones ambientales estuvo acorde a lo descrito para ambas zonas, se observó un patrón más estable en el SCH Centro, mientras que en el SCH Sur las condiciones ambientales variaron estacionalmente. Las señales isotópicas de $\delta^{13}C$ y $\delta^{15}N$ variaron estacionalmente en los diferentes grupos funcionales muestreados (POM, Copépodos y Peces) de ambas zonas del estudio. Los resultados muestran que la anchoveta de ambas zonas mostró rangos estrechos de variaciones estacionales de $\delta^{13}C$ (SCH central: -17,5‰ a -17,85‰; SCH sur: -15,53‰ a -15,85‰) pero marcadas diferencias entre zonas. Las anchovetas del SCH centro mostraron un rango inter-estacional más amplio en los valores de $\delta^{15}N$ (SCH central: 16,68‰ a 20,72 ‰; SCH sur: 16,70‰ -17,59‰), así como una amplitud trófica más amplia, donde el tamaño del Nicho Isotópico de anchoveta en la zona SCH centro fue alrededor de 3 veces superior al tamaño del nicho de la anchoveta en el SCH sur.

El solapamiento del nicho en la zona sur del SCH varió estacionalmente entre *E. ringens* y *S. bentincki* (mayor en verano (68,87% anchoveta, 97,69% S. común) y menor en invierno (30,62% anchoveta, 85,67% S. común)) acorde con la disponibilidad de alimento. Los valores del TP fueron mayores y más estables durante el año en la zona sur (excepto verano). El TP de *E. ringens* fue superior al TP de S. *bentincki* durante todas las estaciones del año.

Los resultados sugieren que aspectos tróficos asociados a variaciones ambientales pueden constituir mecanismos que impulsan la dinámica entre poblaciones de una misma especie en diferentes zonas latitudinalmente

distantes. Este es el primer trabajo que considera la componente estacional en la ecología trófica de *E. ringens* y *S. bentincki* en el SCH. Resulta interesante comprender el rol de los peces pelágicos pequeños en el ambiente marino, las relaciones tróficas interespecíficas y su relación con las condiciones ambientales, ya que entregan información complementaria sobre la dinámica costera, el flujo de energía entre los niveles tróficos y aporta conocimiento fundamental para mejorar la gestión integrada de las pesquerías, cada vez más relevante en un contexto cambiante actual (debido a las modificaciones ambientales de distintas escalas espaciales y temporales (e.g cambio climático) o variaciones directas de origen antropogénico (presión pesquera)).

ABSTRACT

The Humboldt Current System (HCS) is one of the most productive marine environments in the world, sustained by the upwelling of nutrient-rich subsurface waters that ascend to the photic layer, sustaining one of the most productive fishing activities in the world. *Engraulis ringens* and *Strangomera bentincki* represent two species of commercial importance for

Chile's artisanal and industrial fleet. Species with a wide latitudinal distribution range, such as anchoveta, are exposed to diverse environmental conditions, changes in food availability and changes in the trophic structure of ecosystems.

The South Zone of the HCS is characterized by a marked seasonality of environmental and oceanographic conditions, with a variable seasonal input of nutrients through rivers, which contrasts with the Central Zone of the HCS, where freshwater effluents are scarce, and coastal upwelling environmental conditions are persistent throughout the year. How these environmental variations (latitudinal and seasonal) affect the trophic ecology of these small pelagic fishes is still poorly understood.

Recently, stable isotopes (SI) of carbon and nitrogen have been applied to study the structure of trophic webs in marine ecosystems. Nitrogen signals ($\delta^{15}N$) are indicators of the trophic level of organisms, while carbon signals ($\delta^{13}C$) are used to identify the sources of organic carbon supported by consumers, allowing the identification of possible seasonal variations in habitat use. Both SI can provide key information on the trophic structure of the ecosystem, species interactions, and prey assimilation.

Using stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$, the seasonal variability in the trophic ecology of *E. ringens* and *S. bentincki* from two latitudinally distant areas of the Humboldt Current System were analyzed: (Iquique 20°S, HCS Central Zone) and (Talcahuano 36°S, HCS South Zone). The pattern of environmental conditions was in accordance with what was described for both zones, a more stable pattern was observed in the Central HCS, while in the South HCS the environmental conditions varied seasonally. The $\delta^{13}C$ and $\delta^{15}N$ isotopic signals varied seasonally in the different functional groups sampled (POM, Copepods and Fish) from both zones of the study. The results show that anchovy from both zones showed narrow ranges of seasonal variations of $\delta^{13}C$ (central HCS: -17.5‰ to -17.85‰; south HCS: -15.53‰ to -15.85‰) but marked differences between zones. The anchovy in the central HCS showed a wider inter-seasonal range in $\delta^{15}N$ values (central HCS: 16.68‰ to 20.72 ‰; south HCS: 16.70‰ -17.59‰), as well as a wider trophic breadth, where the anchovy Isotopic Niche size in the central HCS zone was about 3 times larger than the anchovy niche size in the south HCS.

Niche overlap in the southern zone of the HCS varied seasonally between *E. ringens* and *S. bentincki* (higher in summer (68.87% anchovy, 97.69% S.

común) and lower in winter (30.62% anchovy, 85.67% S. común)) according to food availability. TP values were higher and more stable during the year in the southern zone (except summer). The TP of *E. ringens* was higher than that of *S. bentincki* during all seasons.

The results suggest that trophic aspects associated with environmental variations may constitute mechanisms that drive the dynamics between populations of the same species in different latitudinally distant areas. This is the first work that considers the seasonal component in the trophic ecology of *E. ringens* and *S. bentincki* in the HCS. It is interesting to understand the role of small pelagic fishes in the marine environment, the interspecific trophic relationships and their relationship with environmental conditions, since they provide complementary information on coastal dynamics, energy flow between trophic levels and contribute fundamental knowledge to improve integrated fisheries management, increasingly relevant in the current changing context (due to environmental modifications of different spatial and temporal scales (e.g. climate change) or direct variations of anthropogenic origin (fishing pressure)).

INTRODUCCIÓN GENERAL

Dentro de la agenda al 2030 para los Objetivos de Desarrollo Sostenible (ODS) se establece un marco de referencia universal para utilizar de manera sustentable los recursos marinos y el océano, avanzando en la ordenación pesquera y su regulación (Naciones Unidas, 2018). Según la Organización de las Naciones Unidas para la Alimentación y la Agricultura (FAO) el consumo humano de recursos acuáticos sigue aumentando, mientras que la proporción de peces marinos explotados dentro de niveles biológicamente sostenibles ha descendido hasta un 62.3% en el año 2021 (FAO, 2024). Tradicionalmente, la gestión pesquera se ha centrado en la sostenibilidad de especies con importancia comercial, ignorando a menudo importantes consideraciones del ecosistema tales como las interacciones entre especies, los cambios en la estructura del ecosistema y sus graves impactos, así como aspectos tróficos esenciales (Link 2002). Cambios en la estructura del ecosistema debido a la intensa explotación pueden aumentar la vulnerabilidad de las poblaciones marinas, provocando que muchos recursos pesqueros puedan ser sobreexplotados o agotados hasta niveles cercanos al colapso (Planque et al., 2010; Pitcher y Cheung, 2013).

Los sectores orientales del océano Pacífico y Atlántico en latitudes subtropicales abarcan grandes áreas de afloramiento costero (Sydeman et al. 2014). Este proceso se caracteriza por un transporte vertical relativamente poco profundo de masas de agua hacia la superficie (Talley et al. 2011). Particularm dente, el Sistema de la Corriente de Humboldt (SCH) en el sureste del Océano Pacífico es una de las áreas marinas más productivas del planeta en términos de producción de peces (Thiel et al., 2007), sustentado por un constante ingreso de nutrientes desde aguas subsuperficiales ricas en nutrientes a la capa fótica, producto del afloramiento costero.

En Chile la intensidad del fenómeno de surgencia costera asociado al SCH varía latitudinalmente. El sistema de surgencia de la zona del Centro del SCH (18ºS - 23ºS) se caracteriza por la ocurrencia permanente de eventos de surgencia durante todo el año, debido a la influencia de vientos débiles, pero persistentes, que fluyen en dirección al Ecuador, y que se intensifican durante primavera-verano (Blanco et al., 2001, Fuenzalida 1990). Algo diferente ocurre en la zona sur del SCH (30°S - 40°S), donde se distingue una marcada estacionalidad en las condiciones ambientales, con eventos de surgencia costera más intensos durante la primavera y verano austral (Gutiérrez et al., 2012, 2017), periodo del año donde dominan los fuertes vientos del sur, y que derivan en un ascenso y transporte de aguas frías subsuperficiales de origen ecuatorial a la zona fótica, con un alto contenido de nitratos y bajo contenido de oxígeno disuelto desde zonas más profundas (Yáñez et al., 2012). Por el contrario, durante los meses de otoño e invierno austral, existe un debilitamiento del viento sur, prevaleciendo condiciones de convergencia costera (no surgencia), con agua de baja salinidad cerca de la superficie debido a lluvias, escorrentía e ingreso de agua dulce proveniente de ríos (Iriarte et al., 2012).

Históricamente, ambas zonas han estado ligadas al desarrollo de intensas actividades pesqueras vinculadas a Peces Pelágicos Pequeños (PPP). Particularmente, la anchoveta o *Engraulis ringens* (Jenyns, 1842), ha sido una de las principales especies objetivos (Gutierrez-Estrada et al., 2007; Freon et al., 2008). El stock de la zona norte de Chile es compartido con Perú, considerándose una pesquería transfronteriza de alta importancia productiva, ya que los desembarques promedios bordean casi 1 millón de toneladas, y representan un ~8% de los desembarques mundiales de PPP (Canales & Cubillos 2021). Diferencialmente, el stock de anchoveta de la zona centro-sur de Chile, es mucho más pequeño y se encuentra constituyendo una pesquería mixta con la sardina común o *Strangomera* *bentincki* (Norman, 1936), un clupeido endémico (Cubillos et al., 2002). Ambas especies sustentan actividades productivas de la flota industrial y artesanal a lo largo de la costa chilena (Castillo et al., 2001; Cubillos et al., 2002; Cubillos et al., 2007a), siendo considerados recursos de alta importancia socioeconómica (Silva & Pequeño, 2007).

E. ringens se distribuye en un amplio rango latitudinal a lo largo del SCH, desde el norte de Perú (Zorritos 4°30′S) hasta el sur de Chile (Chiloé 42°30′S) (Claramunt et al., 2012). A lo largo de su distribución se identifican varias unidades de stock, entre las que destacan el stock del centro-norte del Perú (4ºS - 14ºS), el stock del sur del Perú y norte de Chile (16ºS - 24ºS), el stock que se distribuye en la zona centro-norte (25ºS - 32ºS), entre Caldera y Coquimbo, y otro localizado en el Centro-sur de Chile (34ºS - 41°S) (Alheit y Ñiquen 2004). Por el contrario, *S. bentincki* tiene una distribución más restringida, desde Coquimbo (29°S) hasta Puerto Montt (42°S) (Cubillos et al., 2001). Ambas especies se agregan en cardúmenes de aguas relativamente costeras y poco profundas (Gerlotto et al., 2004), mostrando características biológicas similares en términos de distribución espacial, crecimiento, época de reproductiva, áreas de desove y época de reclutamiento (Cubillos et al., 2001, 2007a). La época de desove en ambas especies tiende a ocurrir en invierno (hemisferio sur) y se extiende de julio a septiembre, con un pico entre agosto y septiembre, para que luego de tres o cuatro meses los juveniles sobrevivientes se incorporan a la población explotada (reclutamiento) (Cubillos et al.,1999, 2001, 2002).

Ambas especies cumplen un rol esencial en el ambiente marino costero, ya que debido a su importante biomasa en los niveles intermedios de la trama trófica, posibilitan la conexión entre los niveles tróficos inferiores y superiores, y por tanto, son claves en el flujo de energía del ecosistema (Cury et al., 2000; Pikitch et al., 2012). A pesar de que estos peces forrajeros se caracterizan por ser especies de vida corta y presentar recambios reproductivos rápidos, son especies sensibles a la variaciones ambientales y al cambio climático impulsado por variaciones climáticas de gran escala (Nakayama et al., 2017; Canales et al. , 2020; Molina-Valdivia et al., 2020).

Las características ambientales varían latitudinalmente entre las dos zonas de estudio (desde la zona cálida del norte de Chile hasta áreas más frías en la zona centro-sur), lo que repercute también en los rasgos de historia de vida (por ejemplo, estacionalidad del desove, tamaño del huevo, el contenido de lípidos y proteína, el éxito de eclosión, tasas de crecimiento larvario, etc)

(Llanos-Rivera & Castro 2004, 2006; Castro et al., 2009; Claramunt et al., 2014; Castro et al., 2020). La zona norte de Chile se caracteriza porque el aporte de agua dulce al sistema marino costero es casi nulo durante la mayor parte del año debido a la ausencia de lluvias. Por el contrario, en la zona centro-sur, la entrada de agua dulce es estacionalmente marcada, con un input mayor durante el invierno y una disminución más tarde en primavera-verano. Se sabe que la escorrentía, y el aporte de los ríos afecta los diversos procesos físicos, químicos y biológicos que ocurren en la columna de agua de regiones costeras (Masotti et al., 2018; Saldías & Lara 2020), afectando con ello a especies pelágicas, sus presas y su composición isotópica (Castro et al., 2020).

Diferencias latitudinales y estacionales en las condiciones ambientales afectan distintamente los ecosistemas marinos a lo largo del SCH, provocando cambios en la disponibilidad del plancton y en las fuentes alimenticias de las especies forrajeras. Diversos estudios tróficos han evaluado la dieta de *E. ringens* y *S. bentincki* en el SCH (Arrizaga et al. 1993, Espinoza & Bertrand 2008; Medina et al. 2015, Nuñez et al. 2018). Sin embargo, la mayor parte de estos estudios se basan en técnicas tradicionales de análisis de contenido estomacal, que únicamente representan el período entre la ingestión y la digestión del alimento (escala de tiempo corta, horas) (Petersen y Fry 1987; Hobson et al., 1996; Madirolas et al., 2000), y no identifica los componentes que realmente son asimilados por los organismos en distintos tiempos de integración (Duffy y Jackson 1986). Recientemente, estudios de análisis de isótopos estables (IE) de Carbono ($\delta^{13}C$) y Nitrógeno ($\delta^{15}N$) en la zona (Espinoza et al. 2017; Pizarro et al. 2019), han permitido ampliar nuestra comprensión de las relaciones tróficas de los PPP en el SCH. Específicamente, los isótopos de $\delta^{15}N$ son buenos indicadores del nivel trófico de las especies, mientras que los valores de $\delta^{13}C$ indican ciertas características del hábitat, posibilitando la discriminación entre diferentes fuentes de producción primaria y con ello seguir posibles variaciones estacionales o explorar diferencias espaciales entre localidades (Fry 2006). Ambos isótopos en conjunto, permiten estudiar diferentes aspectos tróficos de las especies y el ecosistema, caracterizar relaciones interespecíficas y calcular el espacio o nicho trófico de los organismos (Layman et al. 2007, Jackson et al. 2011).

Estudios sobre la composición isotópica en peces costeros de Chile señalan diferencias entre especies y posiblemente entre poblaciones. Sin embargo, estos estudios no han podido determinar diferencias tróficas estacionales, ni su relación con las condiciones ambientales propias del SCH, debido a que no lograron obtener un número de muestras consistentes durante las diferentes estaciones del año, o un lapso de tiempo considerable, utilizaron diferentes tejidos y fuentes basales para el cálculo por ejemplo de la Posición Trófica, entre otras limitaciones (Espinoza et al., 2017, Pizarro et al., 2019, Wiesebron et al., 2022, Cárcamo et al., 2024). De este modo, a pesar de estos avances sobre componente trófica de los PPP en diferentes zonas del SCH, sigue existiendo un importante desconocimiento de muchos aspectos asociados a la ecología trófica de *E. ringens* y *S. bentincki*. La diferencia latitudinal y el efecto de las condiciones ambientales sobre las fuentes alimenticias, la variabilidad trófica estacional de estas especies y los mecanismos tróficos que posibilitan la coexistencia de *E. ringens* y *S. bentincki* en la zona centro-sur de Chile, sobre todo en épocas con poca disponibilidad de alimento, son sólo algunos de los aspectos que siguen siendo poco conocidos.

Para avanzar en la comprensión de estas problemáticas y determinar el rol trófico de estas especies en el ecosistema costero pelágico, esta tesis empleó métodos basados en el análisis de isótopos estables de carbono y nitrógeno ($\delta^{13}C$ y $\delta^{15}N$) para evaluar aspectos esenciales de la ecología trófica de anchoveta y sardina común (amplitud y solapamiento del Nicho Isotópico, su variabilidad estacional y la relación con variables ambientales) durante las 4 estaciones del año, en dos zonas del SCH (norte de Chile (Iquique, 20° S) y centro-sur de Chile (Talcahuano, 36° S)). Este estudio consideró de manera complementaria el muestreo de Material Orgánico Particulado (POM) desde la columna de agua y de organismos zooplanctónicos esenciales en la dieta de estas especies forrajeras (Copépodos), información clave para entender la dinámica estacional de la trama trófica marina pelágica.

Planteamiento del problema

Las variaciones latitudinales y estacionales en las condiciones ambientales y oceanográficas a lo largo del ecosistema costero chileno (una zona norte más cálida, con mayor estabilidad en las condiciones de surgencia costera y un aporte mínimo de ríos, mientras que una zona centro-sur con marcada estacionalidad en la surgencia costera, con eventos más intensos durante primavera y verano, además de un alto aporte de agua dulce proveniente de fuentes terrestres como ríos) han mostrado influir en la composición isotópica de algunos grupos taxonómicos (copépodos) que constituyen presas potenciales de anchovetas en la zona centro y sur del SCH. Estas diferencias isotópicas han sido reportadas adicionalmente en estadios tempranos (huevo y larvas) de anchoveta (Castro et al., 2020) lo que sugiere que la oferta alimenticia para los adultos de peces podría determinar la composición isotópica de sus tejidos y determinar las variaciones tanto estacionales así como inter-poblacionales (latitudinales), aspectos que aún no han sido comprobados. El presente estudio propone las siguientes hipótesis:

HIPÓTESIS

H1: Los valores isotópicos de $\delta^{13}C$ y $\delta^{15}N$ en componentes base de la trama trófica que sostienen a *Engraulis ringens* (POM, Copépodos) difieren latitudinal y estacionalmente entre zonas, debido a la diferencias geográficas y ambientales de cada zona.

H2: Los valores isotópicos ($\delta^{13}C$ y $\delta^{15}N$) de *Engraulis ringens*, presentan menor variabilidad inter-estacional en la zona centro del SCH o norte de Chile, debido a la menor variabilidad ambiental de la zona, mientras que en la zona centro del SCH o centro-sur de Chile existirá una notoria variabilidad inter-estacional en los valores de $\delta^{13}C$ y $\delta^{15}N$ de anchoveta, debido a la condición estacional que caracteriza la zona.

H3: La amplitud y solapamiento del Nicho Isotópico difiere inter-estacionalmente entre *Engraulis ringens* y *Strangomera bentincki* de la zona centro–sur de Chile, lo que facilitaría su coexistencia, especialmente en periodos con menor disponibilidad de alimento.

OBJETIVOS

2.1 Objetivo General

Evaluar aspectos esenciales de la ecología trófica de *Engraulis ringens* y *Strangomera bentincki*, durante las 4 estaciones del año entre dos zonas del SCH (norte de Chile (Iquique, 20°S) y centro-sur de Chile (Talcahuano, 36°S)), mediante la utilización de isótopos estables de $\delta^{13}C$ y $\delta^{15}N$.

2.2 Objetivos específicos

- **1-** Determinar la variabilidad isotópica estacional de $\delta^{13}C$ y $\delta^{15}N$ los diferentes grupos funcionales de la trama trófica (POM, Copépodos y Peces) en ambas zonas del estudio.
- **2-** Utilizando los valores de $\delta^{15}N$ calcular la Posición Trófica (PT) de *E. ringens* y *S. bentincki* durante las 4 estaciones del año en las dos zonas de estudio.
- **3-** Determinar la amplitud y solapamiento del Nicho Isotópico de *E. ringens* y *S. bentincki* durante las 4 estaciones del año.
- **4-** Relacionar y contrastar estacionalmente las señales isotópicas de $\delta^{13}C$ y $\delta^{15}N$ de ambas especies con las variables oceanográficas de las dos zonas de estudio.

CAPITULO 1

Feeding responses to seasonal and latitudinal variations in environmental conditions revealed by stable isotopes in anchovy (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) in the central and south Humboldt Current System.

Garrido Bastián [1, 2], Castro Leonardo [1, 2], Vásquez Sebastián I.[3,4], Gabriel Claramunt [5]

[1] Programa de Magíster en Ciencias con Mención en Pesquerías, Departamento de Oceanografía, Universidad de Concepción, Concepción, Chile. bastian.egarrido@gmail.com

[2] COPAS COASTAL, Departamento de Oceanografía, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción , Chile. lecastro@oceanografia.udec.cl

[3] Departamento de Pesquerías, Instituto de Investigación Pesquera, Talcahuano 4260000, Chile, svasquez@inpesca.cl

[4] Programa de Doctorado en Oceanografía, Universidad de Concepción, Concepción, Chile

5 Universidad Arturo Prat, Iquique, Chile.

Artículo enviado a Marine Ecology Progress Series

ABSTRACT

To improve the understanding of aspects of the trophic ecology of anchovy and common sardine in two areas of the Humboldt Current System (central HCS (20°S) and south HCS (36°S), north and central Chile) we evaluating their seasonal trophic variations and their trophic niche overlap using the stable isotopes $\delta^{13}C$ and $\delta^{15}N$. In addition, the inter-seasonal variability of stable isotopes at different levels of the food web up (POM, copepods, fish) were related the variations of local environmental conditions. The results show that the anchovy from both zones showed narrow ranges of $\delta^{13}C$ seasonal variations (central HCS: - 17.5‰ to -17.85‰ ; south HCS: - 15.53‰ to -15.85‰) but marked differences between zones. Anchovies from the north HCS zone showed a wider inter-seasonal range in $\delta^{15}N$ values (central HCS: 16.68‰ to 20.72 ‰; south HCS: 16.70‰-17.59‰) as well as a wider trophic amplitude (shown by the size of the isotopic niche) compared to anchovies at the south HCS zone. In the south HCS zone, the isotopic values of common sardine and anchovy, showed scarce inter-seasonal variability and relatively stable trophic positions during the year (TP anchovy: 3.15 - 3.43, TP common sardine: 3.08-3.28), being those of common sardine slightly lower than in anchovy. However, the size of the isotopic niche in both species changed inter-seasonally, as did the trophic overlap between them, being winter (low plankton abundance), the period of year with the lowest trophic overlap between species suggesting a trophic partitioning to overcome periods of reduced food availability.

Key words: Small Pelagic Fishes, Trophic ecology, Stable isotopes, Upwelling, Humboldt Current System.

1. INTRODUCCIÓN

The Humboldt Current System (HCS) is the most productive eastern boundary upwelling system in the world (Oerder et al. 2015). The environmental and oceanographic conditions that characterize this ecosystem have facilitated intense fishing activities along the coasts of Chile and Peru (FAO 2024). One of the most important fisheries worldwide is supported by the exploitation of Small Pelagic Fish (SPF), mainly Engraulis ringens, which in terms of catch represents the most important monospecific fishery worldwide (FAO 2024).

In Chile, *E. ringens* (anchovy) and *Strangomera bentincki* (common sardine) are ecologically important due to their role in structuring the coastal pelagic community and economically because they support an intense fishery (Cubillos et al. 2007a, Canales & Cubillos 2021). Both pelagic fish species play a key ecological role in the trophic webs of upwelling ecosystems (Cury et al. 2000), as they represent the main pathway in the flow of energy from lower and middle trophic levels to higher ones (Pikitch et al. 2012, Hilborn et al. 2017). Understanding the interactions of these forage species is fundamental for assessing the dynamics of their marine populations which is key for their sustainable management.

The anchovy has a wide latitudinal distribution range along the HCS, ranging from northern Peru (Zorritos 4° 30′S) to south Chile (Chiloé 42° 30′S) (Claramunt et al. 2012). Three main stocks can be recognized throughout its range: the largest is found in northern Peru, followed by shared central stock from southern Peru - northern Chile and finally, the southern and smallest in central-south Chile. Evidently, the environmental characteristics vary significantly along the wide latitudinal range, from a warm subtropical region in the north to a cold fjord system in northern Patagonia. In contrast, the common sardine has a much more restricted distribution in central-south Chile, from Coquimbo (29°S) to Puerto Montt (42°S) (Cubillos et al. 2001).

Fluctuations in environmental conditions at different time and space scales affect the dynamics of these marine resources. Particularly, SPF are species sensitive to environmental variability during all stages of their life cycle (Cubillos et al. 2007a, Castro et al. 2009, Canales et al. 2020, Castro et al. 2020). Along Chile, environmental conditions change latitudinally from the northern zone, characterized by continuous upwelling during most of the year that cause a favorable feeding environment for SPF (Blanco et al. 2001, Fuenzalida 1990), almost inexistent rain precipitations and very scarce river inputs to the coastal zone, to a central-south zone with a marked seasonality in environmental conditions, with intense coastal upwelling events during spring and summer, and with a significant input of freshwater flows from rivers in winter (Gutiérrez et al. 2012, 2017, Saavedra et al. 2014).

The diverse environmental characteristics that affect coastal marine ecosystems along the HCS drive changes in the food sources for these forage species. Initial trophic studies assessing the diet and feeding of these fishes revealed a high consumption of phytoplanktonic (numerically) (Arrizaga et al. 1993, Espinoza & Bertrand 2008, Medina et al. 2015, Nuñez et al. 2018). However, recent studies have complemented traditional stomach content analysis techniques with stable isotope (SI) analyses have been able to determine that zooplankton organisms are much more important in the diet in terms of carbon assimilated (Espinoza et al. 2017, Pizarro et al. 2019). Despite these advances, several aspects of the trophic ecology of *E. ringens* and *S. bentinc*ki remain unclear, for instance, their seasonal dynamics, the effect of oceanographic conditions, and the trophic interactions between these co-occurring species.

The use of nitrogen and carbon stable isotopes allows the study of trophic relationships over relatively long periods of time, depending on the assimilation rate of organisms (Martínez del Río et al. 2009). Specifically, $\delta\ ^{15}N$ may be used to assess the trophic level of the species, while $\delta\ ^{13}C$ may be used to discriminate between different sources of organic carbon derived from primary producers and thereafter, reveal seasonal variations in carbon consumed by SPF or explore differences between localities (Fry 2006). When used together it is possible to study trophic aspects of the species and of the ecosystem such as characterizing interspecific relationships, estimating the trophic space or niche overlap among organisms (Layman et al. 2007, Jackson et al. 2011).

In central-south Chile, anchovy and common sardine cohabit and are considered a mixed fishery, with high biomass discharges throughout the year sustained by high levels of primary productivity induced by coastal upwelling and nutrient inputs to the photic layer mainly during spring and summer (Chavez et al. 2008). Aspects of the trophic ecology of these SPF and the seasonal dynamics of food sources are key aspects to determine the trophic mechanisms that facilitate their coexistence, especially in times of lower food availability (autumn and winter). Although previous studies have applied stable isotope analyses in small pelagic fishes along the HCS, no studies have assessed the seasonal variability of $\delta^{13}C$ and $\delta^{15}N$ in adult fishes, their food sources and their relationship with environmental variables along the year. Variations of the trophic position (TP), trophic amplitude, and trophic overlap during the year may be relevant aspects to elucidate their coexistence and the sustainable management of the fishery.

This study utilized carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to determine three aspects of the trophic ecology of anchovy and common sardine (trophic position, amplitude and overlap of the Isotopic Niche (IN)), and their relationship with environmental variables during 4 seasons, in two areas of the HCS: central HCS (Iquique, 20°S) and south HCS (Talcahuano, 36°S) in Chile. We hypothesized that, because of the seasonal variations in oceanographic conditions of the south HCS (ie. coastal upwelling, freshwater input from rivers, etc.), there will be a wider inter-seasonal variability in the isotopic values of potential food sources and in anchovy and common sardine in this south HCS zone, while in the central HCS zone the inter-seasonal isotopic variability will be narrower due to the more stable oceanographic conditions during the year. The information generated is relevant to understand the potential impact on these species and their phenology in a context of global change where environmental conditions have already been reported changing, particularly in the south HCS (central Chile: extension of the upwelling season, extreme droughts leading to decreased river inflows, and increased frequency of extreme environmental events such as atmospheric rivers and heat waves) (Silva et al. 2016, Oyarzún & Brierley 2019).

2. METHODS

2.1 Area of Study

Two coastal zones along the Humboldt Current System (HCS) were sampled seasonally along the Chilean coast. A central HCS zone (20°S, Iquique) is characterized by a narrow continental shelf, almost no river input to the coast, relatively stable environmental conditions throughout the year (Blanco et al. 2001) and coastal upwelling during most of the year with greater intensity during the summer months. In contrast, the central HCS zone (36°S, Talcahuano) includes wider continental shelf (~ 65km), a coastline with bays of different extensions, mouths of important rivers, deep submarine canyons and seasonal environmental conditions that include intense upwelling events during spring and austral summer and a coastal convergence (downwelling) due to the weakening of the southerly wind during autumn and winter, and increased precipitations and river flows especially in winter (Sobarzo et al. 2007; Gutierrez et al. 2017).

2.2 Environmental conditions

Profiles of hydrographic characteristics of the water column were obtained in each zone at 3 hydrographic stations using a Seabird 19 plus profiler (CTD). Additionally, to describe the annual cycle of environmental conditions and to visualize differences between sampling locations, data on sea surface temperature (SST), chlorophyll-a (Chl-a) and wind speed and direction at 10 m from sea level (Win10) were analyzed from October 2021 to September 2022 (study period). Daily satellite data from the U.S. Copernicus Marine Service Information program (https://data.marine.copernicus.eu/) for SST (Ostia product, Good et al. 2020) and Chl-a (CMEMS GlobColour product, Garnesson et al. 2019) with 4 x 4 km spatial resolution were used to obtain seasonal averages.

Additionally, hourly zonal and meridional reanalysis wind data from the ERA5 atmospheric product (https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5) with a spatial resolution of 0.25° were used. The annual spatial cycle of SST, Chl-a and Win10 (speed or magnitude and direction) was calculated from seasonal averages considering Summer (January-March), Fall (April-June), Winter (July-September) and Spring (October-December), the same seasons considered during the collection of biological samples in the cruises. Additionally, the monthly variation of SST, Chl-a and the upwelling index (from Win10) was analyzed for both sampling locations (Iquique and central and south HCS) by averaging all pixels located within the quadrants shown in Fig. 2 and 3. The upwelling index was obtained following Bakun (1973) and Bakun & Nelson (1991):

$$\tau_y = \rho_{air} * C_d * V * v$$

Where τ_y is the meridional wind stress, ρ_{air} is the air density (1.22 kg m^{-3}), Cd is the empirical drag coefficient calculated following wind speed intervals according to Trenberth (1990), V is the wind speed or magnitude (in m s-1) and v is the meridional wind component (in m s^{-1}). The upwelling index (UI, $m^{2\ s-1}$ x 1000 m) was estimated from the zonal Ekman transport per 1000 m of shoreline according to:

$$UI = \frac{\tau_y}{\rho_{water} * f}$$

Where τ_y is the meridional wind stress, ρ_{water} represents the mean seawater density (1025 kg m^{-3}) and f is the Coriolis parameter corresponding to the latitudes of Iquique (f = 5.022 x 10^{-5} s^{-1}) and Talcahuano (f = 8.651 x 10^{-5} s^{-1}).

2.3 Sampling

2.3.1 Fish collections

A total of 356 individuals of anchovy and common sardine were collected during the spring 2021, summer, autumn and winter of 2022 (the same months in which the hydrographic cruises were conducted) (Table 1). Approximately, 30 specimens per species were collected from the fishing hauls (central HCS: anchovy; south HCS: anchovy and common sardine), trying to obtain a wide range of adult fish sizes. The specimens were frozen and stored at the Facultad de Recursos Naturales Renovables de la Universidad Arturo Prat (Iquique), and at the Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL) of the Universidad de Concepción, in Concepción.

2.3.2 Seawater and zooplankton samples collection

During each season (spring 2021, summer, fall and winter 2022), cruises were conducted for seawater samples for particulate organic matter (POM) determinations, mesozooplankton sampling, and for obtaining profiles of hydrographic characteristics of the water column.

For POM, seawater samples from 10 and 20 m depths were collected using 5 liter Niskin bottles. A volume of 2.5 liters of seawater were filtered for each depth (2.5L at 10 m and 2.5L at 20 m) at each station, using GFF filters (0.7 µm pore size, pre-combusted). All filters were immediately frozen at -80°C.

Mesozooplankton samples were collected at each station by means of oblique zooplankton stows from the surface to approximately 30 meters depth, using a standard Bongo net of 60 cmmouth diameter, with a 300µm mesh size, with a flowmeter. Two net casts were made for each sampling site, obtaining a total of 4 cod ends per site. The contents of one cod end were preserved in a 5% seawater formalin solution buffered with sodium tetraborate (borax). These samples were used for taxonomic identification of mesozooplankton functional groups. The contents of the other 3 remaining cod ends were utilized for stable isotope analyses. The water of these cod ends was removed using a 300µm sieve, and then the zooplankton was stored in 80 ml vials, frozen at -20°C on board and then (approximately 12 hours later) transferred to -80°C freezer in the laboratory.

2.4. Laboratory analyses

2.4.1. Samples for stable isotope analysis

Samples for stable isotopes determination (carbon and nitrogen) were obtained from fish musculature, mesozooplankton groups and particulate organic material (POM). The fish were measured (total length) and weighted (wet weight, WW), then a piece of dorsal musculature (1 cm^3, aprox.) was extracted and dried for 48 hours in an oven at 60°C, and then using a porcelain mortar, a fine powder was obtained that allowed weights in a micro-balance around 1.25 mg of tissue, which was then encapsulated in tin capsules.

The mesozooplankton samples were thawed and later, using a stereoscopic, the main taxonomic groups were identified and sorted. The number of individuals separated varied depending on the taxonomic group and body size following the recommendations of stable isotopes laboratory (see below). The separated taxonomic groups were dried in an oven at 60° Celsius for 48 hours. Using a porcelain mortar, the dried samples were grounded to a fine powder which was then encapsulated in the tin capsules. All samples were weighed on an electronic microbalance and stored in 98-unit plates until sent for bulk isotope analysis (^{13}C and ^{15}N) at the University of California at Davis Stable Isotope Facility (SIF) (Davis, California, USA).

All samples were analyzed by Isotopic Ratio Mass Spectrometry (IRMS). The isotopic composition was obtained using a PDZ Europa ANCA-GSL coupled to a PDZ Europa/ Sercon 20-20 isotope ratio mass spectrometer. Isotopic values were expressed in delta (δ) values, which denote a difference between the sample value with respect to a known standard value (Criss 1999, Fry 2006). The isotopic compositions of the standards were expressed in parts per thousand (‰) according to the following expression:

$$\delta\, x = [\ (R\ sample\ /\ R\ standard\ -1)]\ *\ 10^{3} \qquad (1)$$

Where x is ^{13}C or ^{15}N, and R corresponds to the heavy isotope/light isotope fraction ($^{13}C/^{12}C$ or $^{15}N\ /^{14}N$) in the sample and standard, respectively. The standards used are Pee Dee Belemnite (PDB) for ^{13}C and atmospheric nitrogen for ^{15}N (Werner & Brand 2001).

To the δ^{13}C data obtained from fish tissues, an arithmetic correction was performed to minimize the effects of the presence of lipids, which causes an enrichment of the δ^{12}C values (Post *et al.* 2007).

$$\delta^{13}Ccorrected = \delta^{13}C\text{sample} - 3.32 + 0.99 * C:N \quad (2)$$

Where the sample δ^{13}C corresponds to the carbon value obtained from the fish tissue, C:N is the carbon:nitrogen ratio and δ^{13}Ccorrected is the resulting carbon value of the samples after applying the correction formula.

The isotopic results were entered into the editor program Notepad++, and then statistically analyzed in R Studio program(R Core Team 2019). Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic values of functional groups were compared between study areas, and inter-seasonally during the year. Normality and homogeneity of variance of the data were determined using the Shapiro-Wilks test.

2.4.2 Trophic Position

To estimate the Trophic Position (TP) of both fish species, nitrogen isotopic values ($\delta^{15}N$) from the base of the trophic web are required. However, organisms as primary producers can vary significantly in $\delta^{13}C$ and $\delta^{15}N$ values both among species and at spatial/temporal scales (Post 2002, McCutchan et al. 2003). For the calculation of TP in our study, a primary consumer (copepods) was utilized, as they are known to be a key component in the diet of these pelagic fishes (Espinoza et al. 2008) and of high abundance in the study areas. Accordingly, the TP of the species was calculated as described by Post (2002):

$$\text{TP predator} = 2.5 + (\delta^{15}\text{N predator} - \delta^{15}\text{N base}) / \text{TF} \qquad (3)$$

where, (2.5) represents the trophic position considered for the primary consumer. Because copepods mostly have an omnivorous diet (Boyd et al. 1980), we assumed that their base value was 2.5 (Espinoza et al. 2017). The predator $\delta^{15}N$ are our fish $\delta^{15}N$ values and the base $\delta^{15}N$ are the $\delta^{15}N$ value of the primary consumer (copepods), and TF was the trophic fractionation factor for general organisms (Post 2002), 3.4 ± 0.98 for $\delta^{15}N$.

2.4.3 Isotopic Niche and overlap between species

As a way to visualize the feeding variability of both fish species as well as to assess possible trophic interactions between species, we estimated the isotopic niche area (as a simile of the trophic niche of each species) and the seasonal niche overlap between species. The isotopic niche and its overlap were estimated based on the probabilistic method of Swanson et al. (2015). This method is not sensitive to variations in sample size and is available as the R package 'nicheROVER'. It uses Bayesian methods to calculate probability distributions of overlaps between the isotopic niche space of species A versus species B, and vice versa (Swanson et al. 2015).

In 'nicheROVER', overlap estimates were made for 10,000 iterations and incorporated 95% of the data to represent overlap in the total niche trophic space. Selection of the proportion of data included in the niche estimates does not affect relative comparisons of niche size between species; however, it can greatly influence estimates of relative niche overlap. Therefore, the total trophic niche (i.e., ellipses incorporating 95% of the data) was used to calculate relative niche overlap and account for individual variability in the sampled population (Shipley et al. 2019). Values were grouped by species and station to assess isotopic niche and percent isotopic overlap (for each study area).

3. RESULTS

3.1 Environmental conditions

The winter (July-September) SST was around 16ºC in the central HCS zone and 12ºC in the south HCS zone, a predominantly cold season when horizontal thermal gradients are not clearly observed, particularly in the south HCS. Spring (October-December) can be considered a transition period from a cold to a relatively warmer period in summer (more clearly observed in the central HCS zone) while the autumn (April - June) is a transition back from warm to cold temperatures (Fig. 2a).

Relatively colder surface water was observed at the coastal zone from October to June in both regions, generating a marked thermal front restricted towards the coast, particularly in the central HCS zone (Figs. 2a and 3a). The extension offshore of the coastal cold water and duration of the frontal structure between regions, plus the mean highest and lowest monthly temperature differ between the central and south HCS. However, the months when the average maxima (January in both zones; 21.5 and 14.5ºC, respectively) and the average minimum occur (September, 16.1 and 11.8ºC respectively) are similar (Fig. 2a and 3a). These seasonal variations in SST be attributed to variations in the net surface heat flux, dominated by solar radiation, which shows a marked annual cycle with a maximum heat flux (about 200 W $^{m-2}$) in January (summer), while from May to July (winter) the ocean loses heat at the ocean-air interface between May and August. The formation of horizontal thermal fronts, in turn, may be attributable to the dynamics of coastal upwelling induced by winds from the south parallel to the coast. The intensity of these winds throughout the study regions is closely linked to the seasonal dynamics of the South Pacific Subtropical Anticyclone (SPSA). In the central HCS zone, no important seasonal variations in the wind are observed, with southerly winds predominating throughout the year (Fig. 2b) that support a moderate upwelling indexes around -350 m^2 s^{-1} x 1000m throughout the entire year (Fig. 2c). In the south HCS, on the other hand, an important seasonality is observed with south winds parallel to the coast that favor upwelling mainly during spring and summer with more intense upwelling indexes around -500 m^2 s^{-1} x 1000m (Fig. 3b, Fig. 3c).

During the austral winter from June to August, when the ASPS migrates north, the south component of the wind weakens and the direction of the coastal winds reversed in June and July in the south HCS zone, leading to coastal convergences (upwelling index greater than 0) that characterize the coastal zone of central Chile (Fig. 4c).

The Chl-a values showed a marked seasonality in the south HCS with comparatively low concentrations during the austral autumn-winter (between April and July; <4 mg m^{-3}) and a highly productive coastal strip in spring and summer (between October and February; > 8 mg m^{-3}) (Fig. 3b, Fig. 4b). In contrast, in the central HCS zone the moderate and permanent upwelling generates a coastal productive band of narrower extension offshore throughout the year (Fig. 4c), without marked seasonality and concentrations around 3.5 mg m^{-3}.

3.2 Small Pelagic Fishes

A total of 236 anchovies were measured, weighted and dissected for stable isotope analyses: 116 from the central HCS zone and 120 from the south HCS zone (Table 1).

From the central HCS, the average anchovy body lengths varied between 12.09 ± 0.96 cm (summer) and 13.23 ± 0.98 cm (spring), while their weight fluctuated between 11.92 ± 2.57 g (summer) and 20.40 ± 3.99 g (spring). From the south HCS zone, the larger average anchovy sizes and weights were also recorded during spring (~ 17.25 ± 0.90 cm and ~ 41.10 ± 6.85 g) and the lowest during autumn (14.43 ± 1.03 cm and 13.79 ± 2.98 g, respectively). Comparing between locations, anchovies analyzed from the central HCS zone were smaller than those from the south HCS zone (Fig. 4).

Out of the 120 common sardines measured and weighted for stable isotope analyses in the south HCS (Table 1), their average body sizes and weights were also higher in spring, varying during the year between 12.37 ± 2.19 cm (autumn) and 15.75 ± 0.98 cm (spring), and between 18.62 ± 10.61 gr and 38.44 ± 6.24 gr in autumn and spring, respectively.

Comparing between species in the central-south zone, the anchovy specimens were larger (in size and weight) compared to those of the common sardine, and in both species a similar pattern of seasonal variation in size was evident during the year (larger sizes in spring and smaller in autumn) (Fig. 4).

3.3 Stable isotopes

More impoverished mean seasonal $\delta^{13}C$ values were observed in anchovy at the central HCS zone, compared to the south HCS zone (Table 2, Fig. 5). In contrast, more enriched mean seasonal values of $\delta^{15}N$ were observed in the central HCS zone compared to the south HCS zone, except during spring where the values were similar (Table 2, Fig. 5).

In the central HCS zone, $\delta^{13}C$ values in anchovy varied slightly between seasons (Kruskal-Wallis, $p<0.05$). The main differences occurred between autumn-winter and spring-winter (Mann-Whitney U, $p<0.05$) (Fig. 5). The values of $\delta^{15}N$ in anchovy from the central HCS zone also varied between the seasons (Kruskal-Wallis, $p<0.05$), with higher values during summer and autumn (Table 2). Only between summer-autumn there was no significant difference. The change in mean seasonal $\delta^{15}N$ in anchovy in the central HCS zone was more marked than in the south HCS zone (Fig. 5).

No seasonal differences were observed in the $\delta^{13}C$ values between common sardine and anchovy in the south HCS zone, except during winter (Mann-Whitney U, $p<0.05$) (Fig. 5). However, more enriched values of $\delta^{15}N$ were observed for anchovy individuals (in all seasons of the year) compared with those of common sardine in this south zone (Kruskal-Wallis, $p<0.05$). The Mann-Whitney U test showed that significant differences between species occurred during winter and spring ($p<0.05$) while during summer and autumn the $\delta^{15}N$ differences between species were not detected ($p=0.22$, and $p=0.35$, respectively). $\delta^{15}N$ values varied (Kruskal-Wallis, $p<0.05$) throughout the year in both species. In anchovy, the inter-seasonal difference was marked between autumn-rest of the year (Mann-Whitney U, $p<0.05$), while in common sardine it was also given by autumn-rest of the year and also between winter-summer (U Mann-Whitney, $p<0.05$).

POM and primary consumer (copepods) presented more impoverished $\delta^{13}C$ and $\delta^{15}N$ values compared to fishes in both study areas (Fig. 6 and 7). The $\delta^{13}C$ values in POM showed a wider intra-seasonal variability in both zones (more marked in the south zone) compared to the variability in small pelagic fishes (Fig. 6 and 7). The $\delta^{13}C$ values in POM and copepods followed a same seasonal trend (higher values in spring and lower in autumn) between the central and south HCS areas. The $\delta^{15}N$ values in POM and copepods were higher in the south HCS zone than in the central HCS zone, and in both zones the seasonal trend (lower levels in spring and higher in autumn) was opposite to that of $\delta^{13}C$, with fluctuations in copepods following the same seasonal trend as the $\delta^{15}N$ values in POM in both zones (except in summer in the central HCS zone).

3.3.1 Trophic Position (TP)

The estimated TP values varied inter-seasonally depending on the study area and the type of base (POM, copepods) of the trophic web used. In the central HCS zone, the anchovy mean TP range varied between 2.52 (spring) and 4.09 (summer) when copepods were used as a base source (using POM as a base source, the values varied between 1.70 and 2.55) (Table 2). In contrast, in the south HCS zone the highest anchovy TP values were recorded in spring (3.43) and the lowest values during summer (3.15) (considering POM as the primary source, TP varied between 2.84 - 3.52). Comparing between areas, the TP of anchovy in the south HCS zone were higher than the TP in the central HCS zone during spring, autumn and winter, and only in summer the TP values in the central HCS zone were higher than those in the south HCS zone (Table 2).

For common sardine, the seasonal TP range was narrower than for anchovy, with value varying between 3.08 and 3.28 (using POM a base, values ranged between 2.77 - 3.28). Comparatively, the TP of anchovy in the south HCS zone were higher than those of common sardine during the four seasons of the year regardless of the base used.

3.4 Isotopic Niche and overlap between species

The Isotopic Niche sizes calculated for anchovy in the central HCS zone varied between 7.98 ± 1.44 (spring) and 11.26 ± 1.84 (summer), while in autumn and winter the values remained relatively similar at an intermediate niche size (Fig. 8A). The elliptical projections of the isotopic niches also varied between season (Fig. 8B), with spring and summer ellipses being the most different between seasons. The isotopic niche values calculated for anchovy in the south HCS zone were lower compared to the central HCS zone during all seasons.

In the south HCS zone, the differences between seasons were less marked compared to the northern zone (Table 3). The anchovy isotopic niches had the largest sizes during winter (3.39 ± 0.65) and the smallest during spring (2.30 ± 0.42). In common sardine, the isotopic niche varied from (2.79 ± 0.52) in autumn, to (1.83 ± 0.35) during summer (Table 3).

The trophic overlap (%) between anchovy and common sardine in the south HCS zone varied inter-seasonally (Table 3). In summer and autumn occurred the highest trophic overlap of the anchovy isotope ellipses (68.87% and 78.35%) and the common sardines’, while the lowest occurred in winter (30.62%). In general, the isotopic niche of common sardine was seasonally smaller than that of the anchovy. The isotopic niche overlap of common sardine versus anchovy exceeded 80% during summer, autumn and winter, while in spring it only reached 57.05% (Table 3). Consequently, especially during winter and spring anchovy and common sardine tend to use different trophic spaces and separate their trophic niches (Fig. 9). On the contrary, during summer and autumn both species tend to use similar trophic spaces (as revealed by $^{\delta13}$C and $^{\delta15}$N) and the isotopic niche ellipses are closer and overlapping each other (Fig.9).

4. DISCUSSION

This study, through the use of stable isotopes $\delta^{13}C$ and $\delta^{15}N$, sought to improve the understanding of aspects of the trophic ecology of anchovy and common sardine in two areas of the HCS (central and south HCS, north and central Chile) by evaluating their seasonal trophic variations and their isotopic niche overlap. In addition, the inter-seasonal variability of stable isotopes at different levels of the food web up to both small pelagic fishes were related the variations of local environmental conditions. The results show that the anchovy from both zones showed narrow ranges of $\delta^{13}C$ seasonal variations but marked differences between zones. Anchovies from the north HCS zone showed a wide inter-seasonal range in $\delta^{15}N$ values as well as a wider trophic amplitude (shown by the size of the isotopic niche) compared to anchovies at the south HCS zone. In the south HCS zone, the isotopic values of common sardine and anchovy, showed scarce inter-seasonal variability and relatively stable trophic positions during the year. However, the size of the isotopic niche in both species changed inter-seasonally, as did the trophic overlap between them, being winter the period of year with the least trophic overlap between species occurred.

4.1 Variability of $\delta^{13}C$ in fish and the food web

Our results showed that the POM and copepods followed a similar $\delta^{13}C$ seasonal trend in both areas studied (spring enrichment). In addition, the northern zone presented more impoverished mean values of $\delta^{13}C$ in the three food web components analyzed (POM, copepods and fish) compared to the central-south zone during all seasons (Fig. 6). These difference between areas located at different latitudes is the result of local variations in the carbon sources that enter the food web associated with large-scale processes (changes in the position of the South Pacific anticyclone) that generate latitudinal differences in the wind direction patterns, which in turn produces changes in the duration and intensity of coastal upwelling at different latitudes (Aguirre et al. 2018, Castro et al. 2020, Weidberg et al. 2020). In the central HCS (northernChile), the coastal upwelling process is relatively continuous throughout the year, inducing an almost permanent entry of deep waters into the coastal zone. This ocean water is saltier, lower in temperature and poor in dissolved oxygen as a result of the degradation of organic matter that occurs in the deeper layers and whose $\delta^{13}C$ content is impoverished (Hill et al. 2006). In the south HCS zone (central Chile), instead, the upwelling is seasonal, more intense in spring and summer, a period when primary production increases to higher values than in the central HCS (Fig. 3B), driving a strong incorporation of organic carbon of marine origin (phytoplankton, enriched $\delta^{13}C$) into the system, which masks the low values of $\delta^{13}C$ coming from deep water that emerge at the coast associated with seasonal upwelling. Complementarily, the complex coastline and the presence of important bays, as well as the wider extension and shallower continental shelf, play a role in the contribution of enriched $\delta^{13}C$ from bento-pelagic sources (macroalgae), increasing the presence of carbon sources enriched in $\delta^{13}C$, this considering that $\delta^{13}C$ values of marine benthic algae are approximately 5‰ higher than those of phytoplankton (France 1995, Doi H et al. 2010 Trueman & St Jhon Glew 2019, Castro et al. 2020). Previous studies in other locations have also reported that the baseline $\delta^{13}C$ is generally more enriched in coastal and shallow regions compared to deeper zones (Fry, 1988, Graham et al. 2010). In the south HCS zone studied, there is an additional source of organic carbon that enters the coastal area and which is not almost not present in the central HCS (northern Chile): the organic carbon from terrestrial origin driven by rivers and runoff. This organic carbon is very impoverished in $\delta^{13}C$ (-33‰ to -26‰; Castro et al.

2020) and therefore, might have affected the isotopic values along the trophic web, particularly in winter. However, the year our study was carried out coincided with the year of most intense drought that has affected central Chile for more than 10 years (Garreaud et al. 2017), which reduced river flows, reaching low historical levels (Castro et al. 2020). The contribution of carbon from terrigenous origin with a very depleted $\delta^{13}C$ values entering to the coastal zone the year we studied, therefore, either was too small to counteract the higher contribution of marine carbon sources or was restricted to very coastal areas near the river mouths.

Inter-seasonal changes of $\delta^{13}C$ in anchovy and common sardine tissues were less marked than those observed in POM and copepods at both localities, suggesting that isotopic variability in $\delta^{13}C$ tends to decrease with increasing trophic levels, a trend previously observed also from POM to adult fish and their eggs (Castro et al. 2020). The $\delta^{13}C$ values determined in our study (-17.8 ‰ to -15.5 ‰) are within the ranges reported in adult anchovy along the Humboldt Current System (-18.7 ‰ to -15.5 ‰)). In northern Peru, Espinoza et al. (2017) reported mean $\delta^{13}C$ values of -16.3 ± 1.2 ‰ for the muscle of *E. ringens*, and in northern Chile (Antofagasta, 23°S) Pizarro et al. (2019) reported $\delta^{13}C$ values between -18.7 ‰ and -16.1 ‰ also for adult anchovy. Hückstädt et al. (2007) reported more enriched values of $\delta^{13}C$ (-15.56 ‰) off central Chile during the austral spring, and Castro et al. (2020) reported seasonal values of $\delta^{13}C$ for the same zone (Talcahuano) between -18.3 (winter) and -16.79 (spring), while values of -16.88 ± 0.59 (winter) for anchovies from the central HCS (Iquique). The $\delta^{13}C$ values we observed, also fall within the ranges reported for anchovies in other systems such as for *Engraulis encrausicolus* (-18.4 ± 0.4 ‰) in the Bay of Biscay (Chouvelon et al. 2014), *E. encrausicolus* (-20.9‰ to -18.1‰) and *S. pilchardus* (-22.4‰ to -18.7‰) in Adriatic Sea (Fanelli et al. 2023), *E. japonicus* (-20.6‰ to -14.2 ‰) in Japan (Tanaka et al. 2008), and *E. capensis* (-16.2 ‰) in Benguela Current (Iitembu et al. 2012).

Finally, when assessing potential latitudinal effects in *E. ringens* adults, our average $\delta^{13}C$ values in anchovies from the central HCS zone varied between -17.5 ‰ and -17.85 ‰, while in the south HCS zone they ranged between -15.53 ‰ and -15.85 ‰, which coincides with the latitudinal variation observed in POM and Copepods in both zones (more enriched $\delta^{13}C$ values in the south HCS). As mentioned above, these enriched $\delta^{13}C$ values at all levels of the food web of the central-south zone (Fig. 6) are apparently the result of the higher concentration of phytoplankton in the southern area (as revealed by the chlorophyll-a images, fig. 3B) and possibly of benthic macroalgae in the environment, compared with the central HCS.

4.2. Variability of $\delta^{15}N$ in fish and the food web

The $\delta^{15}N$ values in the different trophic levels (POM, Copepods and fish) in our study followed a similar seasonal trend in both study areas (except in summer in the northern area). However, more enriched values of $\delta^{15}N$ in all trophic components occurred throughout the year the central HCS zone (Fig. 7). The more enriched values of $\delta^{15}N$ in the central HCS zone apparently are largely due to the permanent presence of a broader and shallower Oxygen Minimum Zone (OMZ) than in central-south Chile (Morales et al. 1999). Denitrification processes within the OMZ cause isotopic fractionation in which bacteria respire isotopically lighter nitrate ($\delta^{14}N$) and leave subsurface nitrate enriched in $\delta^{15}N$, affecting nitrogen dynamics at lower trophic levels (Chavez & Messié 2009, Fuenzalida et al. 2009). The enriched $\delta^{15}N$ rises in the water column due to coastal upwelling (Mollier-Vogel et al. 2012, Doering et al. 2019) and are absorbed by plankton organisms and transferred through the trophic web at higher levels. In the south HCS the OMZ is less intense and deeper, and hence, the deeper oxycline allows pelagic species to occur within a broader and more oxygenated shallow layer, without necessarily be exposed to the low oxygen concentrations (Morales et al. 1999, Fuenzalida et al. 2009) and the nitrogen isotopic fractionation occurring at the bottom of food web. The enrichment in $\delta^{15}N$ values of POM, copepods and fish in our northern area of study (Table 2; Fig. 7) coincides with previous reports in the same groups and areas (except in winter 2016, Castro et al.because , 2020)), and the latitudinal decrease of $\delta^{15}N$ observed in sea lions (anchovy predators) along the Chilean coast (Barrios-Guzmán et al. 2024), and also with the latitudinal pattern in $\delta^{15}N$ observed in sediments along the coast (18°S to 30°S)(De Pol-Holz et al. (2009). However, the latitudinal trend here described is not sustained along the entire HCS as further north (Ecuador - Peru), higher $\delta^{15}N$ values in fishes have been described in areas of high denitrification (Argüelles et al. 2012, Espinoza et al. 2017, Massing et al. 2022).

A wider inter-seasonal $\delta^{15}N$ variability was observed in adult *E. ringens* tissues in the central HCS zone compared with those from the southern zone (Fig. 7). The $\delta^{15}N$ in the central HCS coincides with the enriched values of $\delta^{15}N$ reported for the same fish species for that area (Docmac et al. 2017).

Dietary analyses that could explain inter-seasonal differences in the range of $\delta^{15}N$ observed between zones have not been conducted yet. However, the wider -over the shelf- distribution of this species in the south HCS (Talcahuano area), compared with the narrow distribution in the central HCS (Iquique), allow anchovies in the later zone to prey on food sources of different origin (oceanic and/or coastal) (González et al. 2019), and therefore, feed on sources differentially enriched in $\delta^{15}N$. Previously studies on *E. ringens* diet in the central HCS (Iquique) have classified this species as a generalist utilizing a broad trophic spectrum and showing great plasticity in its diet (Medina et al. 2015). More recently, Pizarro et al. (2019) observed that anchovies in northern Chile varied widely in their $\delta^{15}N$ content according to their feeding preferences, being able to feed along a diverse trophic spectrum depending on food availability. Our results showing seasonal variability in $\delta^{15}N$ values in anchovy tissues from central HCS (Fig. 7) confirm that the diet of these fish can vary locally in a seasonal time scales and also between areas located latitudinally apart (18° vs. 36° latitude).

4.3. Baseline and Trophic Positions (TP)

Our study is the first study that reports the inter-seasonal variations of TP of *E. ringens* during an entire year, in two latitudinally distant areas, utilizing functional groups with different trophic positions as base (POM, Copepods). In both areas, the calculated anchovy TP values were slightly lower when POM was considered as a baseline, but they followed the same trend as those estimated using copepods as a baseline (Table II). From the information reported to date, no obvious conclusion can be obtained about latitudinal variations of the anchovy TP along the HCS because there is no uniformity with respect to the seasons sampled and baselines used to estimate of the TP. For example, recently, Massing et al. (2022) reported values between 3.0 and 3.4 for anchovy during spring 2018 and summer 2019 along the Peruvian coast using POM using salps as a base. In the same area Espinoza et al. (2017) reported values between 3.4 - 3.7 during 2008 (unreported sampling season) using Copepods as a base. In northern Chile (central HCS) variable trophic positions (between 2.62 - 4.16) were reported for anchovy sampled in winter 2008 using POM as a base (Pizarro et al. 2019). In the south HCS zone, in turn, while Hückstädt et al. (2007) reported anchovy trophic positions of 3.63 (spring of 2001 - 2002) using POM as base, Castro et al. (2020) reported values between 3.03 and 3.37 during the winter of 2016 and 3.34 during spring 2017, utilizing POM as base.

The estimated higher trophic positions of anchovies from the south HCS zone in our study (Table 2) (except during summer) compared to those of central zone, are associated with the wider differences in $\delta^{15}N$ between the source used (Copepods) and the predator (Fish). These results are of interest because they indicate that copepods from the South HCS zone were incorporating more phytoplankton (hence, lower $\delta^{15}N$) in their diet zone (where phytoplankton concentrations were higher in spring and summer, see satellite chlorophyll a images) than copepods at the central HCS (higher $\delta^{15}N$). There was one season when unexpectedly high trophic positions (TP>4) occurred in anchovy (summer) in the central HCS zone and these values resulted from lower-than-expected $\delta^{15}N$ values in copepods (15.29‰ versus more than 16.6‰ in other seasons) (Figure 7). Anomalous $\delta^{13}C$ values also occurred in copepods in the same central HCS in summer (higher than expected, fig. 6) and, because, other components of the trophic web such as POM or fishes did not follow this trend, we believe the zooplankton samples might have been contaminated with residues of gelatinous organisms that increase in abundance during summer in the central HCS (Pagès et al. 2001, Pavéz et al. 2006).

The results of the present study indicate also that *E. ringens* in the south HCS zone have higher trophic positions than *S. bentincki* during all seasons, regardless of the base used (POM or Copepods). This suggests that the common sardine feeds on preys with a lower trophic position compared to anchovy. Differential trophic resource use among small pelagic forage fish species such as anchovies and sardines has also been described in other coastal upwelling systems (Van der Lingen et al. 2006). Other recent studies in the northern Chilean Patagonia have described small differences in gill raker spacings, being those of the common sardine narrower than those of the anchovy, allowing them to access different size fractions of plankton as food (Wiesebron et al. 2022). Same as in the small pelagic fishes in Patagonia, the small trophic differences revealed by stable isotopes in our study seem to facilitate the coexistence of small forage species in the coastal pelagic environment along the HCS.

4.4. Isotopic niche and coexistence mechanisms

A trophic niche size about 3 times wider was observed in *E. ringens* from the central HCS zone, compared to the southern zone (Table 3). This zonal difference in *E. ringens* may be associated with the continuous access to food due to the year-round upwelling (Fig. 3) as well as the wide east-west distribution of *E. ringens* in this former zone, therefore, with access to food sources of oceanic and coastal origin (González et al. 2019). Recently, in the same area, using stable isotope analysis and mixing models, Pizarro et al. (2019), observed that anchovy individuals fed on different fractions of zooplankton, from crustacean larvae to anchovy eggs and larvae, causing variations in the trophic position of this species, revealing in this way, the plastic feeding behavior of the species. Our results coincide with Pizarro et al. 2019 appreciation in terms that the central HCS *E. ringens* might have access to different trophic sources, explaining this way their larger isotopic niche compared with south HCS anchovy throughout the year (Fig. 8B).

In the South HCS, where common sardine and anchovy coexist, there is little previous information that clarifies the mechanisms that allow their coexistence, particularly in season of reduced food availability. While previous studies describe that *S. bentincki* feeds preferentially on small prey associated with phytoplankton (Cubillos & Arcos, 2002), more recent ones have shown small differences in feeding among cohabitant small pelagic fishes in the northern Chilean Patagonia during autumn (Wiesebron et al. 2022). Interestingly, in our study the percentage of niche overlap between common sardine and anchovies varied inter-seasonally (Fig. 9), the highest values were observed during the summer (Table 4), just when upwelling conditions were favorable (Fig. 4C) and therefore, when food availability increased in the system. In contrast, during winter there was a decrease in the trophic niche overlap between species (Fig. 9 winter). Therefore, our results suggest that during winter *E. ringens* and *S. bentincki* use different food sources, and thereafter, this generates a separation of their trophic niches. This finding suggests that during winter when environmental conditions are unfavorable and there is less food availability, the anchovy and the common sardine opt for different trophic preferences, in order to avoid interspecific competition as a coexistence mechanism (Schoener, 1974). Thus, diet partitioning could play an important role in mediating the feeding dynamics between forage species.

The results obtained in this study shed light on the inter-seasonal variability of the food sources that support SPF populations along the HCS and document these changes in localities located at different latitudes where contrasting environmental conditions prevail. The inter-seasonal variability in the values of both stable isotopes ($\delta^{13}C$, $\delta^{15}N$) in the different components of the food web studied (POM, copepods, fish) seems closely associated with oceanographic processes that affect both areas but with different intensity and duration, modifying the characteristics of the water column (coastal upwelling, Castro et al. 2020). The anchovy from the central HCS zone showed a larger isotopic niche than in the south HCS zone, which seems associated with its wider coast-ocean distribution and a quasi-permanent upwelling season throughout the year. In the south HCS zone, instead, the smaller isotopic niche appears to be associated with a shorter high-abundance feeding season, a narrower coastal distribution, and the presence of other small pelagic fishes that feed on similar trophic sources. The trophic niche overlap between anchovy and common sardine in the south HCS zone varied depending on the time of year (higher in summer and lower in winter) according to food availability. These results are interesting since they allow us to understand some of the mechanisms that drive the feeding dynamics between populations of the same species in different environments as well as the differences in the feeding dynamics between species of small pelagic fish that coexist in the same habitat. Our study is the first that includes seasonal isotopic variability of two key small pelagic fishes along the central and south HCS and their relationship with environmental variables. Our study only considers inter-seasonal isotopic variability over one year cycle and in only two different zones which does not allow us to evaluate larger spatial scale trophic changes in the HCS (e.g. northern Peru) nor to expand our conclusions to longer time scales (El Niño – La Niña events, interdecadal oscillations, global change). Increasing the time scale and incorporating other study areas are part of the next challenges that we must include in future studies. However, the results here reported indeed suggests that feeding behavior (eg. food partitioning under low food scenarios) might be among the possible factors that modulates the small pelagic fishes resilience to current and future environmental changes at different locations.

Acknowledgments

Funding for this study and partial financial support to B.G. and L.C. during the writing of the manuscript was provided by the COPAS COASTAL Center FB100021. We thank C. Azocar, A. Arcos, J. Charlin and A. Rojas for help in cruises in north Chile (Iquique) and N. Cruces, E. Escalona, H. Diez and C. Veroes in south Chile (Talcahuano). We thank also P. Barrientos and R. León for her support during laboratory work and sample processing and S Soto for the hydrographic data cleaning and storage. Instituto de Fomento Pesquero (IFOP), Instituto de Investigaciones Pesqueras in Talcahuano (INPESCA) and Centro de Investigaciones Aplicadas del Mar (CIAM) provided adult fish samples. C. Torres collaborated on correcting an English version of this manuscript.

References

Aguirre C, Garcia-Loyola S, Testa G, Silva D, Farias L (2018) Insight into anthropogenic forcing on coastal upwelling off south-central Chile. Elementa-Sci. Anthro. 6: 59. doi:10.1525/elementa.314

Argüelles J, Lorrain A, Cherel Y, Graco M, Tafur R, Alegre A, Espinoza P, Taipe A, Ayón P, Bertrand A (2012) Tracking habitat and resource use for the jumbo squid *Dosidicus gigas*: a stable isotope analysis in the Northern Humboldt Current System. Mar. Biol. 159: 2105-2116. DOI:10.1007/s00227-012-1998-2

Arrizaga A, Fuentealba M, Espinoza C, Chong J, Oyarzún C (1993) Trophic habits of two pelagic fish species *Strangomera bentincki* (Norman, 1936) and *Engraulis ringens* Jenyns 1842 in the littoral of the Biobío Región, Chile. Bol. Soc. Biol. Concepción, Chile. Tomo 64.

Bakun A (1973) Coastal Upwelling Indices, West Coast Of North America, 1946-71. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Bakun A**,** Nelson CS (1991) The seasonal cycle of wind-stress curl in subtropical eastern boundary current regions. J. Phys. Oceanogr. 21 (12), 1815-1834. http://dx.doi.org/10.1175/1520-0485(1991)021<1815:TSCOWS>2.0.CO;2.

Barrios-Guzmán C, Harrod C, Guerrero A, Muñoz L, Pavez G, Quiñones R, Reyes H, Santos-Carvallo M, Zárate PM, Newsome SD, SepúlvedaM (2024) Bottom-up processes drive isotopic variation in the South American sea lion *Otaria flavescens* across a 2300 km latitudinal gradient. Marine Environmental Research. (202), 106732, 0141-1136. https://doi.org/10.1016/j.marenvres.2024.106732.

Blanco JL, Thomas AC, Carr ME, Strub PT (2001) Seasonal climatology of hydrographic conditions in the upwelling region off northern Chile. Journal of Geophysical Research. 106(6): 11451-11467.

Boyd CM, Smith SL, Cowles TJ (1980) Grazing patterns of copepods in the upwelling system off Peru. Limnol. Oceanogr. 25:583-596. doi:10.4319/lo.1980.25.4.0583

Canales TM, Lima M, Wiff R, Contreras-Reyes JE, Cifuentes U, Montero J (2020) Endogenous, climate, and fishing influences on the population dynamics of small pelagic fish in the Southern Humboldt Current ecosystem. Front. Mar. Sci. 7:82. https://doi:10.3389/fmars.2020.00082

Canales TM, Cubillos LA (2021) Empirical survey-based harvest control rules in a transboundary small pelagic fishery under recruitment regime shifts: The case of the northern Chilean-southern Peruvian anchovy. Marine Policy. 134: 104784. https://doi.org/10.1016/j.marpol.2021.104784

Castro LR, Claramunt G, Krautz MC, Llanos-Rivera A, Moreno P (2009) Egg trait variations in anchovy *Engraulis ringens*: A maternal effect to changing environmental conditions in contrasting spawning habitats. Mar. Ecol. Progr. Ser. 381, 237-248. DOI:10.3354/meps07922

Castro LR, González V, Claramunt G, Barrientos P, Soto S (2020) Stable isotopes ($\delta^{13}C$, $\delta^{15}N$) seasonal changes in particulate organic matter and in different life stages of anchovy (*Engraulis ringens*) in response to local and large scale oceanographic variations in north and central Chile. Prog. Oceanogr. 186:102342

Chavez FP, Bertrand A, Guevara-Carrasco R, Soler P, Csirke J (2008) The northern Humboldt Current System: Brief history, present status and a view towards the future. Progr Oceanogr 79:95-105. doi:10.1016/j.pocean.2008.10.012.

Chavez FP, Messié M (2009) A comparison of Eastern Boundary Upwelling Ecosystems. Prog. Oceanogr. 83: 80-96. doi: 10.1016/j.pocean.2009.07.032

Chouvelon T, Chappuis A, Bustamante P, Lefebvre S, Mornet F, Guillou G, Violamer L, Dupuy C (2014) Trophic ecology of European sardine *Sardina pilchardus* and European anchovy *Engraulis encrasicolus* in the Bay of Biscay (north-east Atlantic) inferred from $\delta^{13}C$ and $\delta^{15}N$ values of fish and identified mesozooplanktonic organisms. J. Sea Res. 85: 277-291. DOI:10.1016/j.seares.2013.05.011

Claramunt G, Castro LR, Cubillos LA, Hirche HJ, Pérez G, Braun M (2012) Interannual reproductive trait variation and spawning hábitat preferences of *Engraulis ringens* off northern Chile. Rev. Biol. Mar. Oceanogr. 47: 227-243. https://doi.org/10.4067/S0718-19572012000200006.

Criss RE (1999) Principles of stable isotope distribution. Oxford University Press.

Cubillos LA, Bucarey DA, Canales M (2001) Seasonal growth of small pelagic fish off Talcahuano (37°S; 73°W) Chile: a consequence of their reproductive strategy to seasonal upwelling? Aquat. Living Res. 14: 115-124. https://doi.org/10.1016/s09907440(01)01112-3.

Cubillos & Arcos DF (2002) Recruitment of common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off south-central Chile in the 1990s and the impact of the 1997-1998 El Niño. Aquat. Living Resour. 15: 87-94. DOI:10.1016/S0990-7440(02)01158-0.

Cubillos LA, Ruiz P, Claramunt G, Gacitúa S, Núñez S, Castro LR, Riquelme K, Alarcón C, Oyarzún C, Sepúlveda A (2007a) Spawning, daily egg production, and spawning stock biomass estimation for common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off central southern Chile in 2002. Fish. Res. 86: 228-240. https://doi.org/10.1016/j.fishres.2007.06.007.

Cury P, Bakun A, Crawford RJ, Jarre A, Quiñones RA, Shannon LJ, Verheye HM (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist’’ ecosystems. Ices J. Mar. Sci. 57: 603-618. https://doi.org/10.1006/jmsc.2000.0712.

De Pol-Holz R, Robinson R, Hebbeln D, Sigman DM, Ulloa O (2009) Controls on sedimentary nitrogen isotopes along the Chile margin- Deep Sea Res. II 56:1042-1054.

Docmac F, Araya M, Hinojosa I, Dorador C, Harrod C (2017) Habitat coupling writ large: pelagic-derived materials fuel benthivorous macroalgal reef fishes in an upwelling zone. Ecology 98 (8): 2267-2272. https://doi.org/10.1002/ecy.1936

Doering K, Ehlert C, Martinez P, Frank M, Schneider R. (2019) Latitudinal variations in δ^{30}Si and δ^{15}N signatures along the Peruvian shelf: quantifying the effects of nutrient utilization versus denitrification over the past 600 years. Biogeosciences 16: 2163-2180. doi: 10.5194/bg-16-2163-2019

Doi H, Yurlova NI, Kikuchi E, Shikano S, Yadrenkina E, Vodyanitskaya S, Zuykova E (2010) Stable isotopes indicate individual level trophic diversity in the freshwater gastropod *Lymnaea stagnalis*. Journal of Molluscan Studies, 76(4): 384-388. https://doi.org/10.1093/mollus/eyq020

Espinoza P, Bertrand A (2008) Revisiting peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the humboldt current system. Prog. Oceanogr. 79: 215-227.

Espinoza P, Lorrain A, Ménard F, Cherel Y, Tremblay-Boyer L, Argüelles J, Tafur R, Bertrand S, Tremblay Y, Ayón P, Munaron J-M, Richard P, Bertrand A, (2017) Trophic structure in the northern Humboldt Current system: new perspectives from stable isotope analysis. Marine Biology 164:86 https://DOI10.1007/s00227-017-3119-8.

Fanelli E, Da Ros Z, Menicucci S, Malavolti S, Biagiotti I, Canduci G, De Felice A, Leonori I (2023) The pelagic food web of the Western Adriatic Sea: a focus on the role of small pelagics. *Sci Rep* 13:14554. https://doi.org/10.1038/s41598-023-40665-w

FAO (2024) Versión resumida de El estado mundial de la pesca y la acuicultura 2024. La transformación azul en acción. Roma. https://doi.org/10.4060/cd0690es

France RL (1995) Stable isotopic survey of the role of macrophytes in the carbon flow of aquatic foodwebs. Vegetation, 124, 67-72.

Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography, 33, 1182–1190.

Fry B (2006) Stable Isotope Ecology. New York: Springer, 308 pp.

Fuenzalida R (1990) Variabilidad temporal de un índice de surgencia para la zona de Iquique (Lat. 20°S). lnvest. Cient. y Tec., Serie Ciencias del Mar, 1: 37-47.

Fuenzalida R, Schneider W, Garcés-Vargas J, Bravo L, Lange C (2009) Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. Deep-Sea Res. II 56: 1027-1038. doi: 10.1016/j.dsr2.2008.11.001

Garnesson P, Mangin A, Fanton d'Andon O, Demaria J, Bretagnon M (2019) The CMEMS GlobColour chlorophyll a product based on satellite observation: multisensor merging and flagging strategies, Ocean Sci. 15: 819-830, Volume 15, issue 3, https://doi.org/10.5194/os-15-819-2019

Garreaud RD, Alvarez-Garreton C, Barichivich J, Pablo Boisier J, Christie D, Galleguillos M et al. (2017) The 2010-2015 megadrought in central Chile: impacts on regional hydroclimate and vegetation. Hydrol. Earth Syst. Sci. 21:6307-6327. doi:10.5194/hess-21-6307-2017

González CE, Escribano R, Bode A, Schneider W (2019) Zooplankton Taxonomic and Trophic Community Structure Across Biogeochemical Regions in the Eastern South Pacific. Front. Mar. Sci. 5:498. doi: 10.3389/fmars.2018.00498

Good S, Fiedler E, Mao C, Martin MJ, Maycock A, Reid R, Roberts-Jones J, Searle T, Waters J, While J, Worsfold M (2020) The Current Configuration of the OSTIA System for Operational Production of Foundation Sea Surface Temperature and Ice Concentration Analyses. Remote Sens. 12, 720. https://doi:10.3390/rs12040720

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) “Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems,” in Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping, eds J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu (Berlin: Springer), 299-318. doi: https://doi.org/10.1007/978-90-481-3354-3_14

Gutiérrez M, Pantoja S, Lange C (2012) Biogeochemical significance of fatty acid distribution in the coastal upwelling ecosystem off Concepción (36°S), Chile. Organic Geochemistry. 49: 56-67.

Gutiérrez M, Garcés D, Pantoja S, González R, Quiñones R (2017) Environmental fungal diversity in the upwelling ecosystem off central Chile and potential contribution to enzymatic hydrolysis of macromolecules in coastal ecotones. Fungal Ecology. 29: 90-95.

Hill JM, McQuaid CD, Kaehler S (2006) Biogeographic and nearshore-offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa. Mar Ecol Progr Ser 318:63-73. doi:10.3354/meps318063

Hilborn R, Amoroso RO, Bogazzi E, Jensen OP, Parma AM, Szuwalski C, Walters C (2017) When does fishing forage species affect their predators? Fish. Res. 191: 211-221. http://dx.doi.org/10.1016/j.fishres.2017.01.008

Hückstädt LA, Rojas CP, Antezana T (2007) Stable isotope analysis reveals pelagic foraging by the southern sea lion in central Chile. J. Exp. Mar. Biol. Ecol. 2: 123-133. doi:10.1016/j.jembe.2007.03.014

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595-602. doi:10.1111/j.1365-2656.2011.01806.x

Iitembu JA, Miller TW, Ohomori K, Kanime A, Wells S (2012) Comparison of ontogenetic trophic shift in two hake species, *Merluccius capensis* and *Merluccius paradoxus*, from the Northern Benguela Current ecosystem (Namibia) using stable isotope analysis. Fish. Oceanogr. 21 (2-3): 215-225. https://doi.org/10.1111/j.1365-2419.2012.00614.x

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measurements of trophic structure?. Ecology.88: 42-48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2.

Martínez del Rio C, Sabat P, Anderson-Sprecher R, Gonzalez SP (2009) Dietary and isotopic specialization: the isotopic niche of three Cinclodes ovenbirds. Oecol. 161:149-159.

Massing JC, Schukat A, Auel H, Auch D, Kittu L, Pinedo Arteaga EL, Correa Acosta J and Hagen W (2022) Toward a Solution of the "Peruvian Puzzle": Pelagic Food-Web Structure and Trophic Interactions in the Northern Humboldt Current Upwelling System Off Peru. Front. Mar. Sci. 8:759603. doi:10.3389/fmars.2021.759603

McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378-390.

Medina M, Herrera L, Castillo J, Jaque J, Pizarro N (2015) Feeding of Anchovy (*Engraulis ringens*) in the northern Chile (18°25'-24°40S), during December 2010. Lat. Am. J. Acuat. Res. 43(1): 46-58. https://DOI:10.3856/vol43-issue-fulltext-5.

Mollier-Vogel E, Ryabenko E, Martinez P, Wallace D, Altabet MA, Schneider R (2012) Nitrogen isotope gradients off Peru and Ecuador related to upwelling, productivity, nutrient uptake and oxygen deficiency. Deep-Sea Res. I 70: 14-25. doi: 10.1016/j.dsr.2012.06.003

Morales CE, Hormazábal SE, Blanco J (1999) Interannual variability in the mesoscale distribution of the depth of the upper boundary of the oxygen minimum layer off northern Chile (18-24S): implications for the pelagic system and biogeochemical cycling. J. Mar. Res. 57: 909-932.

Nuñez S, Silva J, Luna R (2018) Determinación del contenido estomacal y caracterización del comportamiento trófico de los ejemplares de sardina común y anchoveta en el área comprendida entre la v y x regiones. INPESCA

Oerder V, Colas F, Echevin V, Codron F, Tam J, Belmadani A (2015) Peru-Chile upwelling dynamics under climate change. J Geophys Res Oceans 120(2):1152-1172.

Oyarzún D & Brierley CM (2019) The future coastal upwelling in the Humboldt current from model projections. Climate Dynamics 52:599-615 https://doi.org/10.1007/s00382-018-4158-7

Pagès F, González HE, Ramón M, Sobarzo M, Gili J-M (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). Mar. Ecol. Prog. Ser., 210, 13-24. https://DOI:10.3354/meps210013

Pavez MA, Castro LR, González HE (2006) Across-shelf predatory effect of *Pleurobrachia bachei* (Ctenophora) on the small-copepod community in the coastal upwelling zone of northern Chile (23°S). J. Plankton Res., 28, 115-129. https://doi:10.1093/plankt/fbi105

Pikitch E, Boersma PD, Boyd IL, Conover DO, Cury P, Essington T, Heppell SS, Houde ED, Mangel M, Pauly D, Plagányi É, Sainsbury K, Steneck RS (2012) Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs. Lenfest Ocean Program, Washington, DC.

Pizarro J, Docmac F, Harrod C (2019) Clarifying a trophic black box: stable isotope analysis reveals unexpected dietary variation in the Peruvian anchovy *Engraulis ringens*. PeerJ 7:e6968. https://doi:10.7717/peerj.6968

Post DM (2002) Using stable isotopes to estimate trophic positions: Models, methods and assumptions. Ecology 83, 703-718. https://doi:10.2307/3071875.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179-189. https://doi.org/10.1007/s00442-006-0630-x.

Saavedra A, Catasti V, Leiva F, Vargas R, Cifuentes U, Reyes E et al. (2014) Evaluación Hidroacústica de los Stocks de Anchoveta y Sardina común entre la V y X Regiones, año 2014. Informe Final FIP 2013-05. 306. Chile: Instituto de Fomento Pesquero.

Silva C, Andrade I, Yáñez E, Hormazabal S, Barbieri MA, Aranis A, Böhm G (2016) Predicting habitat suitability and geographic distribution of anchovy (*Engraulis ringens*) due to climate change in the coastal areas off Chile. Progress in Oceanography 146: 159-174. http://dx.doi.org/10.1016/j.pocean.2016.06.006

Shipley ON, Olin JA, Power M, Cerrato RM, Frisk MG (2019) Questioning assumptions of trophic behavior in a broadly ranging marine predator guild. Ecography 42: 1037-1049. https://doi.org/10.1111/ecog.03990.

Schoener TW (1974) Resource partitioning in ecological communities. Science 185: 27-39.

Sobarzo M, Bravo L, Donoso D, Garcés-Vargas J, Schneider W (2007) Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. Progress in Oceanography 75: 363-382. DOI:10.1016/j.pocean.2007.08.022

Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist J (2015) A new probabilistic method for quantifying n-dimensional ecological niches and niches overlap. Ecology 96: 318-324. https://doi.org/10.1890/14-0235.1.

Tanaka H, Takasuka A, Aoki I, Ohshimo S (2008) Geographical variations in the trophic ecology of Japanese anchovy, *Engraulis japonicus*, inferred from carbon and nitrogen stable isotope ratios. Mar. Biol. 154: 557-568.

Trenberth KE (1990) Recent Observed interdecadal climate changes in the Northern Hemisphere. Bull. Am. Meteorol. Soc. 71 (7): 988-993. http://dx.doi.org/10.1175/1520-0477(1990)071<0988:ROICCI>2.0.CO;2.

Trueman CN, St John Glew K (2019) Isotopic tracking of marine animal movement. In Tracking animal migration with stable isotopes (pp. 137-172). New York: Elsevier. https://doi.org/10.1016/b978-0-12-814723-8.00006-4

Van der Lingen CD, Hutchings L, Field JG (2006) Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern benguela: are species alternations between small pelagic fish trophodynamically mediated? Afr. J. Mar. Sci. 28:465-477.

Weidberg N, Ospina-Alvarez A, Bonicelli J, Barahona M, Aiken C, Broitman BR, Navarrete SA (2020) Spatial shifts in productivity of the coastal ocean over the past two decades induced by migration of the Pacific Anticyclone and Bakun's effect in the Humboldt Upwelling Ecosystem, Global and Planetary Change. 193:103259, https://doi.org/10.1016/j.gloplacha.2020.103259.

Werner RA, Brand WA (2001) Referencing strategies and techniques in stable isotope ratio analysis. Rapid Communications in Mass Spectrometry, 15(7): 501-519. https://doi.org/10.1002/rcm.258

Wiesebron LE, Castro LR, Soto S, Castillo J (2022) Small Differences in Diet Facilitate the Coexistence of Three Forage Fish Species in an Inshore Northern Patagonian Habitat. Front. Mar. Sci. 8:792377. https://doi.org/10.3389/fmars.2021.792377

Table 1. Number of fishes sampled per species, study area and season. Average length (cm) and total weight (wt) and their Standard Deviations (± SD) at each season are included.

Central HCS Zone (Iquique)

Specie	Season	n	Mean length ± SD	Mean weight ± SD
Anchovy	Spring	30	13.23 ± 0.98	20.40 ± 3.99
	Summer	30	12.09 ± 0.96	11.92 ± 2.57
	Autumn	30	12.59 ± 0.98	13.79 ± 2.98
	Winter	26	12.91 ± 1.07	14.83 ± 2.51

South HCS Zone (Talcahuano)

Specie	Season	n	Mean length ± SD	Mean weight ± SD
Anchovy	Spring	30	17.25 ± 0.90	41.10 ± 6.85
	Summer	30	16.85 ± 1.04	38.41 ± 6.93
	Autumn	30	14.43 ± 1.03	20.18 ± 4.36
	Winter	30	17.18 ± 0.70	34.63 ± 4.23
Common Sardine	Spring	30	15.75 ± 0.98	38.44 ± 6.24
	Summer	30	14.59 ± 0.78	31.30 ± 5.43
	Autumn	30	12.37 ± 2.19	18.62 ± 10.61
	Winter	30	13.69 ± 1.37	22.03 ± 5.15

Table 2. Seasonal values (mean ± Standard Deviation (SD)) of δ^{13}C and δ^{15}N, C/N ratios, and trophic position (TP) calculated for anchovy and common sardine obtained at the Central HCS and South HCS zones. Copepod and POM values are included. Copepods were used as base for the TP calculations, but TP estimated using POM as base are also included. n= number of samples.

Central HCS Zone (Iquique)

Specie	**Season**	**n**	**δ ^{13}C Mean±SD**	**δ^{15}N Mean±SD**	**C/N Mean±SD**	**TP (2.5)**	**TP POM**
Anchovy	Spring	30	-17.84 ± 0.52	16.68 ± 0.85	3.49 ± 0.23	2.52	1.70
	Summer	30	-17.60 ± 0.47	20.71 ± 1.42	3.42 ± 0.27	4.09	2.44
	Autumn	30	-17.85 ± 0.34	20.72 ± 1.58	3.34 ± 0.14	3.04	2.55
	Winter	26	-17.50 ± 0.54	18.92 ± 1.70	3.18 ± 0.05	2.85	2.41
Copepods	Spring	8	-17.93 ± 0.58	16.60 ± 0.32	5.55 ± 0.53	-	-
	Summer	5	-15.59 ± 0.04	15.29 ± 0.09	5.73 ± 0.02	-	-
	Autumn	10	-21.52 ± 1.19	18.89 ± 0.55	4.91 ± 0.43	-	-
	Winter	9	-21.46 ± 1.21	17.69 ± 0.29	5.18 ± 0.58	-	-
POM	Spring	19	-20.90 ± 1.63	14.28 ± 1.30	6.40 ± 1.24	-	-
	Summer	13	-22.57 ± 1.23	15.81 ± 2.50	5.98 ± 1.01	-	-
	Autumn	24	-24.28 ± 2.19	15.46 ± 2.66	6.26 ± 1.04	-	-
	Winter	12	-23.40 ± 1.54	14.13 ± 1.79	6.18 ± 1.03	-	-

South HCS Zone (Talcahuano)

Specie	**Season**	**n**	**δ^{13}C Mean±SD**	**δ^{15}N Mean±SD**	**C/N Mean±SD**	**TP (2.5)**	**TP POM**
Anchovy	Spring	30	-15.85 ± 0.45	16.82 ± 0.33	3.92 ± 0.58	3.43	3.09
	Summer	30	-15.55 ± 0.35	16.70 ± 0.53	3.49 ± 0.37	3.15	2.84
	Autumn	30	-15.82 ± 0.48	17.59 ± 0.41	3.30 ± 0.10	3.21	3.03
	Winter	30	-15.53 ± 0.45	16.86 ± 0.45	3.48 ± 0.10	3.40	3.52
Common Sardine	Spring	30	-15.78 ± 0.45	16.30 ± 0.34	4.81 ± 1.48	3.28	2.94
	Summer	30	-15.68 ± 0.38	16.47 ± 0.30	5.94 ± 0.82	3.08	2.77
	Autumn	30	-15.77 ± 0.35	17.29 ± 0.54	3.79 ± 0.53	3.12	2.94
	Winter	30	-16.04 ± 0.32	16.04 ± 0.35	3.36 ± 0.18	3.16	3.28
Copepods	Spring	8	-16.22 ± 0.48	13.67 ± 0.21	5.92 ± 0.75	-	-

	Summer	10	-15.53 ± 0.84	14.50 ± 0.11	6.97 ± 1.47	-	-
	Autumn	9	-19.02 ± 0.87	15.18 ± 0.24	6.78 ± 0.73	-	-
	Winter	10	-16.38 ± 0.47	13.81 ± 0.20	6.10 ± 0.37	-	-
POM	Spring	5	-20.39 ± 3.25	9.70 ± 2.10	6.54 ± 0.71	-	-
	Summer	4	-20.76 ± 1.75	10.45 ± 1.64	5.50 ± 0.67	-	-
	Autumn	12	-23.78 ± 2.42	10.70 ± 2.53	6.03 ± 1.72	-	-
	Winter	10	-22.24 ± 2.52	8.29 ± 2.39	6.22 ± 2.56	-	-

Table 3. Isotopic Niche area and percentage of probability of niche overlap (95% of the niche size) between species and during the four seasons of the year.

Central HCS Zone (Iquique)

Specie	**Season**	**Isotopic Niche ± SD**
Anchovy	Spring	7.98 ± 1.44
	Summer	11.26 ± 1.84
	Autumn	9.70 ± 1.81
	Winter	9.78 ± 1.90

South HCS Zone (Talcahuano)

Specie	**Season**	**Isotopic Niche ± SD**	**Overlap (%)**
Anchovy	Spring	2.30 ± 0.42	59.13
	Summer	3.14 ± 0.59	68.87
	Autumn	3.20 ± 0.59	78.35
	Winter	3.39 ± 0.65	30.62
Common Sardine	Spring	2.38 ± 0.43	57.05
	Summer	1.83 ± 0.35	97.69
	Autumn	2.79 ± 0.52	83.36
	Winter	2.06 ± 0.38	85.67

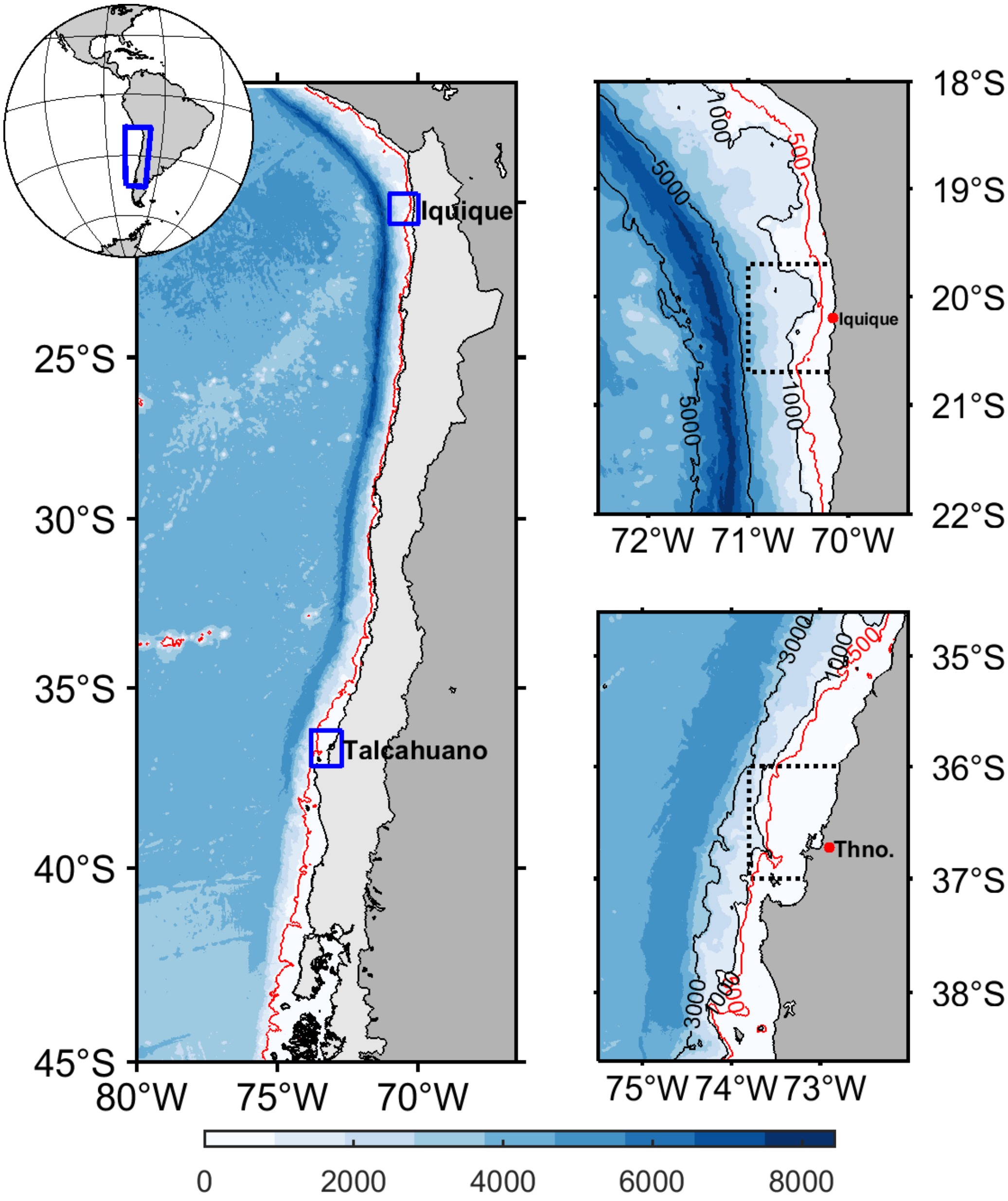

Figure 1. Area of study (left panel) with the two latitudinally separated sampling zones (blue squares) in the HCS, a central HCS zone (20°S, Iquique), and south HCS zone (36°S, Talcahuano). The two right panels show both zones, and the dashed demarcation within them reflects the area where all samples (hydrographic data, fish, zooplankton and particulate organic matter) were collected. The blue scale on the x-axis shows the bottom depth in meters and the lines near the shore represent the depth isobaths.

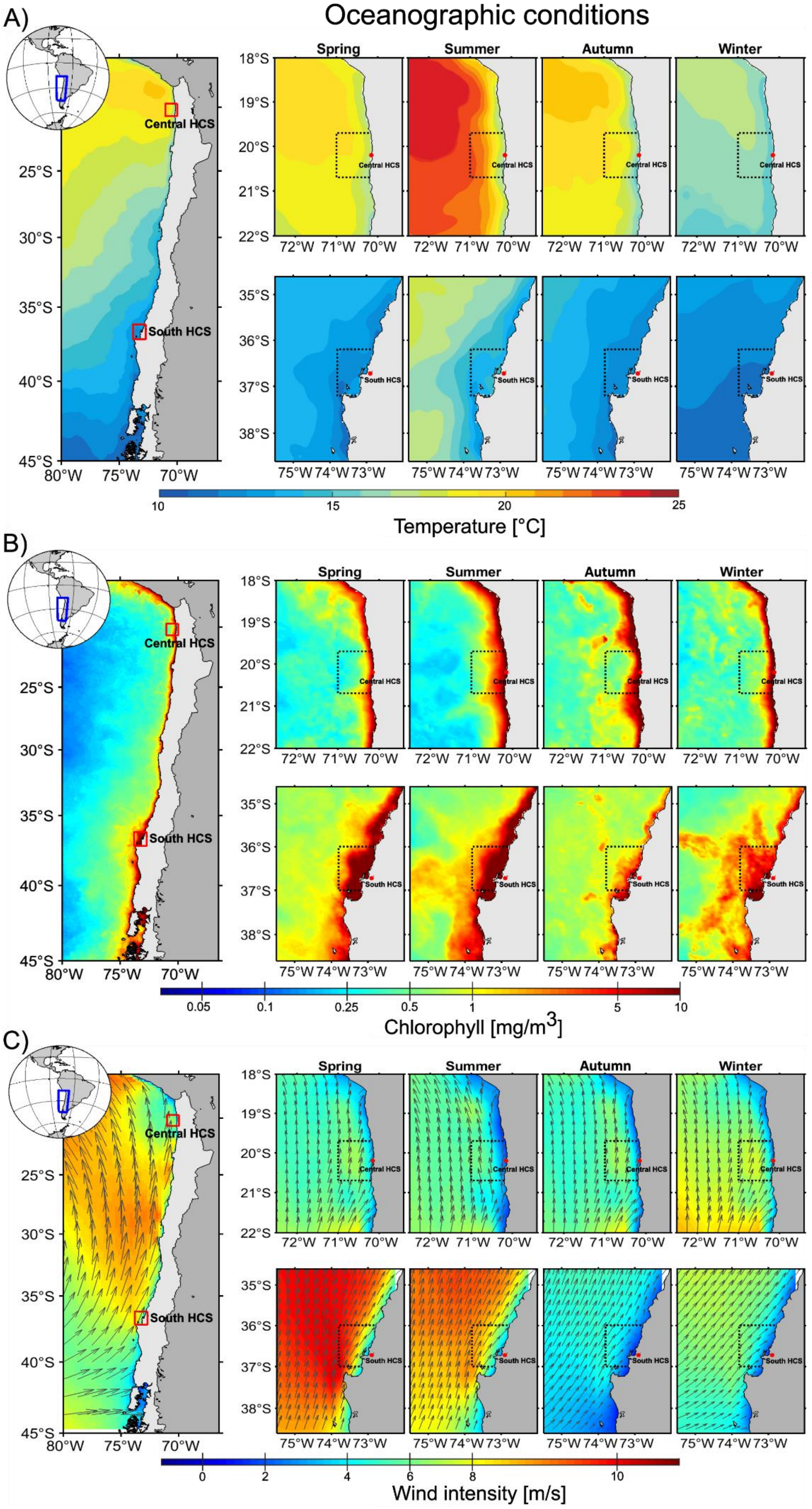
A)
Oceanographic conditions
Spring
Summer
Autumn
Winter
Central HCS
South HCS
18°S
19°S
20°S
21°S
22°S
25°S
30°S
35°S
40°S
45°S
35°S
36°S
37°S
38°S
80°W
75°W
70°W
72°W
71°W
70°W
75°W
74°W
73°W
10
15
20
25
Temperature [°C]
B)
0.05
0.1
0.25
0.5
1
5
10
Chlorophyll [mg/m3]
C)
0
2
4
6
8
10
Wind intensity [m/s]

Figure 2. Seasonal oceanographic variability, A) Seasonal average sea surface temperature (°C), B) chlorophyll concentration [mg/m3], C) average wind intensity [m/s] in the two study sites (Central HCS Zone (Iquique) and South HCS Zone (Talcahuano)) during the 4 seasons of the year.

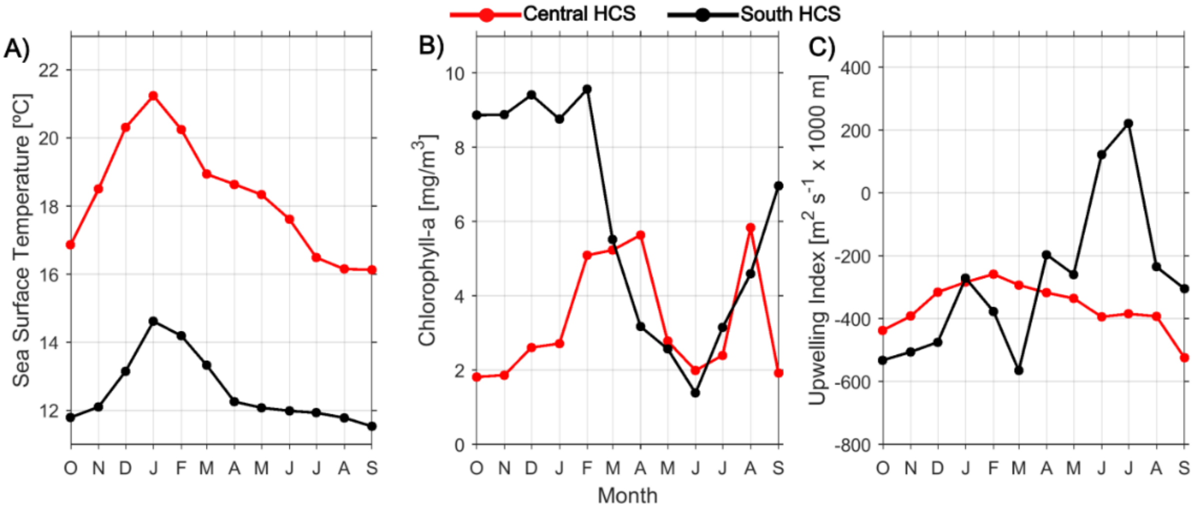

Figure 3. A) Monthly average sea surface temperature (°C), B) chlorophyll concentrations [mg/m3], C) upwelling index [m^2 s^{-1} x 1000 m] in the central HCS zone (Iquique, red line), and south HCS zone (Talcahuano, black line). Negative upwelling indexes (northward winds) denote upwelling conditions.

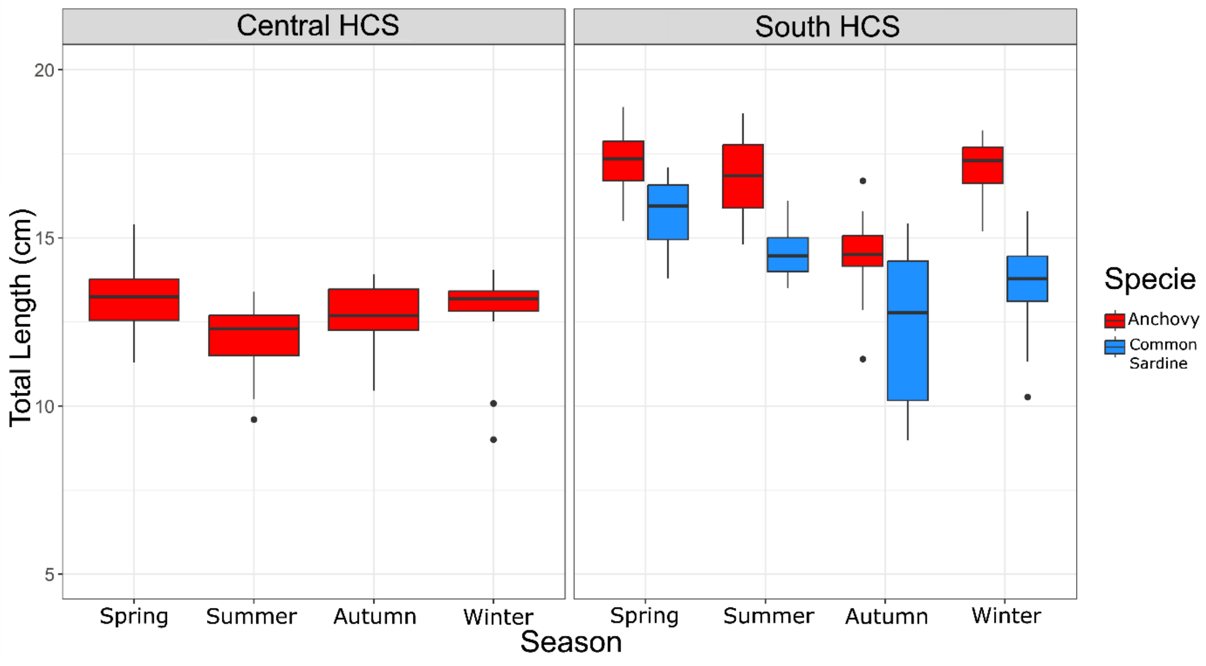

Figure 4. Body length distribution (cm) of anchovy and common sardine in the central HCS sampling zone and south HCS zone, during the 4 sampled seasons. Red symbols are anchovies, and calypso are common sardine.

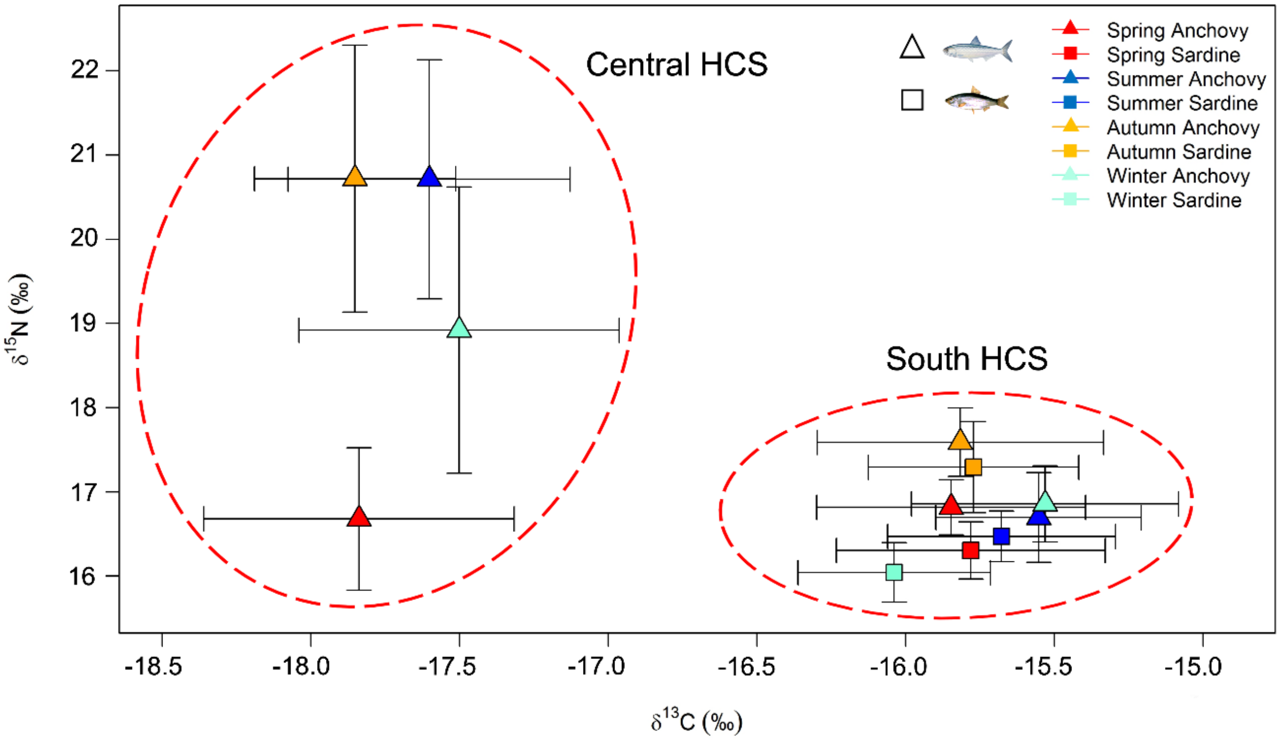

Figure 5. Average seasonal isotopic values (± SD) $\delta^{13}C$ and $\delta^{15}N$ in anchovy (triangle) and common sardine (Square), in the central HCS and south HCS zones along Chile, during the four seasons of the year.

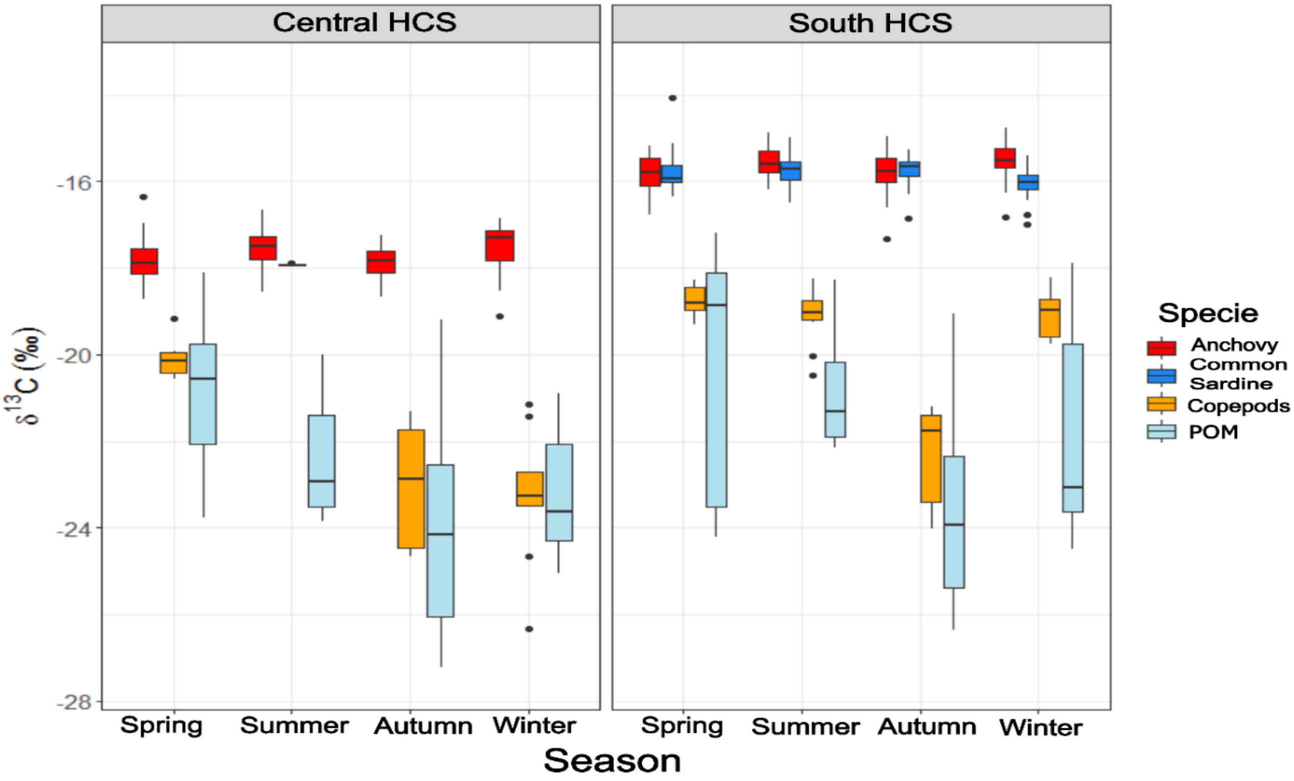

Figure 6. Mean seasonal values (± SD) of δ^{13}C for each functional group in the central HCS and south HCS zones. Colored symbols represent anchovy (red), common sardine (blue), Copepods (orange) and POM (light blue).

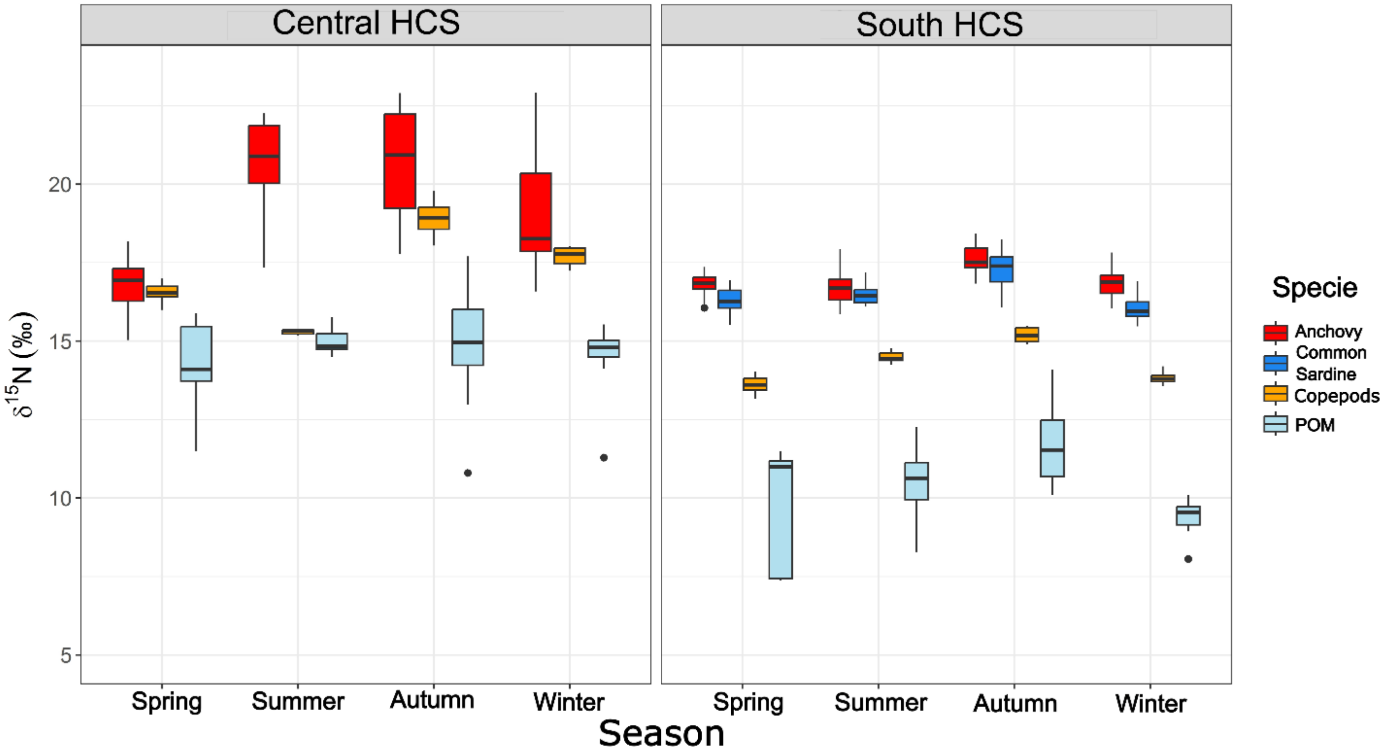

Figure 7. Mean seasonal values (± SD) of δ^{15}N for each functional group in the central HCS and south HCS zones. Anchovy (red), Common sardine (blue), Copepods (orange) and POM (light blue).

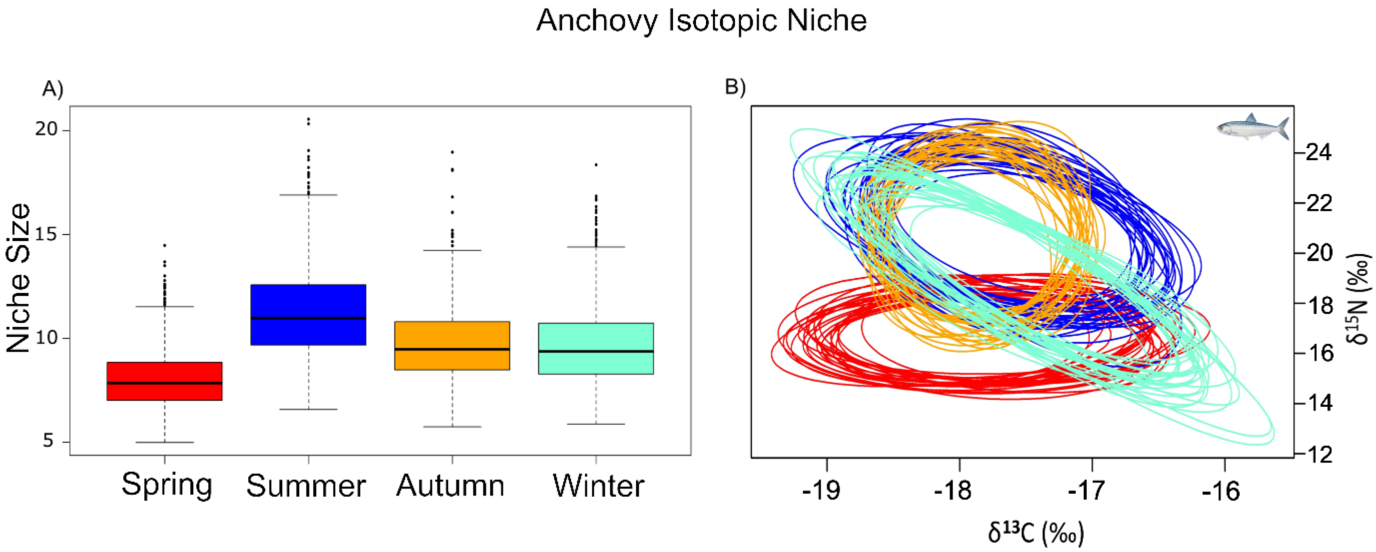

Figure 8. Isotopic niche values of anchovy in the central HCS zone. A) Size of the anchovy isotopic niche of during the four seasons; B) Fifteen random elliptical projections of the anchovy isotopic niche region during the different seasons. Colors for seasons in Figure B) correspond with those in Figure A).

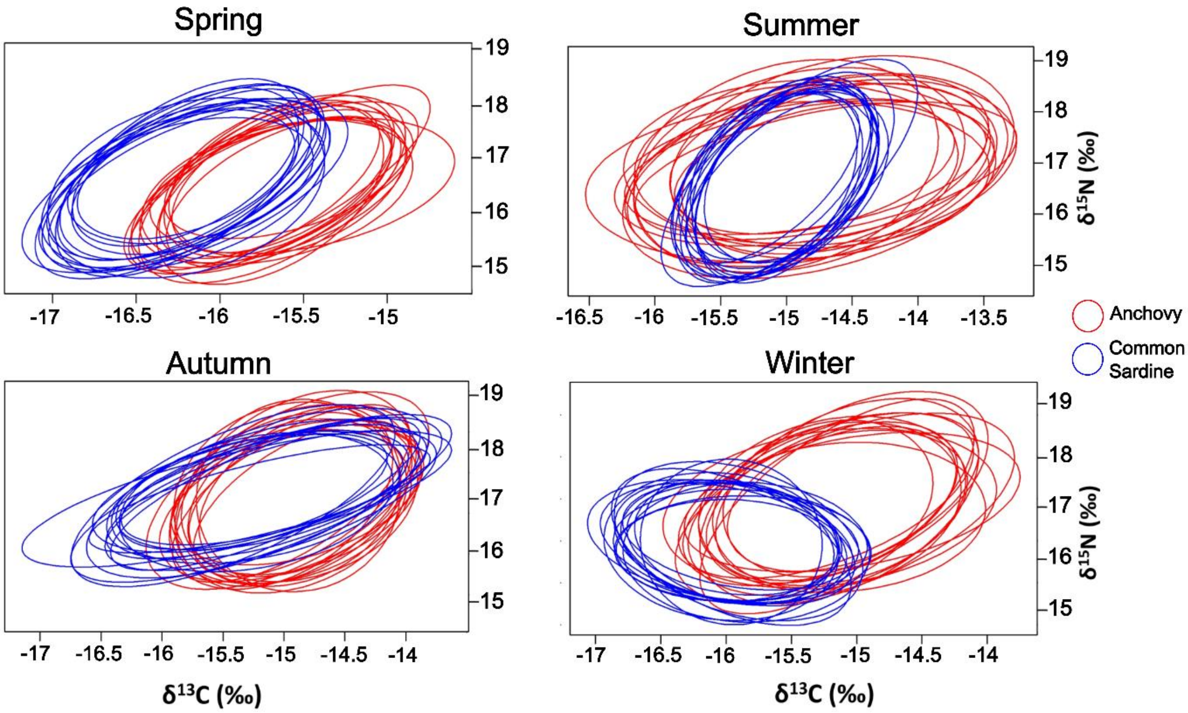

Figure 9. Seasonal random elliptical projections of the isotopic niche for anchovy (red) and common sardine (blue) in the south HCS zone.

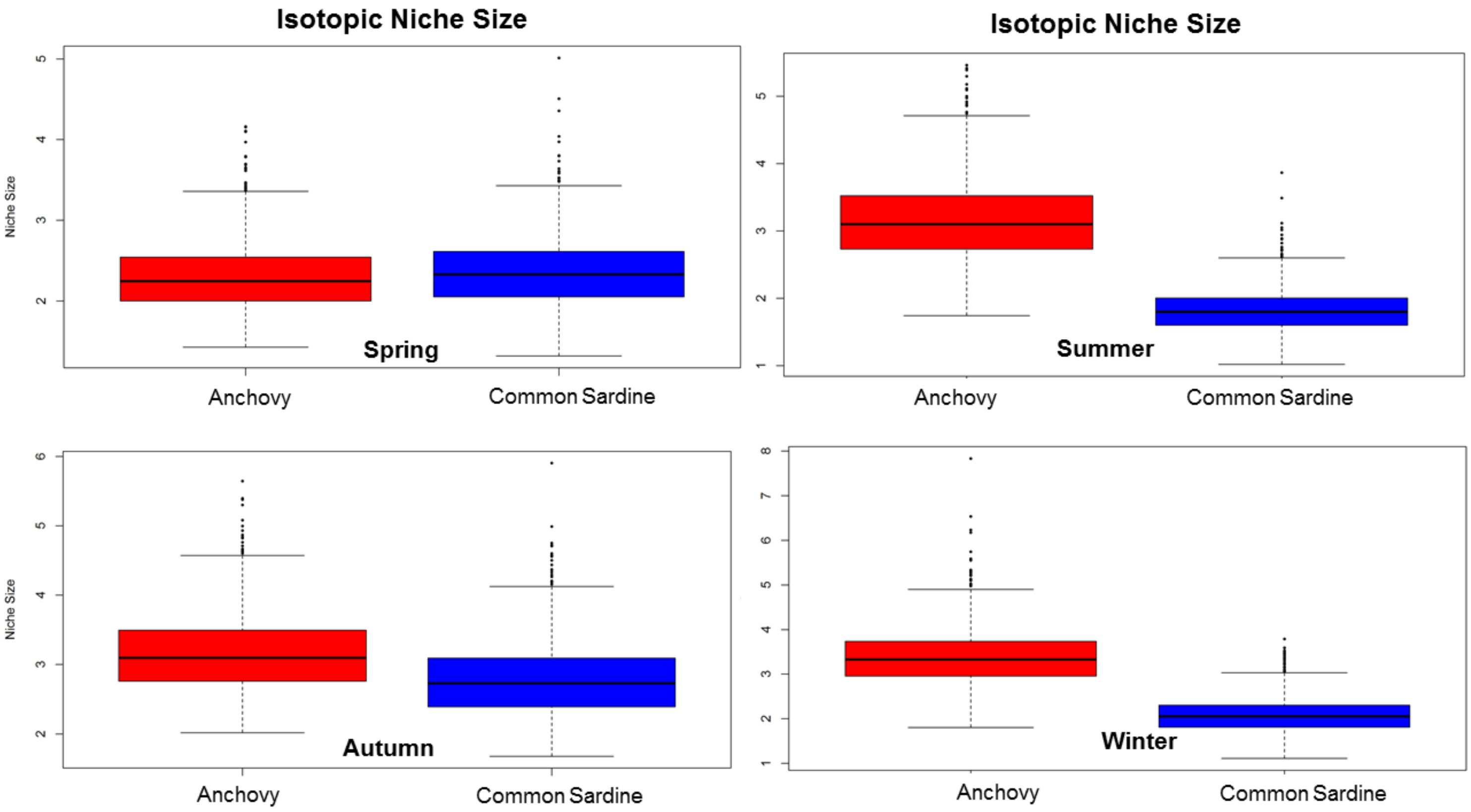

Figura 10. Tamaño del Nicho isotópico calculado para *Engraulis ringens* (rojo) y *Strangomera bentincki* (azul), durante las cuatro estaciones del año.

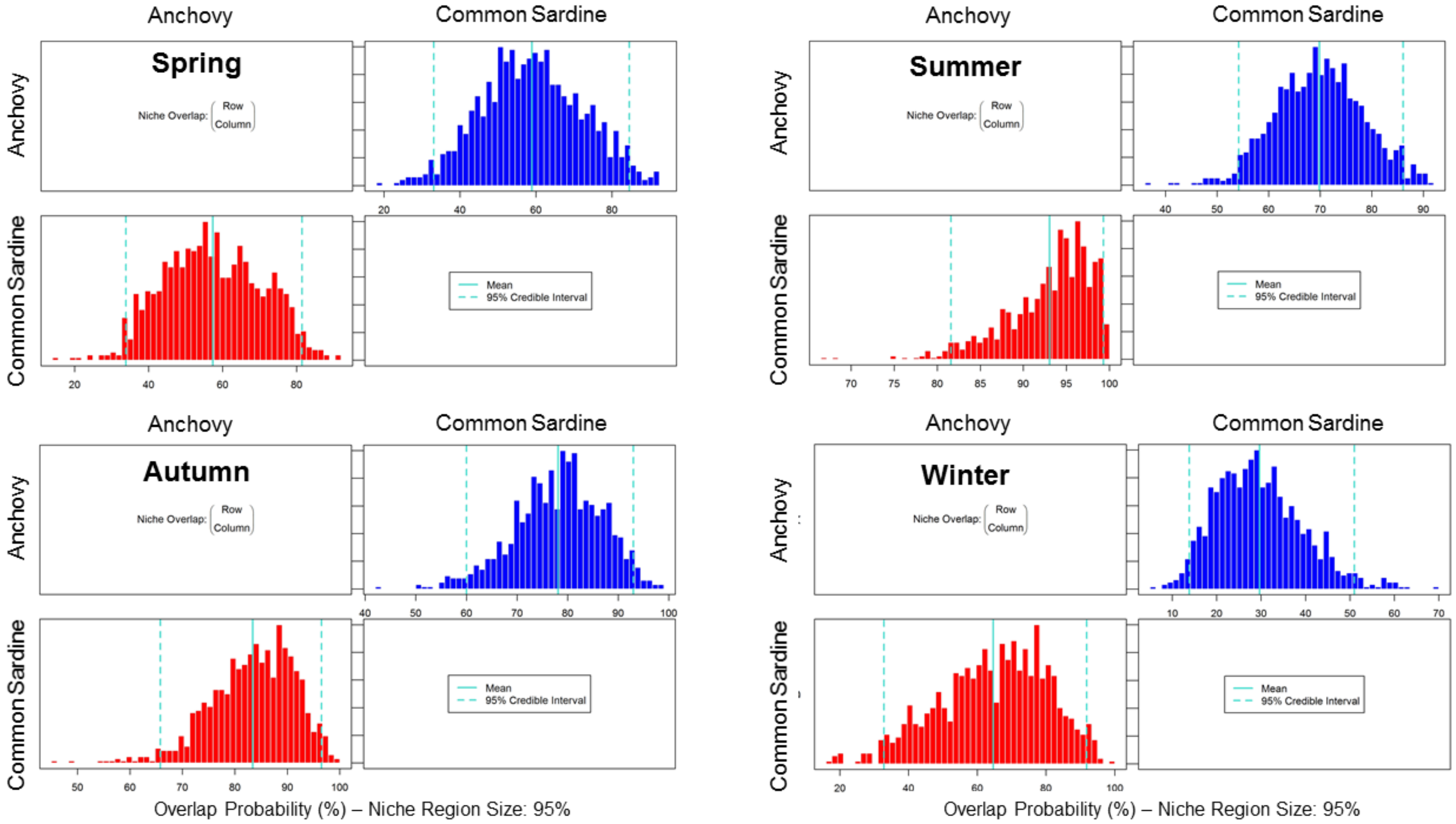

Figura 11. Trophic overlap probability (95%) between *Engraulis ringens* (red) and *Strangomera bentincki* (blue) during the 4 seasons. Solid line (calypso) represents the mean and dashed lines the calculated credible intervals.

CAPÍTULO II

Discusión general

Esta tesis estuvo orientada a entender la ecología trófica de *Engraulis ringens* y *Strangomera bentincki* en dos zonas latitudinalmente distantes del SCH (centro y sur del SCH). Este trabajo es novedoso ya que logró integrar varios aspectos relevantes y complejos desde el punto de vista práctico, la estacionalidad en la obtención de muestras representativas de las cuatro estaciones del año en dos zonas distantes geográficamente fue una de las barreras más compleja que logramos sortear. Asimismo, el muestreo integrado de la comunidad planctónica fue otro aspecto limitante que comúnmente afectan este tipo de estudios. En ese sentido, esta tesis logró incorporar elementos fundamentales para generar una mirada integrada de sistema pelágico costero y los mecanismos tróficos que afectan a *E. ringens* y *S. bentincki* durante el año.

Mediante la utilización de análisis de isótopos estables de $\delta^{13}C$ y $\delta^{15}N$ se obtuvo información sobre las relaciones tróficas durante un periodo de un año, posibilitando estudiar e inferir aspectos tróficos de ambas especies, el ecosistema, y las relaciones interespecíficas (Martínez del Río et al. 2009). De igual manera, se incorporó la caracterización de variables ambientales que afectan ambas zonas de estudio, así como su relación con las fuentes alimenticias disponibles y sus valores isotópicos (δ^{13}C y δ^{15}N). Se observó que las condiciones ambientales se mantuvieron acorde con lo descrito para cada zona (una zona centro del SCH con condiciones favorables a surgencia relativamente continua durante el año, mientras que la zona sur del SCH mucho más estacional en las condiciones ambientales, con principales máximos de surgencia durante primavera y verano (Figura 3 C)). Los valores isotópicos de δ^{13}C y δ^{15}N obtenidos en los primeros niveles de la trama trófica (POM, copépodos) variaron latitudinalmente entre ambas zonas del SCH (figura 6 y 7). Igualmente, se evidenció una mayor variabilidad intra-estacional en los componentes bajos de la trama trófica (POM y copépodos). Se sabe que las proporciones de los isótopos estables de carbono y nitrógeno en la base de la trama trófica pueden variar espacialmente, lo que se refleja en la variabilidad de la composición isotópica de los niveles más bajos (Zanden & Rasmussen, 2001). La diferenciación latitudinal observada en los valores de δ^{13}C (una zona centro del SCH con valores más empobrecidos de δ^{13}C y una zona sur con valores más enriquecidos (Figura 5)) tiene relación con la presencia de diferentes fuentes de carbono dominantes en cada zona. En la zona centro (Iquique) dominó el $\delta^{13}C$ con origen oceánico y, dado el continuo afloramiento de aguas subsuperficiales más empobrecidas en $\delta^{13}C$. En la zona sur del SCH, los valores fueron más enriquecidos de $\delta^{13}C$ y tuvieron relación con la presencia importante de fuentes bentopelágicas, macroalgas que dominan en la zona costera y las altas biomasas de fitoplancton. La mayor extensión de la plataforma continental y la menor profundidad del sistema favorecen la proliferación de estas fuentes más enriquecidas en $\delta^{13}C$ (productores primarios marinos). Por otro lado, el presente estudio coincidió con la fuerte sequía que afectó la zona de estudio durante el periodo muestreado, y por tanto, con un bajo aporte de los caudales durante la época y una débil señal de origen terrígena, más empobrecida en $\delta^{13}C$ comparada con la señal de productores primario marinos. Acorde a lo anterior, se acepta la primera Hipótesis de trabajo propuesta peros solo para el $\delta^{13}C$, ya que los valores isotópicos de $\delta^{13}C$ en la estructura trófica baja (POM, Copépodos) difirieron latitudinalmente entre zonas, debido a las características geográficas y ambientales de cada zona.

Al comparar entre ambas zonas de estudio se observó que los valores isotópicos de *E. ringens* fueron zonalmente diferentes. La anchoveta de la zona centro del SCH presentó una mayor variabilidad inter-estacional en los valores de $\delta^{15}N$ y una mayor amplitud trófica en comparación a la anchoveta de la zona sur (Tabla 3). Al parecer existen características oceanográficas y geográficas originalmente no consideradas (variación de extensión de la distribución costa-océano y diferencias en profundidad del fondo) que moldean la dinámica trófica y el enriquecimiento isotópico de la trama alimenticia primaria. Por un lado, una zona centro del SCH con una reducida plataforma continental (Figura 1) y una Zona mínima de Oxígeno poco profunda afectan el enriquecimiento isotópico del $\delta^{15}N$ de las fuentes alimenticias disponibles (más variadas y enriquecidas en $\delta^{15}N$). Mientras que por otro lado, la zona sur del SCH la presencia de una plataforma continental extendida y poco profunda, resulta en la presencia de fuentes bentónicas de macroalgas y altas biomasas fitoplanctónicas durante más tiempo en el año, y un ambiente costero geográficamente más protegido, parecen dar mayor estabilidad al sistema trófico y por tanto, una menor variabilidad isotópica asociada. Contrario a lo postulado en la Hipótesis 2 de trabajo, se observó una mayor variabilidad isotópica en *E. ringens* de la zona centro del SCH, a pesar de las condiciones más estables de surgencia costera durante el año. Por otro lado, la zona sur del SCH a pesar de tener una marcada estacionalidad en las condiciones oceanográficas y ambientales, presentó valores isotópicos de *E. ringens* menos variables inter-estacionalmente (Figura 5). Igualmente, los valores calculados del TP para la anchoveta en la zona centro variaron notoriamente entre las diferentes estaciones del año, mientras que el TP calculado para anchoveta en la zona sur del SCH se mantuvo relativamente estable durante el año (Tabla 2).

El cálculo del "nicho isotópico" a partir del espacio bidimensional (Newsome et al. 2007) posibilitó comprender estacionalmente las características tróficas de ambos peces, sus similitudes, diferencias, y la variabilidad del solapamiento trófico durante el año. La figura 10 muestra el tamaño calculado del nicho isotópico y la figura 11 ilustra el cálculo del porcentaje estimado de solapamiento trófico con un 95% de credibilidad (Swason et al. 2015). Tanto los valores del tamaño de nicho como el nivel de solapamiento trófico variaron inter-estacionalmente en sardina común y anchoveta en la zona sur del SCH. Los mayores valores de solapamiento trófico se obtuvieron durante verano, lo que coincidió con el máximo de clorofila observado y de productividad, mientras que el menor porcentaje de solapamiento trófico se obtuvo durante invierno donde se evidenció una separación de nicho y coincidió con la época con menor disponibilidad de alimento en el sistema. La teoría de diferenciación de nichos relacionados con la biodiversidad (Cazzolla-Gatti, 2011) postula que dos especies pueden coexistir si cada una usa un nicho diferente de hábitat disponible para reducir la competencia interespecífica. Al parecer ambas especies pelágicas separan sus nichos tróficos durante invierno y utilizan diferencialmente los recursos tróficos como una estrategia de coexistencia. En ese sentido, se aprobó la Hipótesis 3 de trabajo, ya que tanto la amplitud como el solapamiento del nicho isotópico variaron inter-estacionalmente entre *E. ringens* y *S. bentincki* en la zona sur del SCH, hecho que estaría facilitando su coexistencia, especialmente en periodos con menor disponibilidad de alimento. En otras áreas, se ha observado diferencias tróficas entre especies, lo que les posibilita seleccionar alimentos de diferentes tamaños (Balbontín et al., 1979; Van der Lingen et al., 2006; Wiesbron et al., 2022), y de paso les permite coexistir en ecosistemas compartidos (Wiesbron et al., 2022). Además, se ha observado variaciones en el tipo de dieta de estos peces, según su estadio de desarrollo (Llanos et al., 1996; Costalago et al., 2012), la latitud en donde se encuentren (Pauly et al., 1989; Espinoza et al., 2014), y según las condiciones ambientales predominantes (Takasuka et al., 2007).

Este trabajo identifica aspectos esenciales de la ecología trófica de anchoveta y sardina común en el ecosistema pelágico costero del SCH. La comprensión de los procesos ecológicos primarios en los ecosistemas marinos, la variación en las fuentes de alimento, las transferencias energéticas a través de la trama trófica, y la interrelación entre especies, son aspectos fundamentales para relacionar el funcionamiento de los ecosistemas con la gestión y manejo de los recursos marinos. Contar con información trófica complementaria posibilita no solo identificar el rol de estas especies en el ecosistema marino, y comprender las fuerzas que impulsan la dinámica poblacional, sino que también aportan conocimiento fundamental para mejorar la gestión integral de estas pesquerías, hechos relevantes sobre todo en los tiempos actuales cambiantes.

Referencias

Balbontín F, Llanos A, Valenzuela V (1979). Estudio experimental sobre selección de alimento y comportamiento alimentario en anchoveta y sardina de Chile (pisces, clupeiformes). Revista de Biología Marina, Valparaíso (Chile) 16, 211-220.

Cárcamo C, Schultz T, Leiva F, Saavedra A, Klarian SA (2024). A Deep Dive into the Trophic Ecology of *Engraulis ringens*: Assessing Diet Through Stomach Content and Stable Isotope Analysis. Fishes, 9, 475. https://doi.org/10.3390/fishes9120475

Costalago D, Navarro J, Álvarez-Calleja I, Palomera I (2012). Ontogenetic and seasonal changes in he feeding habits and trophic levels of two small pelagic fish species. Mar. Ecol. Prog. Ser. Vol 460: 169-181, doi: 10.3354/meps0975.

Espinoza P & Bertrand A (2014) Ontogenetic and spatiotemporal variability in anchoveta (*Engraulis ringens*) diet off Peru. J Fish Biol 84(422):435. doi:10.1111/jfb.12293

Llanos A, Herrera G, Bernal P (1996). Análisis del tamaño de las presas en la dieta de las larvas de cuatro clupeiformes en un área costera de Chile central. Sci. Mar., 60, 435-42.

Martínez del Rio C, Sabat P, Anderson-Sprecher R, Gonzalez SP (2009). Dietary and isotopic specialization: the isotopic niche of three Cinclodes ovenbirds. *Oecol.* 161:149-159.

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007). A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429-436.

Pauly D, Jarre A, Luna S, Sambilay V, Rojas de Mendiola B, Alamo A (1989). On the quantity and types of food ingested by Peruvian anchoveta, 1953-1982. In The Peruvian Upwelling Ecosystem: Dynamics and Interactions, ed. D. Pauly, P. Muck, J. Mendo and I. Tsukayama. ICLARM Conf. Proc., 18, 109-24.

Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist J (2015) A new probabilistic method for quantifying n-dimensional ecological niches and niches overlap. Ecology 96: 318-324. https://doi.org/10.1890/14-0235.1.

Takasuka A, Oozeki Y, Aoki I (2007). Optimal growth temperature hypothesis: Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? Canadian Journal of Fisheries and Aquatic Science, 64, 768-776. https://doi.org/10.1139/f07-052

Van der Lingen CD, Bertrand A, Bode A, Brodeur R, Cubillos LA, Espinoza P, Temming A (2009). Trophic dynamics. In D. Checkley, J. Alheit, Y. Oozeki & C. Roy (Eds.), Climate change and small pelagic fish (pp. 112-157). Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511596681

Vander Zanden & Rasmussen J (2001). Variation in δ^{13}C and δ^{15}N trophic fractionation: Implications for aquatic food web studies. Limnol. Oceanogr., 46(8), 2061-2066, by the American Society of Limnology and Oceanography, Inc. DOI: 10.4319/lo.2001.46.8.2061

Wiesebron LE, Castro LR, Soto S, Castillo J (2022). Small Differences in Diet Facilitate the Coexistence of Three Forage Fish Species in an Inshore Northern Patagonian Habitat. Front. Mar. Sci. 8:792377. doi: 10.3389/fmars.2021.792377