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► To cite this version:

Pamela Toledo, Edwin Niklitschek, Audrey M. Darnaude, Félix Leiva, Chris Harrod, et al.. The trophic ecology of partial migration: insights from *Merluccius australis* off NW Patagonia. ICES Journal of Marine Science, 2020, 77 (5), pp.1927-1940. 10.1093/icesjms/fsaa065 . hal-03404711

HAL Id: hal-03404711

<https://hal.science/hal-03404711v1>

Submitted on 3 Nov 2021



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Original Article

The trophic ecology of partial migration: insights from *Merluccius australis* off NW Patagonia

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Toledo, P., Niklitschek, E. J., Darnaude, A. M., Leiva, F. P., Harrod, C., Lillo, S., Ojeda, V., Klarian, S., Molina-Burgos, B. E., Gálvez, P., and Canales-Aguirre, C. B. The trophic ecology of partial migration: insights from *Merluccius australis* off NW Patagonia. – ICES Journal of Marine Science, 77: 1927–1940.

Received 27 September 2019; revised 26 February 2020; accepted 4 March 2020; advance access publication 18 June 2020.

Partial migration, where migrant and resident organisms coexist within the same population, has been found in many fishes. Although it seems obvious that different life cycles exploit habitats and food webs differently, few assessments about the trophic consequences of partial migration are available. To unveil part of this complexity, we combined otolith chemistry with stable isotope analyses data for hind-casting *Merluccius australis* habitat use and diet composition at age. By providing detailed information about lifetime variability in diet, trophic position, and prey demand of four *M. australis* life-cycle types, we show that these groups feed differentially in estuarine and oceanic habitats throughout their ontogeny. Although trophic positions were similar between habitats for juvenile and subadults, substantial differences between life-cycle types were found regarding lifetime diet and trophic demand. Thus, the more abundant and heavily exploited oceanic stock of *M. australis* was heavily dependent of estuarine habitats within the Patagonian Fjords System, where it consumes large biomasses of *Macruronus magellanicus*, *Pasiphaea*, *Sprattus fuegensis*, and Euphausiidae at earlier stages. We show ignoring trophic consequences of partial migration and life-cycle diversity may produce highly biased results, both in terms of prey and habitat use, which appears critical for multispecies and ecosystem management approaches.

Keywords: migration ecology, partial migration, Patagonian Fjords, Southern hake, stable isotope, trophic ecology

Introduction

Migration is a biological phenomenon observed in numerous terrestrial and aquatic species and includes a wide range of lifetime habitats, travelled distances, migration periodicity, and timing (Secor, 2015). The evolution of migration seems to have been promoted by several selective advantages, mainly associated with granting migrants the ability to use multiple niches during their ontogeny (Dingle and Drake, 2007). Nonetheless, the coexistence of both migratory and resident groups within a population, currently termed “partial migration” (Chapman *et al.*, 2012), is a common feature in migratory birds and fishes, which greatly increases life-cycle complexity (Dingle, 1996; Secor, 2015), affecting many individual, population, community, and ecosystem processes, at different temporal and spatial scales (Secor and Kerr, 2009; Chapman *et al.*, 2011). Moreover, it remains unclear whether individual life-cycle types are genetically determined or simply reflect phenotypical responses to ecological pressures (Secor, 2015).

Populations exhibiting partial migration and multiple life-cycle types pose multiple challenges to managers and scientists (Secor, 1999) as conventional monitoring and stock assessment approaches will fail to account for distribution, abundance, and demographic differences between life-cycle types. This can lead to biased assessments and result in unsuitable management measures with large repercussions on population resilience and productivity (Quinn and Collie, 2005; Kerr *et al.*, 2017). Multispecies and ecosystem approaches may also fail to account for the unrecognized complexity in trophic between prey and predators of species exhibiting multiple life-cycle types, which will inhabit different habitats and, thus, will consume different prey at different ages (Quinn and Collie, 2005; Hilborn *et al.*, 2015). This is one of the least studied dimensions of partial migration ecology.

Here, we investigate the trophic ecology of southern hake *Merluccius australis*, partially migratory groundfish, of high economic and ecological importance in Sub-Antarctic regions. This species is distributed in the Southern Hemisphere, where it has two large spatially separated populations, one located around Patagonia and the other around the islands of New Zealand (Machado-Schiaffino *et al.*, 2009). Overall, this species inhabits Sub-Antarctic regions, in a depth range between 50 and 600 m and is characterized by delayed sexual maturity (~9 years) and slower growth rates than those seen in most other hakes (Ojeda and Aguayo, 1986).

Merluccius australis uses both estuarine and oceanic habitats along the Patagonian Fjords System (PFS), mainly south from the 40°S (Aguayo-Hernández, 1995). Adults are believed to disperse seasonally from main spawning grounds located around coastal submarine canyons to feeding areas, located either in the PFS or along the Chilean continental shelf (Aguayo-Hernández, 1995; Lillo *et al.*, 2011). A large fraction of the eggs and larvae originated from these oceanic spawning grounds are advected to nursery areas within the PFS (Figure 1), whereas another part remains offshore in oceanic nursery habitats (Bustos *et al.*, 2007). Other eggs and larvae are, instead, produced locally and nursed around secondary spawning areas, within the PFS. Juvenile *M. australis* are then believed to migrate vertically from pelagic nursery habitats (<100 m) used during its first 1–2 years of life (16–22 cm) to demersal habitats (200–600 m depth) used preferentially by older ages.

Recent studies have shown that this population exhibits partial migration, with large variability in the way its different life-cycle types use estuarine and coastal habitats (Toledo *et al.*, 2019).

Using age, growth, and otolith chemistry analysis of juvenile, subadult, and adult individuals, these authors identified four basic life-cycle types for *M. australis* in NW Patagonia: oceanic residents, which remain in oceanic habitats during its whole life, oceanic migratory, which use oceanic nursery areas but migrate later, as subadults, to the PFS, estuarine residents, which remain within the PFS through life, and estuarine migratory, which are nursed in the PFS but migrate to oceanic waters before maturity.

The diet of *M. australis* off NW Patagonia changes with age and size, becoming progressively piscivorous, as also observed in many other fishes (Werner and Gilliam, 1984) and *Merluccius* species, such as *M. capensis* (Punt *et al.*, 1992), *M. merluccius* (Murua, 2010), *M. bilinearis*, *M. albus* (Garrison and Link, 2000), and *M. hubbsi* (Costa *et al.*, 2019), among other examples around the world. Thus, although *M. australis* juveniles mainly feed on pelagic crustaceans and small fishes, adults become almost totally piscivorous (Pool *et al.*, 1997; Dunn *et al.*, 2010; Arkhipkin *et al.*, 2015), preying heavily on *M. magellanicus*, which has been reported to contribute >90% of its diet, by mass (Lillo *et al.*, 2008, 2011). Within this general ontogenetic pattern, a significant degree of spatial, seasonal, sub-seasonal, and bathymetric variability in the diet has been found in some of these species, such as *M. merluccius* (Velasco and Olaso, 1998; Cartes *et al.*, 2009).

Despite sharing the general trophic pattern previously described, large differences in diet are believed to exist between *M. australis* inhabiting estuarine and oceanic habitats (Pool *et al.*, 1997; Lillo *et al.*, 2011). Given the existence of different life-cycle types, which exhibits a quite distinct habitat use patterns, there is an evident need to integrate the effects of overall and habitat-specific ontogenetic shifts in diet, prey availability, and migratory behaviours upon the lifetime trophic ecology of *M. australis* in this area (Toledo *et al.*, 2019). We believe this is a fundamental step needed to get a better understanding and more accurate estimates about the trophic role-played and the trophic pressures exerted by this predator upon the PFS and the continental shelf ecosystems.

Although the demographic and trophic consequences of life-history diversity have not been evaluated for *M. australis*, they might result particularly relevant for managing this currently overexploited population (Quiroz and Pérez, 2018), while moving from its current mono-specific management towards multi-specific or ecosystem approaches (Hilborn *et al.*, 2015; Kerr *et al.*, 2017). Of particular interest for this purpose is improving current understanding about trophic interactions between *M. australis* and *M. magellanicus* (Payá, 1992; Pool *et al.*, 1997), which is not only one of the most important forage species in the system but also the main target for the Chilean fishing industry (Niklitschek *et al.*, 2014). Interestingly, both species exhibit largely overlapping spawning areas (Bustos *et al.*, 2008) and partial migration within and between estuarine and oceanic habitats (Niklitschek *et al.*, 2014; Toledo *et al.*, 2019).

In the present work, we investigated the trophic ecology of *M. australis* at the individual, contingent (life-cycle type), habitat, and population scales by combining otolith chemistry data, that allowed us to hind-casting *M. australis* habitat use at age

(Toledo *et al.*, 2019), with carbon and nitrogen stable isotope analyses of fish soft tissues, suitable for estimating diet composition at the age in each habitat (DeNiro and Epstein, 1976; Hobson and Wassenaar, 2019). By doing so, we sought to evaluate the extent of trophic segregation between *M. australis* life-cycle types, compare their trophic position (TP) and assess the consequences of partial migration upon lifetime diet and trophic demand of *M. magellanicus* and other prey in estuarine and oceanic habitats. As a working hypothesis guiding our analyses, we expected to find evidence that the dominant estuarine-resident life cycle was selected to maximize the predation of *M. australis* upon *M. magellanicus*.

Material and methods

Over the last decades, stable isotopic analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) have been increasingly used to successfully identify the assimilated diet, food sources, TPs, feeding strategies, and movements of migratory species and quantify organic matter flows among ecosystems (Peterson and Fry, 1987; Post, 2002; Michener and Lajtha, 2008). Meanwhile, the chemical analysis of fish otoliths (ear stones) has been proved particularly efficient for recognizing the successive habitats inhabited by an individual throughout its life (Elsdon *et al.*, 2008; Secor, 2010; Darnaude *et al.*, 2014). In this work, both techniques were combined to provide unprecedentedly detailed information about lifetime variability in diet, TP, and prey demand of *M. australis* life-cycle types.

Study area

Our study focused on the NW Patagonian coast (40–47°S, Figure 1), which hosts the largest spawning and nursery grounds for *M. australis* around South America (Aguayo-Hernández, 1995). This is a highly heterogeneous seascape, notoriously shaped by the Patagonian Fjords and Channels System, PFS (Acha *et al.*, 2004; Iriarte *et al.*, 2010). Two main habitat types can be distinguished here, estuarine habitats, characterized by saline stratification and a superficial layer of estuarine water (salinity ≤ 31), and oceanic habitats, located west from the PFS, and whose upper layer is dominated by Sub-Antarctic water (Sievers and Silva, 2008). It must be acknowledged that, given this simplified classification, estuarine habitats include some deep basins (up to 400 m), whose deeper layers can be dominated by Modified Sub-Antarctic Water of salinity 31–33. As observed in other estuarine systems, the PFS host nursery areas essential for several demersal and pelagic fishes (Bustos *et al.*, 2008; Niklitschek *et al.*, 2014).

Sampling

Otolith and tissue samples from *M. australis*, as well as tissue/whole animal samples used to produce isotopic baselines for its putative prey, were collected between 2013 and 2016 from varied locations within each habitat type (Figure 1). As for estuarine habitats, most of the 111 invertebrate prey samples collected here were obtained thorough diagonal IKMT tows, whereas most of the 347 fish prey samples and all *M. australis* individuals

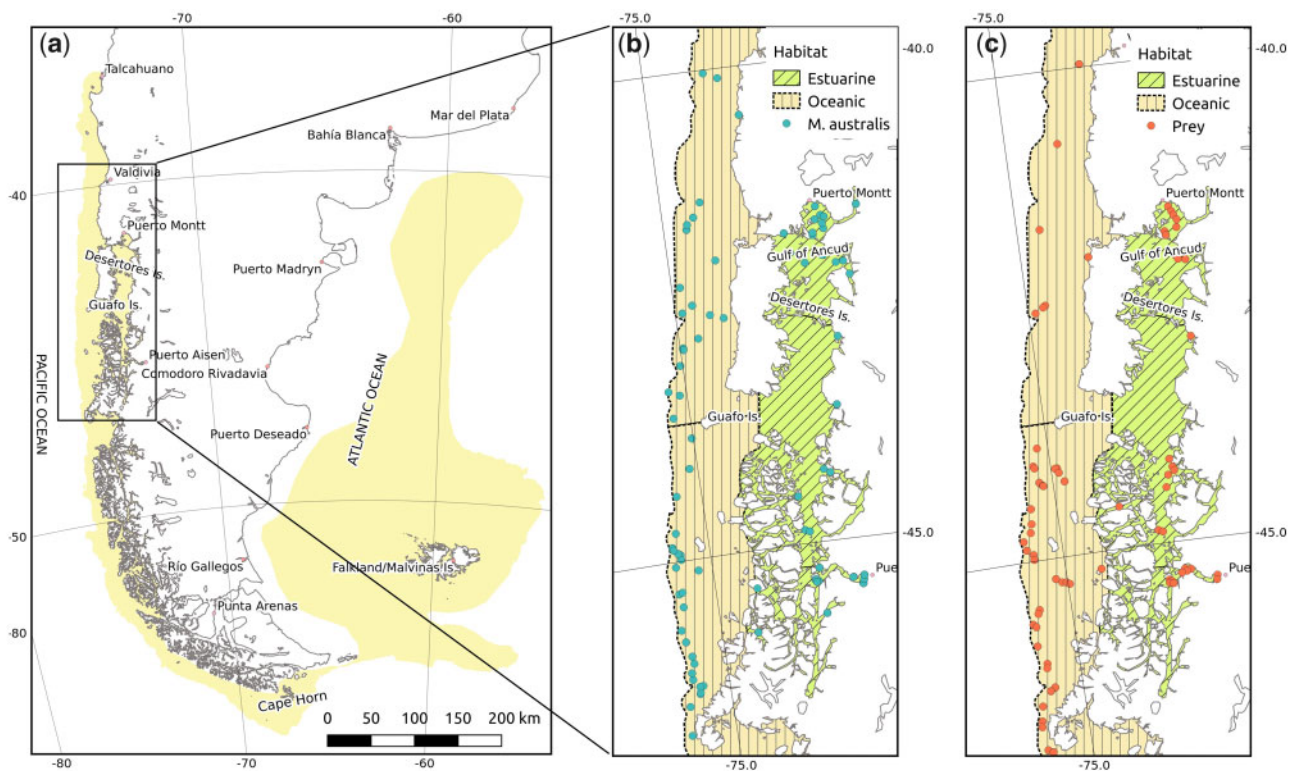


Figure 1. (a) Distribution of *Merluccius australis* around Patagonia and study area, (b) *M. australis* sampling locations, and (c) prey sampling locations in estuarine and oceanic habitats off NW Patagonia. Only prey and *M. australis* sampling locations for which exact coordinates were available are shown.

($n = 476$) were collected by sampling the catch and bycatch of artisanal longlines and purse-seines. All invertebrate ($n = 121$), fish prey ($n = 267$), and *M. australis* ($n = 206$) samples from the oceanic habitat were collected by zooplankton, midwater, and bottom trawls during winter hydroacoustic surveys carried out by the Chilean Fisheries Institute to assess *M. australis* and *M. magellanicus* spawning aggregations.

Some additional invertebrates and fish prey samples, also used for producing isotopic baselines of potential prey for each habitat type, were obtained from *M. australis* gut content but used only if no visual sign of digestion was observed. Primary consumer baselines for TP analysis (Post, 2002) were built using a collection of 122 Euphausiidae samples obtained using bongo, Tucker, and IKMT trawls, between August and December of 2013–2018, from both estuarine ($n = 74$) and oceanic ($n = 48$) habitats (Supplementary Tables SM 1-1 and SM 1-2).

Fish ageing and growth models

All 179 *M. australis* samples were sectioned and aged following standardized procedures based upon Ojeda and Aguayo (1986), setting the first of January as the arbitrary birth date. To back-calculate age as a function of otolith distance from the core (S), we combined a linear model, for all ages ≤ 0.5 years old, and a generalized von Bertalanffy growth model (VBGM, Pauly, 1981), re-parametrized according to Ogle and Isermann (2017), for older individuals. This combined otolith growth function was found to be more informative [lower Akaike (1973)'s Information Criterion, AIC] than either a single linear or a single VBGM function. As a result,

$$S = \begin{cases} S_0 + \beta_1 \cdot \text{age}, & \text{if age} < a_r \\ S_r + (S_\infty - S_r) \times \left\{ 1 - \exp[-D_r \cdot K \cdot (\text{age} - a_r)]^{b/D_r} \right\}, & \text{if age} \geq a_r, \end{cases} \quad (1)$$

where $S_0 = 30 \mu\text{m}$ (distance at age 0; Landaeta et al., 2018), β_1 is the initial slope, S_r is the distance from the core at the reference minimum age ($a_r = 0.5$ years), D_r is the estimated distance at a_r , $b = 1$, and S_∞ , K , and D are original VBGM parameters. All parameters were estimated through non-linear regression through the Levenberg–Marquardt algorithm (Moré, 1978), implemented in the R package minpack.lm (Elzhov et al., 2016). The inverse function used then to back-calculate age was defined as

$$\text{age} = \begin{cases} (S - S_0)/\beta_1, & \text{if } S < S_r \\ S_r + \frac{\log[-1/(a' - 1)]}{D \cdot K}, & \text{if } S \geq S_r, \end{cases} \quad (2)$$

where

$$a' = \left(\frac{S - S_r}{S_\infty - S_r} \right)^{D/b}. \quad (3)$$

Total length (TL) at age, back-calculated age at length and VBGM parameters required by Temming and Herrmann's (2009) consumption model (see below) were estimated by fitting (1) to TL instead of to otolith distance. Here, a_r was set to 1 year old, and S_0 to 3 cm (Landaeta et al., 2018). Separate otolith and body length growth models were fitted for estuarine and for oceanic *M. australis* samples, as the combination of two separate models was

found to be more informative (lower total AICs) than common models in both cases.

Life-cycle type identification

Sagittal otoliths from all *M. australis* samples were prepared and analysed for elemental composition following the same strict protocols and facilities described by Toledo et al. (2019). Final concentrations and limits of detection were computed off-line with the R package ElementR (Siroto et al., 2017). Raster data were discretized and averaged within 29- μm sampling intervals, which were then grouped into sequential triplets. To reduce autocorrelation among overlapping readings within triplets, each triplet was finally represented by its median, addressed from now on as a spot.

Random forest models (Cutler et al., 2007), which outperformed multinomial and linear discrimination models, were used to identify life-cycle types in 117 subadult and adult individuals ($>60 \text{ cm}$, ≥ 7 years old). One origin discriminant model (ODM) and two habitat discriminant models (HDMs) were fit using otolith concentrations of B, Na, Mg, Mn, Sr, and Ba. The ODM aimed to identify nursery origin was fitted using solely early-life otolith chemical records (264–1200 μm from the core) from pre-migratory (<2 years old) individuals (Toledo et al., 2019). HDMs were fitted using otolith chemical records from marginal otolith regions defined to represent the last 3 months of life of each individual. Depending on fish age and growth, this marginal region was defined to start between 38 and 630 μm inward from the edge. Higher accuracy was reached by fitting two separate HDMs: one for fish <2 years old (HDM1) and another for fish ≥ 2 years old (HDM2). Out of the bag, error rates were 2.84% for the ODM, 3% for the HDM1, and 6% for the HDM2 models.

To hind-cast nursery origins, the ODM was applied to estimate the probability of each spot analysed between 264 and 1200 μm from the core, for each modelled origin (estuarine or oceanic). Single spot probabilities were then averaged within individuals and used to assign a putative origin to each fish, which corresponded to the habitat reaching the highest mean probability. HDMs were applied to hind-cast habitat use probabilities for all spots lying between 264 μm from the core and the otolith edge and then averaged within back-calculated intervals to represent a season (0.25 years) of life. As before, the putative habitat assigned to each of these life intervals corresponded to the one reaching the highest mean probability. As a result, seasonal habitat use profiles were made available for 117 subadult and adult individuals ≥ 7 years old collected at estuarine ($n = 59$) and oceanic ($n = 58$) habitats. Using this information, all fish were classified into one of the four life-cycle types defined by Toledo et al. (2019).

Stable isotope analysis

Muscular tissue ($\sim 1 \text{ cm}^3$) or whole organism samples from fish and invertebrates, respectively, were transported in ice and frozen as soon as possible (-20°C). Before analysis, samples were thawed ($\sim 20^\circ\text{C}$), rinsed, oven-dried at 60°C , and ground to a fine powder (Jardine et al., 2003). To increase the precision of some small and/or abundant prey, we pooled and homogenize samples from 2 to 15 individuals from the same species, fishing event, and class size ($<10\%$ difference in length or mass).

Subsamples of 0.8–1.2 mg were analysed either at the Stable Isotope Facility of the University of California-Davis (UCD),

using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd, Cheshire, UK), or at the Isotope Analysis Laboratory of the University Andrés Bello (UNAB), using a Eurovector elemental analyser coupled to a mass spectrometer (Nu-instruments). Isotopic compositions were expressed using the conventional δ notation and the standards Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen (Peterson and Fry, 1987). Reported analytical precisions were 0.06‰ for $\delta^{13}\text{C}$ and 0.13‰ for $\delta^{15}\text{N}$ at UCD and 0.1‰ for $\delta^{13}\text{C}$ and 0.2‰ for $\delta^{15}\text{N}$ at UNAB.

$\delta^{13}\text{C}$ values were corrected to account for lipid depletion as suggested by Kiljunen *et al.* (2006), Post *et al.* (2007), and others, when C:N ratios exceeded 3.5 (Skinner *et al.*, 2016). Algorithms proposed by Kiljunen *et al.* (2006) and Logan *et al.* (2008) were used for fish and invertebrate signatures, respectively. To reduce variability caused by laboratory and year effects, we fitted multiple regression models for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measured in *M. australis* as a function of TL, laboratory, and year of analysis. By subtracting the coefficients from these regressions, we standardized all data, using the data produced at UCD in 2013 as the arbitrary reference dataset.

Diet composition

All sampled *M. australis* individuals were classified into five size classes based on TL: class I: (9–25) cm, class II: (25–40) cm, class III: (40–55) cm, class IV: (55–70) cm, and class V: >70 cm (size-frequency histograms within classes and habitats provided as Supplementary Figure SM 1). To estimate the relative contribution of all sampled prey to each size class, we used a mixing models approach (Everitt and Hand, 1981), as implemented in the Bayesian oriented R package “simmr” (Parnell, 2016). Trophic discrimination factors (TDFs) corresponded to those proposed by McCutchan *et al.* (2003): $\delta^{13}\text{C} = 1.3 \pm 0.30\text{‰}$ and $\delta^{15}\text{N} = 2.9 \pm 0.32\text{‰}$.

Putative prey was defined and their corresponding priors estimated for each size class and habitat pooling and averaging information from several authors (details available in Supplementary Tables SM 1-1 and SM 1-2). Because of limitations related to the use of only two discriminant isotopes, small sample sizes, similar isotopic signatures, and/or uncertain identification, only prey exhibiting priors >0.001 were included in the analysis. Moreover, some prey were combined into higher taxonomic levels as done for the order Clupeiformes, the family Euphausiidae, and several members of the order Decapoda. Cannibalism was assessed for size classes III–V (≥ 40 cm), using *M. australis* baselines computed by averaging all isotopic data available from size classes I and II.

Food consumption models

Individual food consumption (C_{ai} in g) at discrete age intervals (Δt) of 0.25 years, throughout the lifespan of each fish, was estimated using Temming and Herrmann’s (2009) model, which is largely based in VBGM parameters, following the relationships:

$$C_{ai} = Q \cdot W_{ai}^m \cdot \Delta t, \quad (4)$$

and

$$Q = \frac{1}{k_3} \cdot b \cdot K \cdot W_{\infty}^{D/b}, \quad (5)$$

where, W_{ai} is the mean individual mass at age a , m is the theoretical allometric scaling factor for consumption, assumed to be 0.75 following (West *et al.*, 2001), $k_3 = 0.59$ (net conversion efficiency, Temming and Herrmann, 2009), b is the allometric exponent of the mass-length relationship, K and W_{∞} are VBGM parameters. Different allometric exponents (b) were estimated for fish from the estuarine and the oceanic habitat.

Food consumption per season of life (C_{ai}) was assumed to occur in one of the two habitat types (h) following the habitat use profiles previously hind-casted for each individual from its otolith chemical profiles. After back-calculating size from age through (1), the seasonal contribution of prey j to the diet of each individual i (P_{ajh}) was assumed equal to the mean contribution observed for prey j at habitat h for the corresponding (back-calculated) size class.

Thus, lifetime individual consumptions of each prey and habitat for each life-cycle types were computed as

$$LC_{ijhl} = \sum_{a=0}^{a=\text{age}} C_{ai} \cdot P_{ajhl}. \quad (6)$$

Lifetime contributions of different preys and habitats to the diet of each *M. australis* life-cycle type (l) were then computed as

$$P_{jhl} = \frac{1}{n_l} \sum_{i=1}^{n_l} \left(\frac{LC_{ijhl}}{\sum_{j=1}^J LC_{ijhl}} \right). \quad (7)$$

Population trophic demand

To provide a gross but still informative estimate of the trophic demand of the estuarine and oceanic stocks of *M. australis* in NW Patagonia, after accounting for partial migration effects, we considered the maximum sustainable yield (MSY) scenario defined by Quiroz and Pérez (2018), which sets biomass (B_{MSY}) and fishing mortality (F_{MSY}) goals of 171 740 t, and 0.24-year⁻¹, respectively. Given a minimum age of capture of 9 years old and a natural mortality rate (M) of 0.21, abundances at age (N_a) were computed from B_{MSY} assuming a stable population, 50% of which feeds in the study area. Proportional distributions of the stock between the estuarine and the oceanic habitats (pH) of 0.175 and 0.825, respectively, resulted from averaging winter hydroacoustic results available for years 2003, 2005, and 2009 (Lillo *et al.*, 2010, 2011). Proportional abundance by life-cycle type (pL) was assumed equal to those reported by Toledo *et al.* (2019). Thus, summing over ages 0–25 and the four life-history types, total trophic demands per habitat and prey (TD_{jh}) were computed as

$$TD_{jh} = \sum_{a=0}^{25} \sum_{l=1}^L N_a \cdot pH \cdot pL \cdot C_a \cdot P_{ajhl}. \quad (8)$$

Trophic position

TGs for each size class and habitat were computed following the general equation of Cabana and Rasmussen (1996):

$$TP = \lambda + (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{base}})/TEF, \quad (9)$$

where $\lambda = 2$ corresponded to the baseline trophic level assumed for filter-feeding bivalves and TDF (TEF, Trophic Enrichment Factor) = $2.9\text{‰} \pm 0.32 \text{ SD}$ (McCutchan et al., 2003). To account for uncertainty both in baseline and consumer isotopic values, we follow the Bayesian approach described by Quezada-Romegialli et al. (2018). To reduce both the effects of seasonal variability and summer migration/dispersal upon TP estimates and their comparison between habitats, only fish samples collected in winter were used for size classes II–V. No samples from size class I were excluded, however, given the limited number of available samples and the low probability of long-range seasonal movements corresponding to this group.

Baseline TPs ($\delta^{15}N$) of $10.6\text{‰} \pm 2.26$ (SD) and $11.4\text{‰} \pm 1.09$ (SD) were estimated from different filter-feeders (*Aulacomya atra*, *Mytilus chilensis*, *Perumytilus purpuratus*, and *Venus antiqua*). Although filter-feeder sample sizes were small, our mean $\delta^{15}N$ estimates were almost identical to values previously reported in the same study area (Mayr et al., 2011; Klarian et al., 2018). All analyses and figures (apart from the location map, generated in QGIS v2.18) were implemented and generated in R version 3.5.1.

Results

Prey contributions to *M. australis* diet by size class and habitat

The diet of *M. australis* changed with size and habitat (Figure 2). In estuarine habitats, size class I juveniles (9–25 cm TL) mainly consumed Euphausiidae and *Pasiphaea*, whose contributions (credibility intervals) reached 58–64% and 18–25%, respectively.

Macruronus magellanicus represented the main diet-item for all remaining size classes in the estuarine habitat, with credibility intervals raising from 44 to 55% for size class II to 91–97% for size class V (Figure 2). *Sprattus fuegensis* was identified as a relevant prey for *M. australis* size classes II and III (25–55 cm), with median contributions of 7 and 16%, respectively.

In the oceanic habitat, the main prey identified for size class I juveniles corresponded to *Pasiphaea* (64–72%) instead of Euphausiidae, which contributed only 14–21% (Figure 2). Size class II juveniles in the oceanic habitat showed a relatively more diverse diet composed by *Pasiphaea*, mesopelagic fishes, *M. magellanicus* and Euphausiidae, whose median contributions ranged between 14 and 34%. Starting from subadult size class III, there was an evident increase in the estimated contribution of *M. magellanicus* associated with a strong decrease in the estimated contributions of pelagic crustaceans and other fishes. This tendency was accentuated in the largest fish (>60 cm), where the proportional contribution of *M. magellanicus* represented 87–94% of *M. australis* diet (Figure 2).

In summary, the diet of *M. australis* in both habitats showed a similar ontogenetic increase in the contribution of *M. magellanicus* to *M. australis* diet, with median values rising from 3% (size class I) to 95% (size class V) in the estuarine habitat and from 1 to 91% in the oceanic habitat. Although *S. fuegensis* (up to 16%), cannibalism (up to 13%), and *Merluccius gayi* (up to 6%) were relevant in the estuarine habitat (Figure 2), prey such as Macrouridae, *Micromesistius australis*, and *Sergestes* only appeared to have some trophic relevance (1–6%, Figure 2) in the oceanic habitat. Detailed information about prey

contribution quantiles is provided as Supplementary Tables SM 1-3 and SM 1-4.

Life-cycle type diversity and lifetime diets

Otolith chemistry analysis allowed us to discriminate life-cycle types for a total of 86 subadult (>55 cm) and adult (>70 cm) individuals. Out of 40 fish sampled in the estuarine habitat, 20 were classified as estuarine-resident, 18 as estuarine-migratory, and only 3 as oceanic-migratory types. From 46 samples captured in the oceanic habitat, only 7 corresponded to oceanic-resident, 15 to oceanic-migratory, and 24 to estuarine-migratory life-cycle types. When lifetime diets were hind-casted for these fish, several differences in trophic ecology emerged between life-cycle types (Figure 3).

Although all life-cycle types were found to rely heavily on *M. magellanicus*, both migratory life-cycle types were shown to access and exploit a greater diversity of prey than resident life-cycle types. Moreover, resident life-cycle types would exploit some prey, such as *M. magellanicus*, *Pasiphaea*, and Euphausiidae, in both habitats, with relatively similar intensities (Figure 3). Although large individual variability was found within both migratory life-cycle types, the estuarine habitat tended to contribute a large fraction of the lifetime diet consumed by the oceanic-migratory type, which tended to be greater than what was contributed by the oceanic habitat to the estuarine-migratory life cycle (Figure 3).

TP of *M. australis* by habitat and size classes

The TP of *M. australis* increased with size, from overall median values of 4.0 at size class I to 4.7 at size class V (Figure 4). Moreover, TP was consistently higher ($\Delta_{TP} = 0.24$ – 0.62) in the oceanic than in the estuarine habitat, across all size classes (Figure 4), being larger for size classes I–II ($\Delta_{TP} \geq 0.52$, posterior- $p \leq 0.079$). Within habitats, the TP of *M. australis* increased steadily with size, from a median (95% credible interval) of 3.7 (3.34–4.36) to 4.6 (4.08–5.33) in the estuarine habitat and from 4.3 (3.77–5.03) to 4.8 (4.25–5.65) in the oceanic habitat (Figure 4). Differences in TP between size classes were larger within the estuarine habitat than within the oceanic one. For instance, the median difference between size classes V and I reached 0.87 (posterior- $p = 0.019$) in the estuarine habitat, but only 0.56 (posterior- $p = 0.11$) in the oceanic one.

Trophic demand of oceanic and estuarine stocks of *M. australis* in the NW Patagonia under an MSY scenario

We found that the estuarine stock depended, fundamentally, of prey consumed within the estuarine habitat such as *M. magellanicus* (66%), *Pasiphaea* (8%), *S. fuegensis* (6%), and Euphausiidae (4%), with a total annual prey demand of 120 700 t under an MSY scenario (Figure 5). Annual prey demand by the oceanic stock was much higher (438 000 t) and also highly dependent of prey consumed in the estuarine habitat, which had supplied ~60% of the total demand of this stock, including 174 800 t of *M. magellanicus*, 25 900 t of *Pasiphaea*, and 19 700 t of *S. fuegensis*. Overall, sustaining the whole *M. australis* population, under MSY, would require 383 200 t of prey consumed in the estuarine habitat, mainly *M. magellanicus*, *Pasiphaea*, and *S. fuegensis*, and 175 600 t of prey consumed in the oceanic habitat, mainly *M. magellanicus*, *Pasiphaea*, and mesopelagic fishes (Table 1). If analogous estimates had been obtained neglecting migration (i.e.

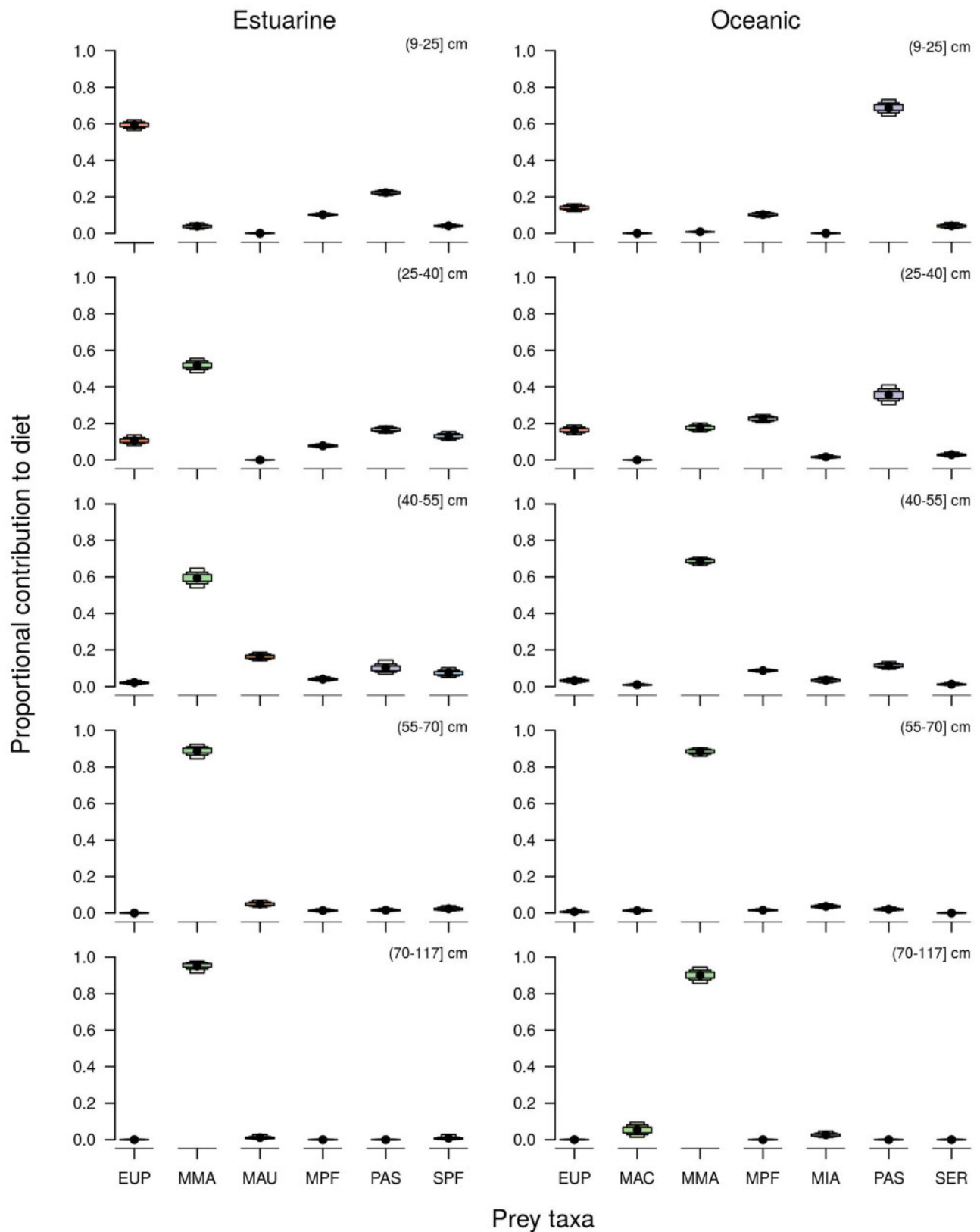


Figure 2. Median, 50, 75, and 95% credibility intervals of the estimated contributions from main prey to the diet of *Merluccius australis* during its ontogeny in estuarine and oceanic habitats from NW Patagonia by size classes (class I: 9–25 cm, class II: 25–40 cm, class III: 40–55 cm, class IV: 55–70 cm, and class V: >70 cm). Only taxa contributing >2% to the diet of *M. australis* are shown. EUP, Euphausiidae; MMA, *Macruronus magellanicus*; MAU, *Merluccius australis*; MPF, Mesopelagic fishes; PAS, *Pasiphaea*; SPF, *Sprattus fuegensis*; MAC, Macrouridae; MIA, *Micromesistius australis*; SER, *Sergestes*.

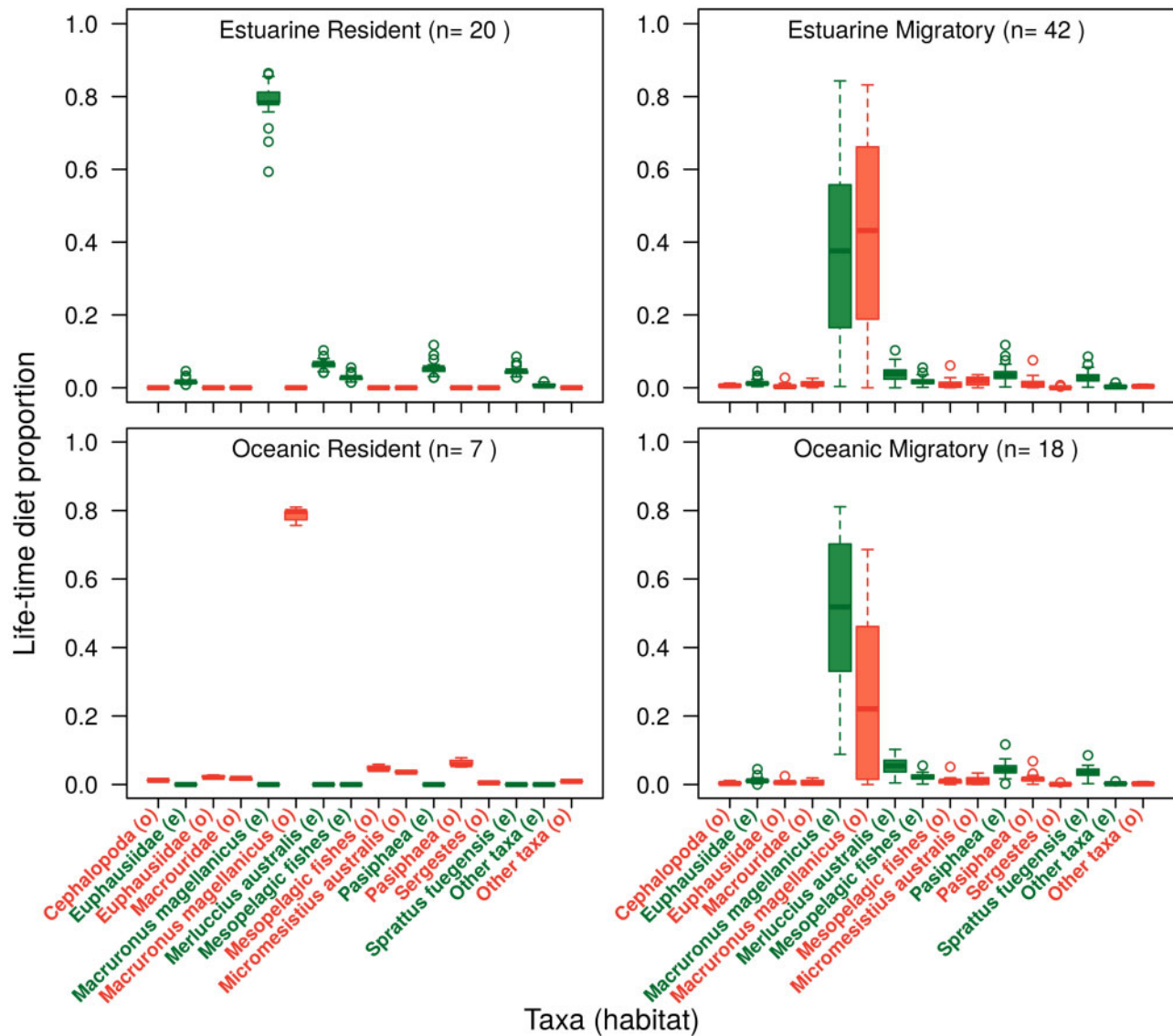


Figure 3. Estimated lifetime contributions of prey from estuarine (in green) and oceanic (in orange) habitats to the four main life-cycle types identified in *Merluccius australis* off NW Patagonia. Only taxa contributing >2% to the lifetime diet of *M. australis* are shown. Although boxes represent percentiles 25 and 75%, whiskers extend up to the more distant observation or to 1.5 times the interquartile range, whichever limit is reached first.

assuming all sampled fish were resident), an average underestimation bias of 68% had affected prey demand estimates upon the estuarine habitat, whereas an average overestimation bias of 145% had affected estimates corresponding to the oceanic area (Table 1).

Discussion

Most trophic studies deliver snapshots of diet composition, prey consumption, or trophic relationships for a given population and habitat, without considering individual variability, life-cycle diversity, and the effects of migrations upon the sequential use of different habitats during ontogeny (Garvey and Whiles, 2016). In this study, we show how partial migration and the existence of different life-cycle types can affect diet, TP, and prey demand of a fish

population. Selecting *M. australis* off NW Patagonia as a case study, we gain precious knowledge on how partial migration and the existence of different life-cycle types may affect lifetime diet, TP, and prey demand of top predators. Important differences were found between the four basic life-cycle types described recently for this species (Toledo et al., 2019), yielding quite new insights about the sequential exploitation of different habitats and prey by *M. australis*. To tackle these questions, we had focused on horizontal and long-term movements between major habitat types, lacking of enough resolution for exploring smaller scale and/or shorter-term effects, such as seasonal migrations, sub-seasonal movements, and/or bathymetric displacements upon food web dynamics expected for this species and already reported for other *Merluccius* species (Velasco and Olaso, 1998; Velasco et al., 2003; Cartes et al., 2009).

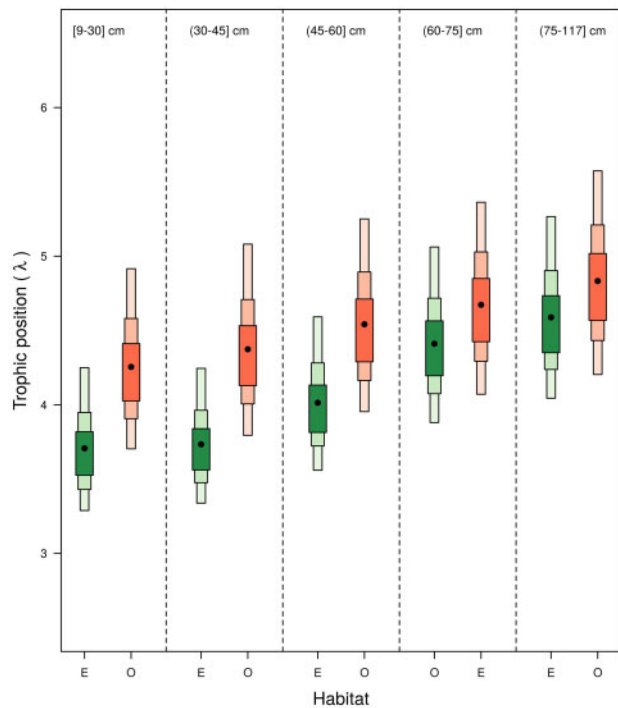


Figure 4. Median, 50, 75, and 95% credibility intervals of estimated TPs for different size classes of *Merluccius australis* in estuarine (E, green) and oceanic (O, orange) habitats off NW Patagonia.

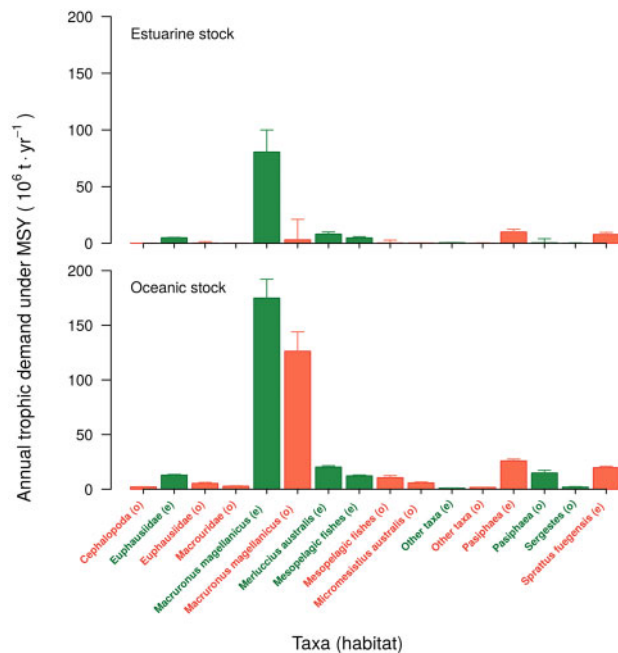


Figure 5. Annual trophic demand of estuarine (e, green) and oceanic (o, orange) prey by estuarine and oceanic stocks of *Merluccius australis*, estimated under a scenario of MSY. Only taxa contributing >2% to the lifetime diet of *M. australis* are shown.

Ontogenetic changes in diet

The ontogenetic diet we have found in *M. australis* can be summarized as a progressive decline in the feeding importance of

invertebrates (*Pasiphaea* and Euphausiidae), accompanied by an equivalent increase in the consumption of fishes, particularly *M. magellanicus*, ending in a piscivorous and almost mono-specific adult diet, particularly in the estuarine habitat. These were not unexpected results because similar ontogenetic changes had been previously found for this species in the same area (Payá, 1992; Pool *et al.*, 1997), and elsewhere (Dunn *et al.*, 2010; Arkhipkin *et al.*, 2015; Giussi *et al.*, 2016), as well as in other members of the same genus, which also tend to consume larger and deeper prey with age (e.g. Punt *et al.*, 1992; Garrison and Link, 2000; Murua, 2010; Costa *et al.*, 2019). Adult *M. australis*, on the other hand, appear to be a much more specialized predator than other members of this genus, particularly those inhabiting shallower strata, such as *M. merluccius* (Murua, 2010), *Merluccius paradoxus* (Punt *et al.*, 1992), and *M. gayi* (Cubillos *et al.*, 2007). Nonetheless, a greater contribution of other prey, such as blue whiting, could be expected south from our study area, where *M. australis* becomes particularly abundant.

Highly piscivorous adult diets are rather common features not only in *Merluccius* but also in many other fish taxa. Although this change seems facilitated by the ontogenetic development of better hunting capabilities (greater mouth size and swimming speed), it has been probably selected to satisfy larger energy requirements derived from migration and reproduction (Werner and Gilliam, 1984; Snover, 2008). For instance, *M. magellanicus*, the main prey of *M. australis*, contains almost twice as much energy per unit of mass than most invertebrate prey consumed by this predator (Ciancio *et al.*, 2007). How these ontogenetic diet changes towards increased piscivory interact with migratory movements to modify the role of a predator in different habitats and/or ecosystems remains poorly explored (McCauley *et al.*, 2012), particularly when multiple life-cycle types and migratory patterns exist within the same population. Although largely based on models and assumptions, we believe the preliminary quantifications provided in the present work result useful to illustrate how relevant maybe integrating life-cycle diversity and trophic ecology for migratory top predators.

Cannibalism

Species from the *Merluccius* genus are characterized by relatively high cannibalism rates, with values between 23 and 70% observed in species such as *M. bilinearis*, *M. capensis*, *M. gayi*, and *M. merluccius* (Stobberup, 1992; Juanes, 2003; Mahe *et al.*, 2007). Even considering some potential overestimation owing to isotopic proximity between juvenile *M. australis* and *M. gayi*, our results show that cannibalism in *M. australis* would be very moderate, with maximum values of only 10–16%, found at intermediate sizes, in the estuarine habitat (Figure 2). Cannibalism trade-offs are habitat- and species-specific and expected to maximize average fitness (Juanes, 2003). Although we are uncertain about ecological or evolutionary reasons for the low cannibalism rate observed in *M. australis*, it may be related to the large availability of small *M. magellanicus* in the estuarine habitat and to the massive emigration of subadults of estuarine origin to oceanic waters (Toledo *et al.*, 2019), which substantially contributes to the spatial segregation between predominantly estuarine juveniles and predominantly oceanic adults, in the local population (Bustos *et al.*, 2007; Toledo *et al.*, 2019).

Table 1. Total consumption of prey (TC) by *Merluccius australis* estimated under hypothetical abundances expected for each habitat under an MSY scenario.

| Prey habitat | Taxa | Partial migration TC (SE) | Naive TC (SE) | Nominal bias (%) |
|--------------|---------------------------------|---------------------------|---------------|------------------|
| Estuarine | Euphausiidae | 17.7 (0.78) | 10.7 (2.77) | -40 |
| | <i>Macruronus magellanicus</i> | 255.3 (26.05) | 72.3 (5.4) | -72 |
| | <i>Merluccius australis</i> | 28.3 (2.29) | 7.7 (0.72) | -73 |
| | Mesopelagic fishes | 17 (1.39) | 6.5 (0.77) | -62 |
| | <i>Pasiphaea</i> | 35.9 (2.92) | 14.2 (1.88) | -60 |
| | <i>Sprattus fuegensis</i> | 27.5 (2.26) | 10.6 (1.25) | -61 |
| | Other taxa | 1.5 (0.27) | 0.5 (0.09) | -63 |
| | Total | 383.2 (26.46) | 122.6 (6.56) | -68 |
| Oceanic | Cephalopoda | 2.2 (0.29) | 5.7 (0.08) | 161 |
| | Euphausiidae | 5.5 (1.58) | 28.1 (3.47) | 414 |
| | Macrouridae | 2.9 (0.42) | 5.3 (0.17) | 84 |
| | <i>Macruronus magellanicus</i> | 129.3 (25.36) | 239.9 (17.28) | 86 |
| | Mesopelagic fishes | 10.9 (3.14) | 47.3 (3.98) | 335 |
| | <i>Micromesistius australis</i> | 6 (0.83) | 11.7 (0.81) | 94 |
| | <i>Pasiphaea</i> | 15.3 (4.38) | 80.2 (10.33) | 426 |
| | <i>Sergestes</i> | 1.9 (0.63) | 6.4 (0.63) | 230 |
| | Other taxa | 1.7 (0.39) | 5.6 (0.26) | 229 |
| | Total | 175.6 (26.00) | 430.1 (20.84) | 145 |

Partial migration TC corresponds to estimates produced after reconstructing lifetime habitat use and migratory patterns for each sampled fish. Naive TC estimates produced assuming all sampled fish were resident.

Trophic position

As observed in most fishes, we found the TP of *M. australis* tended to increase progressively with ontogeny, from minimum median values of 3.7–4.3 in juvenile fish to maximum values of 4.6–4.8 in adults. Although these positions seem quite high when compared with values of 3.6–4.0 reported for *M. gayi* (Hückstädt et al., 2007) and *M. merluccius* (Loc'h and Hily, 2005), they are similar to those reported by Ciancio et al. (2007) for the same species (4.4) and *M. hubbsi* (4.9) in the Atlantic Ocean. Differences in TP between habitats were moderate, suggesting a similar trophic role is played by juvenile and subadult *M. australis* in both habitats.

The slightly higher trophic levels found for juveniles size classes in the oceanic habitat may be related to more diverse diets in the oceanic habitat, with higher consumptions of *Pasiphaea* and mesopelagic fishes in this habitat. Moreover, isotopic differences between habitats may result also from a well-documented ecosystem and food web differences between these habitats (Iriarte et al., 2010; Vargas et al., 2011). From a methodological point of view, the TP of Euphausiidae, assumed here to be 2.0, requires further validation in each of these habitats.

Trophic relationships under partial migration

One of the main adaptive advantages of migration is the expansion of the resource base for a given population (McCauley et al., 2012). Thus, either different or common prey can be exploited from different ecosystems or food webs by a single predator species. The complexity of these relationships increases as these exploitation patterns may change substantially for each life-cycle type. Although all life-cycle types of *M. australis* exploit similar prey, migratory contingents gain access to Euphausiidae, *M. magellanicus*, and *Pasiphaea* from two relatively independent food webs: the estuarine web, mainly based upon dinoflagellates, and the oceanic one, mainly based upon diatoms (Medina et al., 2014). As a downside of migratory life cycles, fish may be forced to face a larger diversity of diseases and parasites than resident

ones, which may affect their survival, energetic performance, and fitness (Piertney and Oliver, 2006).

When partial migration increases life-cycle diversity in both predators and prey, the complexity of their predator–prey interactions can increase largely (Brodersen et al., 2008). Trophic interactions between *M. australis* and *M. magellanicus* seem conditioned by their extensive and largely overlapping areas of distribution, the oceanographic and bathymetric heterogeneity of the different habitats that shape these areas, and the diversity of life-cycle types presented by both species (Niklitschek et al., 2014; Toledo et al., 2019). Because *M. magellanicus* is the main prey for all life-cycle types in *M. australis*, we speculate that the dominant migratory pattern of *M. australis* (estuarine migratory) allows for maximizing energetic returns obtained from this prey.

Estuarine habitats within the PFS are known to harbour high concentrations of subadults (age 2–4 years) of *M. magellanicus*, corresponding to a mix of both estuarine-resident and, mainly, oceanic-migratory contingents of this species (Niklitschek et al., 2014). These subadults are potentially hunted by both the estuarine-resident and the estuarine-migratory contingents of *M. australis* as well as by the oceanic-migratory contingent entering early in life to the PFS. Then, as *M. magellanicus* approaches sexual maturity, most individuals emigrate to adjacent coastal oceanic zone, where they become available to the oceanic-resident and the estuarine-migratory contingents of *M. australis*, as well as to the oceanic-migratory contingents that had returned to the ocean after entering the PFS. Following this logic, the estuarine-migratory contingent of *M. australis* is the best suited to track the dominant migratory life cycle of *M. magellanicus*, without incurring in the cost of a double migration, as would be the case for the oceanic-migratory contingent of *M. australis*.

Lifetime diet and trophic demand from different habitats

Assessing the ecosystem impact of fisheries implies, among many other aspects, to quantify in detail the trophic relationships of

exploited populations (Agardy, 2000). The same applies to over-come mono-specific approaches, which tend to ignore not only trophic interactions but also the physical and biological factors conditioning ecosystem productivity, community structure, population dynamics, and trophic roles of predators and their prey (Agardy, 2000; Hilborn, 2011; Skern-Mauritzen *et al.*, 2016). Additional levels of complexity are granted if such a task is focused on populations exhibiting diverse life-cycle types, as illustrated here for *M. australis*.

We have shown that treating life-cycle types as separate trophic entities lead to much more accurate estimates of lifetime diet compositions and total trophic demands than assuming a homogeneous population. Estimating the proportion of life-cycle types and hind-casting population size at age are, however, challenging but not unrealizable tasks we have tackled using a hypothetical population size scenario, set equal to MSY, a composition of life-cycle types constant and equal to Toledo *et al.* (2019), and a constant mortality rate of 0.25. Our results show the larger oceanic stock, exploited exclusively by industrial vessels and largely composed by estuarine-migratory fish (Toledo *et al.*, 2019), is unexpectedly and highly dependent of prey from the estuarine habitat, such as *M. magellanicus*, *Pasiphaea*, *S. fuegensis*, and Euphausiidae. Less surprising, the estuarine stock, less abundant and exploited exclusively by artisan fishermen, relies heavily (almost exclusively) on prey inhabiting this same estuarine habitat.

Conclusions and final remarks

Identifying and understanding the diversity of life-cycle types that coexist in a species or population may be fundamental for management and conservation purposes (Secor, 2015). Although we unveiled here some fundamental consequences of this diversity upon the diet and prey demand of a top fish predator, we are yet to investigate further the implications of these new insights on predator-prey regulations and dynamics. Overcoming these knowledge gaps is an essential requirement both at global and regional scales to improve management and conservation of species and ecosystems, particularly when involving overexploited predators and prey, such as *M. australis* and *M. magellanicus* (Wiff *et al.*, 2016; Quiroz and Pérez, 2018), and vulnerable ecosystems, such as the PFS (Iriarte *et al.*, 2010).

The coexistence of multiple life cycles and the diversity of habitat, prey, and food web exploitation patterns are believed to entail increased population resilience to anthropogenic pressures natural sources of ecosystem variability (Kerr *et al.*, 2010). Under this logic, growth, survival, and/or fitness of certain life-cycle types (e.g. resident fish) may be favoured by certain conditions but affected by others. Prey life-cycle types, on the other hand, may exhibit in phase or out of phase responses to the same environmental changes, leading to increasing or decreasing levels of stability. Among many dimensions to be understood, establishing triggering mechanisms and thresholds that determine residence or migration in predators and prey, such as *M. australis* and *M. magellanicus*, may be key to understand and predict their sensitivity to anthropogenic and natural environmental changes.

Although our results may be affected by some methodological limitations and inaccuracies, they clearly show the need to incorporate life-cycle diversity into future ecosystem modelling approaches, aimed to help management or conservation of *M. australis* and *M. magellanicus*. They also show that conserving the estuarine productivity for *M. magellanicus* and other prey is

critical for conserving the productivity and abundance of *M. australis* both in estuarine and oceanic waters. This is not a trivial conclusion given the multiple anthropogenic pressures affecting and threatening the PFS, which include aquaculture, deforestation, and power generation, among others (Iriarte *et al.*, 2010; Niklitschek *et al.*, 2013; Molinet *et al.*, 2018).

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Acknowledgements

We thank C. Cárcamo, I. Quintanilla, and D. Campos for their valuable cooperation in the development of this article.

Funding

This work was partially funded by the National Commission for Scientific and Technological Research (FONDECYT 1131143) and by the Universidad de Los Lagos New Researchers Fund (FNI 01-16). CH and CBC-A were supported by Nucleo Milenio INVASAL funded by Chile's government programme, Iniciativa Científica Milenio from the Ministerio de Economía, Fomento y Turismo. This work was partly carried out during the stay of CH in the University of Exeter, UK (MINEDUC-UA project ANT 1855). FPL was supported by CONICYT Becas-Chile (Scholarship No. 72190288).

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Handling editor: Caroline Durif