



Original Article

Partial migration and early size of southern hake *Merluccius australis*: a journey between estuarine and oceanic habitats off Northwest Patagonia

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Partial migration is a key adaptive strategy, increasingly observed across multiple taxa. To investigate partial migration and life-cycle diversity of *Merluccius australis* in northwestern Patagonia, we analysed isotopic ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) and elemental (^{11}B , ^{23}Na , ^{24}Mg , ^{55}Mn , ^{86}Sr , ^{138}Ba) compositions of otoliths from juveniles, sub-adults, and adults to identify nursery origins, habitats used, and migratory behaviours of multiple cohorts (1990–2005). Influence of early size upon migration was assessed by comparing back-calculated sizes at demersal recruitment between resident and migratory adults. Although partial migration occurred at both estuarine and oceanic nursery habitats, migratory behaviour was more frequent in fish of estuarine origin (59%) than in fish of oceanic origin (17%). Adults of estuarine origin dominated both estuarine (92%) and oceanic (77%) sampling areas. Although we found no significant differences in size at demersal recruitment between oceanic-resident and oceanic-migratory fish, a strong relationship between size at demersal recruitment and migratory behaviour appeared in fish of estuarine origin, whose probability of migration increased from 5% to 95% as demersal recruitment size increased from 18.8 to 23.6 cm. Further research on *M. australis* life cycle is required to incorporate sub-population processes into the stock assessment and management models being used for this overexploited species.

Keywords: early size, *Merluccius australis*, nor-Patagonia, otoliths, partial migration.

Introduction

Many organisms, as part of their life cycle, move at different frequencies and spatial or temporal scales. When these movements are of behavioural, collective, and directional nature, and associated with changes in their habitat, they are called “migration” (Dingle and Drake, 2007; Secor, 2015). Diverging from the idea

that each species or population has a unique and characteristic migratory cycle (Harden Jones, 1968), there is strong and growing evidence showing great variability in migratory behaviours within species, including the coexistence of migratory and resident contingents within a single population (Secor, 2015), nowadays referred to as “partial migration” (Dingle, 1996; Secor and

Kerr, 2009; Suryan *et al.*, 2009; Chapman *et al.*, 2011a). With species exhibiting obligatory migration seemingly increasingly vulnerable to anthropogenic pressures (e.g. habitat fragmentation, climate change, introduction of exotic species, etc.) (Wilcove, 2008), partial migration could be an adaptive strategy that enhances the resilience of populations subject to high levels of environmental variability (Kerr *et al.*, 2010; Secor, 2015).

The documentation of cases of partial migration has been increasing across taxonomic groups, as have the technological advances necessary to study it (Newton, 2008). Although more extensively documented in bird species (Reznick *et al.*, 1990; Shaw and Levin, 2011), evidence of partial migration has also been found in a growing number of fishes (Jonsson and Jonsson, 1993), terrestrial mammals (Ball *et al.*, 2001), marine mammals (Gales *et al.*, 2009), and invertebrates (Slager and Malcolm, 2015). In fishes, anadromous species attracted greater attention until new evidence began to show that partial migration is more frequent in marine species than previously thought (Kerr *et al.*, 2009; Chapman *et al.*, 2012). Identifying the mechanisms that determine the migratory behaviour adopted by an individual is key to fully understand the dynamics of a population (Dingle and Drake, 2007). Diverse studies have shown that these control mechanisms can be facultative (i.e. responding plastically to physiological, environmental, behavioural, or demographic variables or stimuli) or forced (i.e. completely genetically predefined) (Gadgil and Bossert, 1970; Roff, 1988; Jonsson and Jonsson, 1993; Secor, 1999; Petitgas *et al.*, 2006; Mueller *et al.*, 2011; Chapman *et al.*, 2012).

A large fraction of the research related to the mechanisms controlling partial migration has focused on identifying indicators and/or trigger thresholds associated with the morphological and physiological condition of pre-migratory individuals (Berthold, 1999; Chapman *et al.*, 2011b). The physiological indicators most commonly used in fishes are early life and/or pre-migratory growth rates, body size, and condition factor (Chapman *et al.*, 2011b). Evidence of a pre-migratory growth rate and/or body size threshold has been observed in several salmonids, such as *Salvelinus alpinus* (Nordeng, 1983), *Salmo trutta* (Økland *et al.*, 1993; Olsson *et al.*, 2006), and *Salmo salar* (Økland *et al.*, 1993), whose migratory individuals tend to present higher pre-migratory growth rates and larger body size than their resident counterparts. The opposite pattern has been found, however, in other species, such as *Morone americana* (Kraus and Secor, 2004) and *Plecoglossus altivelis* (Tsukamoto *et al.*, 1987). Here, increased growth and size at an early age seems to stimulate residency instead of migration. Moreover, in some species where migratory fish correspond to the largest individuals within a cohort, habitats providing poorer growth conditions have been found to present greater migratory rates (Økland *et al.*, 1993).

Several hypotheses have arisen to reconcile the apparent contradictions in the previously described patterns under a common theoretical framework. First, there is evidence supporting the idea that instead of being triggered by absolute growth rate or body-size thresholds, migration is a response to increased limitations to growth imposed by the habitat (Økland *et al.*, 1993). Thus, migration is triggered when the energetic demands of fast-growing/larger individuals cannot be further sustained by the environment. Second, multiple size thresholds, operating at different times, may be determining migratory behaviours in some fish populations, such as *S. salar*, where a first threshold, which induces early migration in the largest body size group, is followed by a

second threshold that determines precocious maturation in intermediate body size fish and 1-year delayed migration for the lowest body-size group (Dodson *et al.*, 2013).

Evidence of significantly higher condition index has been found (Näslund *et al.*, 1993) and experimentally corroborated (Chapman *et al.*, 2012) in migratory individuals of *S. alpinus*. However, in other species, pre-migratory condition factor has been found to be less informative than pre-migratory size (Skov *et al.*, 2010). For most species, however, control mechanisms and/or trigger thresholds have not been investigated and remain unknown. This is explained, to a large extent, by the logistic difficulties of sequentially sampling individuals or cohorts, limiting many studies to the retrospective analysis of the first years of life of migratory and resident adults.

Among the tools available for the retrospective study of migration in fishes, the structural and chemical analyses of otoliths stand out. The combination of these two approaches may allow for the simultaneous estimation of age, growth rate, environmental history, and life cycle of an individual (Pannella, 1971; Secor, 1992; Campana *et al.*, 1995; Francis and Campana, 2004; Campana, 2005; Bradbury *et al.*, 2008). The growth of the otolith is closely related to somatic growth (Pannella, 1971) and often reflected in daily, seasonal, and/or annual rings, whose width and density also register periods of physiological or environmental stress, making it possible to estimate the size at different ages or life stages in many fish species (Campana, 1990). Furthermore, chemical elements and their corresponding isotopes in the otolith are closely related to the environment surrounding the fish (Kalish, 1989, 1991). Therefore, the chemical analysis of the otolith provides relevant information about the habitat used and/or about the habitat shifts performed by an individual throughout its life (Campana, 1990; Secor *et al.*, 1992; Campana *et al.*, 1995; Mahé *et al.*, 2017).

Fish migration research presents important differences between hemispheres and continents, exhibiting a relative lack of attention given to marine species around South America. Within this group, gadiforms of commercial importance, such as *Micromesistius australis* (Arkhipkin *et al.*, 2009; Niklitschek *et al.*, 2010), *Macruronus magellanicus* (Schuchert *et al.*, 2010; Niklitschek *et al.*, 2014), and *Merluccius australis* (Bricke *et al.*, 2016), have received the greatest attention. Available evidence shows that all these, partially sympatric, species perform extensive ontogenetic migrations. Moreover, *M. australis* and *M. magellanicus* combine the use of estuarine nursery and feeding habitats located within the Western Patagonian Fjords and Channels, with properly oceanic nursery and feeding areas located along the Atlantic and Pacific coasts. Although the existence of partial migration and multiple life cycles has been recently identified in *M. magellanicus* (Niklitschek *et al.*, 2014), the evaluation of its existence and importance in *M. australis* is one of the main focuses of this work.

Merluccius australis is of great ecological importance as top fish predator within its community (Pool *et al.*, 1997), and sustains one of the most important fisheries around Patagonia. Given the intensity of this fishery, its current status in the Eastern Pacific ocean is overexploited (Quiroz *et al.*, 2014). This species exhibits a disjointed geographical distribution with two main populations, one in South America and the other in New Zealand (Aguayo-Hernández, 1995; Horn, 2015), that present low connectivity (Machado-Schiaffino *et al.*, 2009). In the South Eastern Pacific, *M. australis* is mainly distributed south of 40°S, in a

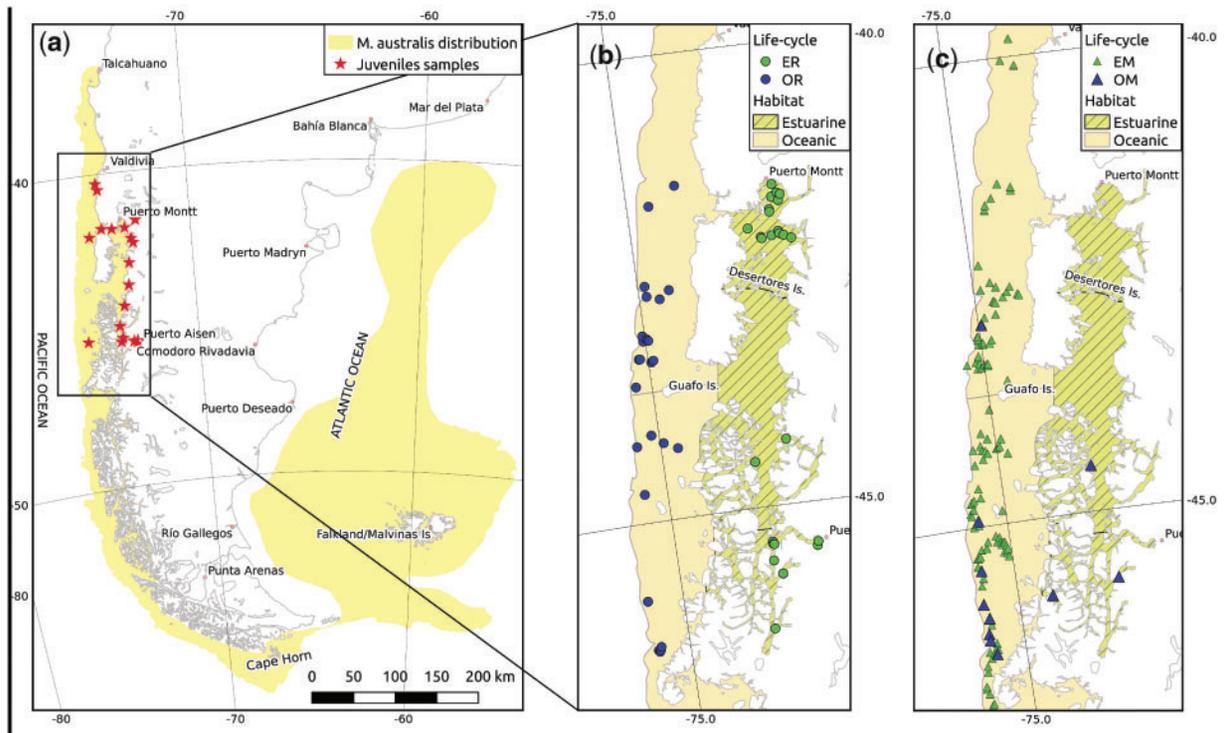


Figure 1. (a) Study area, approximated distribution of *M. australis* around South America, and location of juvenile samples used to produce nursery baselines; (b) adult fish exhibiting resident life-cycle types; and (c) adult fish exhibiting migratory life-cycle types. Life-cycle types classified by origin and behaviour as ER, estuarine-resident; EM, estuarine-migratory; OR, oceanic-resident; and OM, oceanic-migratory.

vertical range (adults) between 60 and 1000 m depth (Aguayo-Hernández, 1995; FAO, 2008).

Merluccius australis is a long-lived species (maximum observed age ~30 years old) that exhibits slow growth rates and late maturity (Ojeda and Aguayo, 1986). Although its life cycle is not well known, Aguayo-Hernández (1995) have proposed a conceptual model for its South American population that considers one annual reproductive migration to spawning grounds located in coastal areas, between Guafo Island and Taitao Peninsula (44–47°S), followed by trophic migrations to estuarine and oceanic waters (Figure 1). Payá and Ehrhardt (2005) suggested that, after spawning, an unknown, but large proportion of eggs and larvae is advectively transported from coastal spawning grounds to estuarine waters within the Patagonian Fjords and Channels System (Figure 1). Remnant eggs and larvae would remain in oceanic nursery areas (Bustos *et al.*, 2007; Lillo *et al.*, 2008, 2011). On the other hand, the existence of secondary spawning areas within the Patagonian Fjords and Channels System has been observed (Bustos *et al.*, 2007; Medina *et al.*, 2014; Brickle *et al.*, 2016), and confirmed by the presence of eggs and early larvae in these estuarine waters (Bustos *et al.*, 2007; Lillo *et al.*, 2011; Landaeta *et al.*, 2018). Nonetheless, and despite its ecological and economic importance, the life cycle(s) and connectivity of the estuarine and oceanic habitats used by *M. australis* are largely unknown, as is the contribution of each nursery habitat to the adult population exploited in each area.

In the present study, we investigated the diversity of life cycles of *M. australis*, following the theoretical framework of partial migration. We estimated and compared the relative frequency of resident and migratory behaviours between fish of oceanic and

estuarine nursery origins, and evaluated whether early growth rates and juvenile size at demersal recruitment were suitable variables for explaining these differences. To do so, we combined isotopic and elemental analyses of juvenile, sub-adult and adult fish otoliths, measurements of the diameter at the demersal recruitment ring in the whole otolith, and back-calculation of body size at demersal recruitment, in resident and migratory individuals.

Material and methods

Study area

The study area (Figure 1) corresponded to the northwestern (NW) Patagonian coast (40–47°S), where the main known spawning and nursery areas of *M. australis* in the SE Pacific are located (Aguayo-Hernández, 1995). This zone consists of a heterogeneous landscape that can be divided into two main habitat types: oceanic waters and estuarine waters. The oceanic waters are strongly influenced by the Western Drift that oscillates latitudinally according to the season, and is divided forming the Humboldt Current to the North, and the Cape Horn Current to the South (Siefeld and Vargas, 1999; Camus, 2001; Thiel *et al.*, 2007). Estuarine waters, on the other hand, exhibit different degrees of spatial and temporal stratification, and provide reproductive grounds and nursery habitats for larvae and juveniles of several marine species (Cushing, 1975; Bustos *et al.*, 2008, 2011; Landaeta *et al.*, 2011).

Sampling

The sampling of early juvenile fish (yearlings and young of the year, YOY) presented severe difficulties given their low capture

rates by both scientific and commercial gear. During 2014–2016, a significant sampling effort was made which combined pelagic trawling surveys, gill-net deployments, and a reward program directed at local fishermen. Despite these efforts, only 62 juvenile specimens were collected. Sagittal otoliths from sub-adult and adult fish were obtained by sampling commercial catches of artisan and industrial vessels (2013–2015) and were complemented with otoliths from the historical archive curated by the Instituto de Fomento Pesquero (IFOP), corresponding to fish captured between 2002 and 2012. Otolith-based ageing (Ojeda and Aguayo, 1986) was performed by IFOP personnel, indicating that these fish belonged to cohorts born between 1999 and 2015. Thus, of the total sample, 297 otoliths corresponded to fish captured in oceanic habitats (21 juveniles, 276 sub-adults and adults), and 204 otoliths to fish captured in estuarine habitats (38 juveniles, 166 sub-adults and adults). Each sampled individual was measured (total length, mm), weighed (total weight, g), and sexed. After extraction, otoliths were cleaned, sonicated, dried under clean conditions, and stored following protocols as described in Secor *et al.* (1992).

Demersal recruitment ring measurements

After being hydrated in ultra-pure water for 12 h, whole otoliths were photographed (Canon EOS Rebel T5 camera, Nikon SMZ800 stereo-microscope, 0.5 \times , reflected light) in lateral external view (sulcus down). Considering the difficulties of ageing species of genera *Merluccius* (Wysokiński, 1983; Horn, 1996; Piñero and Saínza, 2003), we selected the main axis diameter of the first translucent ring as a proxy for early size. This ring corresponds to the most noteworthy and conspicuous otolith ring found in *M. australis*, observable both in sectioned and whole otoliths (Supplementary Figures S1 and S2) for most individuals and in other *Merluccius* species (Wysokiński, 1983; Morales-Nin *et al.*, 1998; Lombarte *et al.*, 2003). Our daily micro-increments results suggest that this ring is formed during the first year of life (Darnaude *et al.*, unpublished data), when the otolith reaches an average main diameter of 7.7 mm \pm 0.09 (SE). Measurements of this ring, hereafter referred to as “demersal recruitment ring”, as well as of the total diameter of each otolith, were made along the main otolith axis using the program ImageJ (Schneider *et al.*, 2012). Only entire otoliths, where the demersal recruitment ring was clearly identified, were measured and used for subsequent analyses.

Preparation of otoliths for chemical analysis

The whole otolith was embedded in clear epoxy resin (Araldite 2020) and cut along the transverse plane containing the core, using a diamond-coated saw (Buehler Isomet[®]1000). Each otolith section (\sim 1000 μ m thick) was ground down to 500–600 μ m, glued (anterior side) on a glass slide using epoxy resin, and further polished using diamond-coated polishing paper (ESCIL) to expose its core. Glass slides were sonicated once more (5 min), triple-rinsed with ultra-pure water, and stored until analysis.

Origin and contingent discrimination

Discrimination of origin (nursery habitat) and migration pattern in adult fish was based on two types of otolith micro-chemistry data: elemental composition (EC) analysis of six selected trace elements (¹¹B, ²³Na, ²⁴Mg, ⁵⁵Mn, ⁸⁶Sr, and ¹³⁸Ba) and stable isotope (SI) analysis of oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$). Combining

otoliths from fish of different ages, and 1–3 different sections within each otolith, we aimed to create reliable baselines to characterize otolith signatures imprinted at different habitats and life stages, and use this information to hindcast the habitat types being used by each adult throughout its life span. Habitat use hindcasting was carried out by fitting multinomial models (Venables and Ripley, 2002) where habitat was modelled as a response to EC and/or SI variables, as detailed below. Three life stages were considered for all analyses: nursery life (0–1 year old), sub-adult life (3–6 years old), and adult life (\geq 9 years old).

Elemental composition analysis was carried out by laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS), using a 193-nm Excimer Laser System (CompEx 102, Lambda Physik) coupled to an Element XR sector field ICPMS (Thermo Fisher), at the University of Montpellier (UMR 5243 Geosciences). Helium gas was used as a carrier, whereas NIST 612 and calcium (⁴³Ca) were used as external and internal standards, respectively, with a stoichiometric value of 56% CaO. The laser was operated in scanning mode, at a scan speed of 20 $\mu\text{m}\cdot\text{s}^{-1}$, 7 Hz, and a constant fluence of 10 $\text{J}\cdot\text{cm}^{-2}$ (nominal ablation depth \sim 10 μ m). Final concentrations and limits of detection were computed off-line with the R package ElementR (Sirot *et al.*, 2017). Raster data was discretised and averaged within 29 μ m sampling intervals, which were then grouped into sequential triplets. In order to reduce auto-correlation among overlapping readings within triplets, each triplet was finally represented by a single value corresponding to its median, referred to as a “spot” hereafter.

Stable isotope analysis for oxygen (¹⁸O/¹⁶O) and carbon (¹³C/¹²C) followed EC for most of the same otoliths, although an additional set of otolith samples were analysed for EC only, after being prepared following mounting and polishing protocols analogous to those described above. Target otolith sections were drilled out as powder or prisms (see details below) using a New Wave Research micro-mill, and then sent to the University of Arizona Isotope Geochemistry Laboratory for further analysis. Following procedures detailed by Kerr *et al.* (2007), and using an automated carbonate preparation device (KIEL-III) attached to a gas-ratio spectrometer (Finnigan MAT 252), otolith samples were reacted with dehydrated phosphoric acid under vacuum at 70°C, and the resulting CO₂ was analysed for its relative isotopic concentrations of ¹²C, ¹³C, ¹⁶O, and ¹⁸O. All results were reported as per mil relative to a standard ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$), which corresponded to Vienna Pee Dee Belemnite (VPDB, international standards NBS-18 and NBS-19) for both isotopes.

Baseline data used to fit discriminant models (see below) aimed at hindcasting nursery-life (origin) habitat from otolith EC and/or SI were obtained from 59 YOY and yearling juveniles, collected in both estuarine and oceanic habitats, between 2013 and 2015. Nursery-life sections selected for EC analyses out of the LA-ICPMS transect corresponded to spots lying between 250 and 1200 μ m from the core. These limits were set to exclude material deposited before metamorphosis (<250 μ m), as well as after the demersal recruitment ring, formed 1200–1700 μ m from the core (A. Darnaude, pers. comm.). Nursery-life material used for SI analysis was extracted as powder from two circular spots (diameter \sim 500 μ m, depth \sim 200 μ m), defined inward from the inner side of the demersal recruitment ring, at both (dorsal and ventral) sides of the core, along the main section axis.

Baseline data used to fit discriminant models (see below) aimed at hindcasting habitat use at sub-adult and adult-life stages

from otolith EC and/or SI data were obtained from 58 sub-adult and 99 adult fish otoliths, sampled between 2003 and 2015. All marginal spots lying within the last 38–198 μm of each LA-ICPMS transect were selected for this purpose. This marginal width was calculated to represent the last year of life of each sampled fish. EC data from both sub-adult and adult individuals were pooled into a single baseline model, which was more informative (lower Akaike criterion information, AIC) than two separate baseline models for each stage.

As part of a preliminary work, we compared the accuracy of multinomial, random forest, and linear discrimination models (Pella and Masuda, 2005; Mercier *et al.*, 2011; Jones *et al.*, 2017) when used for self-classifying baseline samples for nursery-, sub-adult-, and adult-life stages. Multinomial models outperformed the other two for all baselines and, therefore, were used to identify (hindcast) the origin and habitat used by adults at different stages. Since the availability of baseline data (EC, SI, or both) was uneven among and within individual otolith samples, we fitted three types of multinomial models, both for origin and habitat-use discrimination purposes: (i) EC models, fitted using only EC data, (ii) SI models, fitted using only SI data, and (iii) combined models, fitted using both EC and SI data. Given relative differences found in their corresponding accuracy (see results), and depending upon what data was available for each sample, origin and habitat hindcasts were carried out prioritizing combined over SI models, and SI over EC models.

Origin and habitat-use patterns of adults were finally hindcasted by applying predictive multinomial models to standardized otolith sections, selected to represent “nursery” (origin), “sub-adult”, and “adult” life stages within each adult sample. For EC data, the selection of LA-ICPMS from adult fish used to represent their nursery life matched the one used to produce baselines from yearlings and YOY fish (250 and 1200 μm from the core). LA-ICPMS transect sections selected to represent sub-adult and adult-life were, instead, variable, as they were back-calculated to identify otolith material deposited between 3 and 6 years-old (sub-adult life) and over 9 years-old (adult life). These back-calculations were based on the total distance from the core at the age of capture, estimated following Ojeda and Aguayo (1986) and fitted using Ogle and Isermann’s (2017) re-parametrization of the von Bertalanffy (1938)’s growth model (VBGM), which allowed for explicit (more accurate) estimations of the distance from the core corresponding to each selected age.

For SI data, nursery-life (origin) sections sampled from adult fish otoliths, matched those sampled from yearlings and YOY (two circular spots inward from the demersal recruitment ring, at both sides of the core). Sub-adult-life SI samples were drilled out as irregular prisms from a standardized parallelogram drawn on the ventral side of the otolith section, between annuli 5 and 7. Adult-life SI sampling collected, as powder, all material deposited after the penultimate winter annuli, whenever it was evident. Otherwise, all material deposited within 100 μm from the edge was removed. Recent life samples used to hindcast habitat use at sub-adult- and adult-life stages from otolith SI corresponded to powder milled out in raster mode along the interior edge of the section, in most cases, over its ventral side. Raster path was designed to remove material deposited after the penultimate winter annuli, whenever it was evident. Otherwise, all material deposited within 100 μm from the edge was removed.

Life-cycle characterization and analysis

Adults were classified into four life-cycle types, defined by combining their hindcast nursery origin (estuarine vs. oceanic) and contingent (migratory vs. resident). All fish exhibiting any habitat shift among nursery, sub-adult, or adult of capture site habitat were assigned to the migratory contingent. Mean proportions of contingents by nursery origin were estimated using a generalized linear mixed model (GLMM) (Bolker *et al.*, 2009), which permitted accounting for the binomial nature of the response and the possible correlation of observations within cohorts and tows. Mean proportions of life-cycle types by capture habitat were estimated using a multiplicative approach (Begg and Gray, 1984), as the product between the proportions estimated for each origin and for each contingent within each capture habitat.

Estimation of size at demersal recruitment and probability of migration

Individual size at demersal recruitment was retro-calculated (Campana, 1990) from the proportionality between total otolith diameter and total fish length at capture. Average size at demersal recruitment was then compared between life cycles using a linear mixed modelling approach (Searle, 1987), oriented to account for possible correlations between observations belonging to the same cohort and/or tow. Since a preliminary analysis showed no significant differences in size at demersal recruitment between sexes within life cycles, data from both sexes were pooled for all remaining analyses. The relationship between migratory behaviour (resident or migratory) and size at demersal recruitment was evaluated for each nursery area (oceanic or estuarine) fitting a GLMM (Bolker *et al.*, 2009), expected, as before, to account for the binomial nature of the data and the lack of independence within cohorts and tows, and suitable for obtaining unbiased predictions of the probability of migration as a function of fish size at demersal recruitment.

Hypotheses testing

No significant departures from normality, evaluated when applicable using quantile–quantile diagrams (Venables and Ripley, 2002), or homoscedasticity, evaluated by Levene’s test (1960) were found throughout the different models applied. Tukey’s test was used for all multiple comparison analyses. All analyses were done in R (The R Core Team, 2017), fitting all models with the package “lme4” (Bates *et al.*, 2012). All analyses of variance were based on likelihood ratio tests, performed using the package “car” (Fox, 2008). Correlation between annual averages of size at demersal recruitment and probability of migration was based on by Spearman non-parametric index (Zar, 1999). Null hypotheses were rejected under a significance level (α) of 0.05. All values are reported as the means \pm standard error (SE).

Results

Discriminant models accuracy

Elemental composition and stable isotope concentrations showed important univariate and multivariate differences between estuarine and oceanic samples regarding both core otolith sections from juveniles and marginal otolith sections from sub-adult and adult fish (not shown). Thus, multinomial discriminant models used to hindcast both nursery origin and habitat use throughout life showed high self-classification accuracies. For nursery origin, jackknife (one-out) accuracy estimates reached 92%, 71%, and

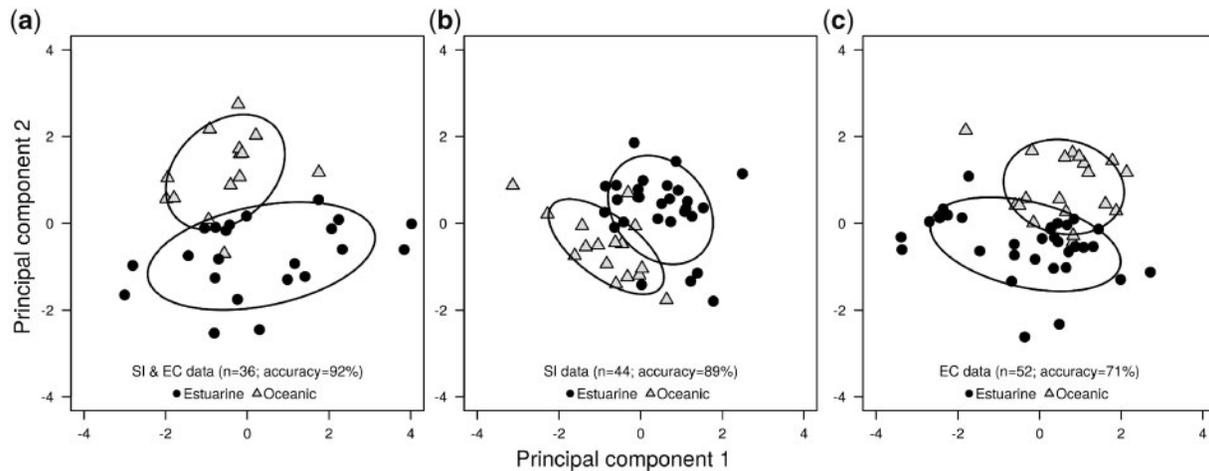


Figure 2. Principal components representation of the multivariate dispersion observed in SI, stable isotope ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) and/or EC, elemental (^{11}B , ^{23}Na , ^{24}Mg , ^{55}Mn , ^{86}Sr , and ^{138}Ba) compositions of otolith sections from juvenile *M. australis* collected at estuarine and oceanic habitats off NW Patagonia. Accuracy values correspond to jack-knife self-classification values produced by three different multinomial discriminant models, fit to different datasets as (a) both SI and EC; (b) only SI; or (c) only EC data were available.

89% for models based upon combined sets, EC, and SI data, respectively (Figure 2). For habitat-use models, estimated accuracies were somewhat lower, reaching 72%, 62%, and 100% for models based on combined sets, EC, and SI data, respectively.

Diversity of life cycles in *M. australis*

Considering a total of 383 adults whose nursery origin was discernible, 314 individuals were identified as coming from estuarine habitats and only 69 from oceanic habitats. In both nursery groups, it was possible to observe both resident fish that remained all their life in the same habitat, and migratory fish, which exhibited evidence of a habitat switch, with or without evidence of fidelity (posterior return) to their nursery habitats. Thus, the combination of origins and patterns allows for the identification of fish representative of four general life-cycle types: estuarine-resident, estuarine-migratory, oceanic-resident, and oceanic-migratory (Figure 3). It must be acknowledged that no YOY or yearlings were available from the time when sampled adults inhabited their corresponding nursery areas (1990–2006). YOY/yearling fish samples available to produce EC and SI nursery baselines were, instead, captured between 2013 and 2015. Although this important temporal mismatch could introduce some bias when hindcasting the nursery origins for these adults, we found that inter-annual variability within habitats was much smaller than overall variability between habitats.

In fish of estuarine nursery origin, estimated proportions (\hat{p}) of migratory ($\hat{p}=0.59 \pm 0.143$, $n=185$) were higher than resident ($\hat{p}=0.41 \pm 0.143$, $n=129$) contingents. On the other hand, in fish of oceanic nursery origin, there was a clear predominance of the resident contingent ($\hat{p}=0.82 \pm 0.045$, $n=57$) over the migratory contingent, which was represented by only 12 individuals ($\hat{p}=0.17 \pm 0.045$). This oceanic-migratory life-cycle type was, in general, poorly represented in all our samples. We found important differences in the contribution of each nursery habitat to the adults captured at each habitat (Figure 3). Most adults captured in both estuarine and oceanic waters were identified as having estuarine nursery habitats. Thus, the estuarine-resident life-cycle type dominated in estuarine waters ($\hat{p}=0.92 \pm 0.017$), whereas the

estuarine-migratory life-cycle type dominated in oceanic waters ($\hat{p}=0.77 \pm 0.048$). The contributions of estuarine-migratory and oceanic-migratory life cycles to the adults captured in estuarine waters were quite low, with estimated proportions of $\hat{p}=0.04 \pm 0.017$ and $\hat{p}=0.04 \pm 0.008$, respectively. Oceanic-resident fish corresponded to only 17% ($\hat{p}=0.17 \pm 0.034$) of the adults captured in this habitat. The contribution of oceanic-migratory fish that showed evidence of returning to this habitat after using estuarine waters at some intermediate life stage was also very low ($\hat{p}=0.06 \pm 0.034$), with this life cycle being the one exhibiting the lowest frequency among all identified life-cycle types.

Variability in size at demersal recruitment between life cycles

A significant effect of the life-cycle type on the diameter of the demersal recruitment ring and on the size (back-calculated) at the demersal recruitment (ANOVA, $p < 0.0001$ for both models) was found. Mean diameter of the demersal recruitment ring and mean back-calculated size tended to be lower in estuarine-resident fish than in all other life-cycle types (Figure 4). Pairwise comparisons showed the mean back-calculated size of estuarine-resident fish (16.6 ± 0.34 cm) was significantly lower (Tukey's test, combined sexes and cohorts, $p < 0.0001$) than the mean back-calculated size of estuarine-migratory (22.1 ± 0.34 cm), oceanic-resident (24.1 ± 0.77 cm), and oceanic-migratory (21.9 ± 0.96 cm) fish. No significant pairwise differences in mean back-calculated sizes were found among estuarine-migratory, oceanic-resident, and oceanic-migratory life-cycle types. Despite the observed variability, we did not find evidence of significant differences in mean size at demersal recruitment between cohorts, nor a significant interaction between cohort and life cycle (ANOVA, Table 1). However, there was a consistent tendency of estuarine-resident fish to show a smaller size at demersal recruitment than other life cycles across all analysed cohorts (Figure 5).

Migration probability

Average migration probability was significantly affected by mean size at demersal recruitment, nursery habitat, and their interaction

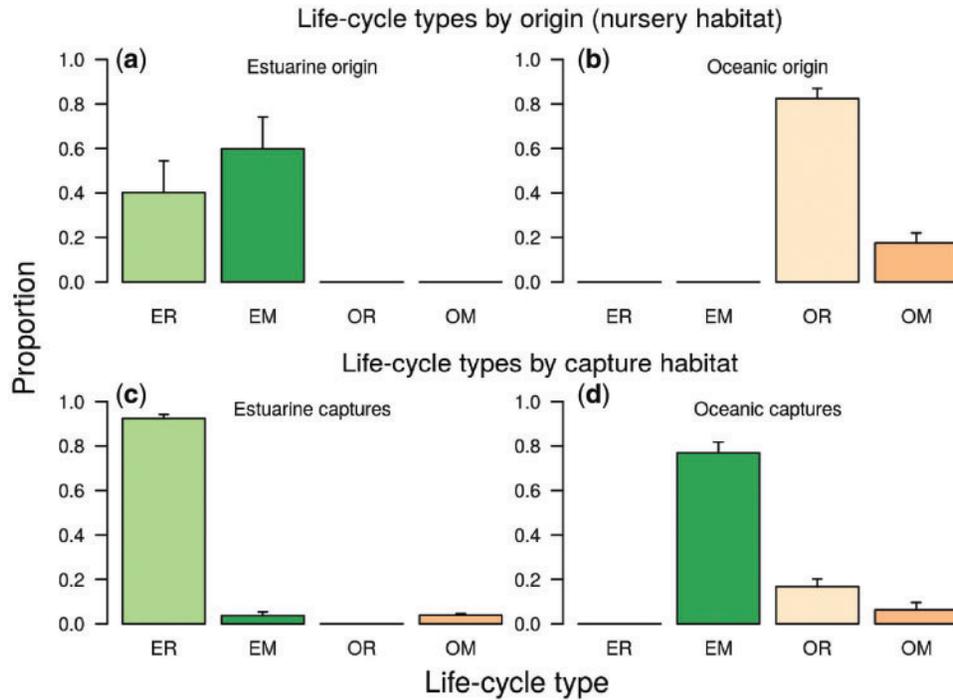


Figure 3. Relative frequency of life-cycle types by nursery origin (panels a and b) and capture habitat (panels c and d) identified in *M. australis* off NW Patagonia. Life-cycle types classified by origin and behaviour as ER, estuarine-resident; EM, estuarine-migratory; OR, oceanic-resident; and OM, oceanic-migratory. All cohorts and sexes combined.

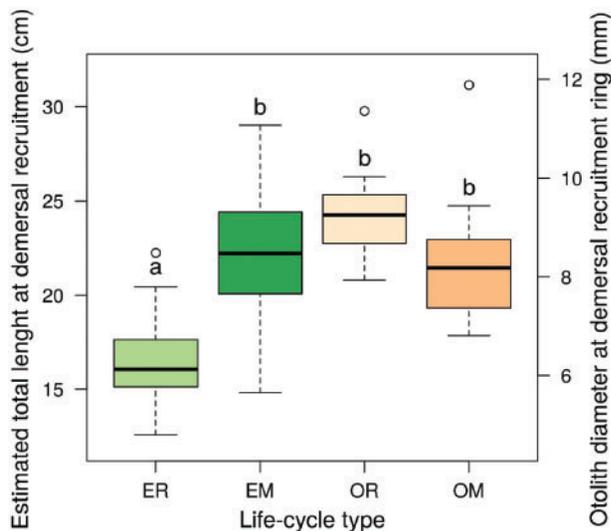


Figure 4. Otolith diameter (main axis) and retro-calculated total length at size of demersal recruitment by life-cycle type in *M. australis* off NW Patagonia. Life-cycle types classified by origin and behaviour as ER, estuarine-resident; EM, estuarine-migratory; OR, oceanic-resident; and OM, oceanic-migratory. Different letters indicate significant differences. All cohorts and sexes combined.

(ANOVA, $p < 0.0001$). When each nursery origin was analysed separately, it was possible to observe that the probability of migration was significantly affected by size at demersal recruitment only in fish of estuarine nursery origin ($p < 0.0001$), but not in those of oceanic nursery origin ($p > 0.2$). The reduced representation of

oceanic-migratory fish in our sample ($n = 12$), however, affected the power of this and all related analyses, thus only the results for fish of estuarine nursery origin are reported. From the logistic GLMM that explained migration probability as a function of size at demersal recruitment, we estimated a migrating probability of 50% for fish that had reached a size at demersal recruitment of 18.8 ± 0.50 cm. For a migration probability of 95%, the estimated size at demersal recruitment was 23.6 ± 0.50 cm (Figure 6). An additional corroboration of this relationship was provided by the positive and significant inter-annual correlation (Spearman 0.92; $p = 4.7 \times 10^{-4}$) found between the proportion of the migratory contingent and the mean size at demersal recruitment computed for each cohort (Figure 7).

Discussion

Migration is a generalized phenomenon of strong ecological and evolutionary consequences. Over the last 2–3 decades, it has also become evident that partial migration and multiple life cycles characterize many species and populations, and that they are more common than previously thought (Kerr and Secor, 2009; Chapman et al., 2012; Gillanders et al., 2015). Therefore, it seems reasonable to speculate that the existence of such migratory behaviours does not occur by chance, but correspond to an adaptive strategy that provides selective advantages, such as enhanced population resilience and persistence under increased environmental variability (Wilcove, 2008; Secor et al., 2009). In the present study, we present important evidence of partial migration in *M. australis*. Crossing nursery origins and migratory behaviours allowed us to identify and estimate highly unequal frequencies for four life-cycle types. Besides potential bias related to the temporal mismatch between early juvenile, sub-adult, and adult samples,

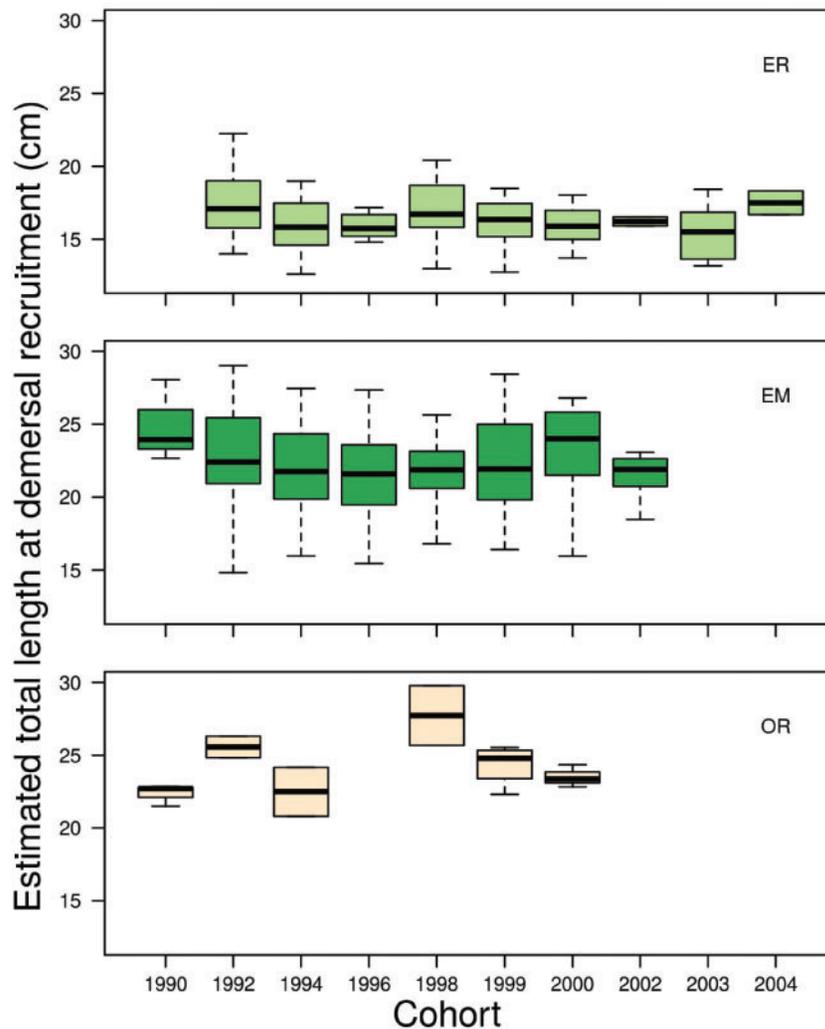


Figure 5. Inter-annual variability in estimated total length at size of demersal recruitment of life in adult of *M. australis* by life-cycle types classified by origin and behaviour as ER, estuarine-resident; EM, estuarine-migratory; OR, oceanic-resident; and OM, oceanic-migratory. Oceanic-migratory life-cycle type, which was extremely rare is not shown. Both sexes combined within cohorts.

Table 1. Inter-annual variability in otolith diameter at size of demersal recruitment for adults of *M. australis* of estuarine and oceanic origin (sexes, migrants, and residents combined).

	Sum squares	GL	F value	Pr(>F)
Life cycle	45.2901	3	123.26	<2e-16
Cohort	0.7291	9	162.65	0.6818
Interaction	0.8722	15	162.44	0.5963

most fish originated from estuarine nursery areas had migrated toward the adjacent ocean (estuarine migratory), whereas a much smaller fraction (~1/4) of this group had remained in estuarine habitats throughout their life (estuarine resident). In contrast, most fish from oceanic nursery areas exhibited a resident behaviour, whereas only a small fraction of them exhibited an oceanic-migratory life cycle.

Over the years (1990–2005), adults originating from estuarine nurseries dominated in both estuarine and oceanic habitats, revealing that this nursery habitat has a fundamental importance in

sustaining *M. australis* populations and fisheries both in estuarine and oceanic waters. This essential role of estuarine habitats observed for *M. australis* is clearly consistent with previous findings by [Brickle et al. \(2016\)](#), who sampled a much larger geographic area, on both sides of Patagonia, and concluded that most adults they sampled had been exposed to highly variable (estuarine) salinities during the first months of life.

Although our results contribute to a better understanding of life-cycle diversity and connectivity of *M. australis* in NW Patagonia, we lacked relevant pieces of information about the individuals we sampled and analysed. We ignored the spawning habitat and the possible transport mechanisms and pathways followed by the as eggs and larvae. Thus, the relevance of estuarine nursery origins cannot be linked necessarily to an equivalent relevance of estuarine spawning grounds and/or of estuarine-resident spawning adults. In fact, existing hydro-acoustic surveys show much higher spawning biomasses in oceanic waters ([Lillo et al., 2011, 2013](#)), whereas lower densities of *M. australis* larvae have been reported in estuarine waters by [Landaeta et al. \(2018\)](#).

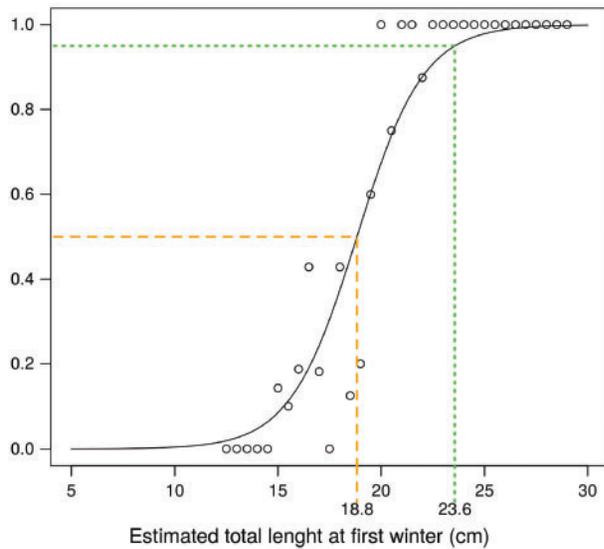


Figure 6. Migration probability estimated for *M. australis* off NW Patagonia as a function of retro-calculated size at demersal recruitment (all cohorts and sexes combined). Dashed and dotted lines indicate 50% and 95% migration probability, respectively.

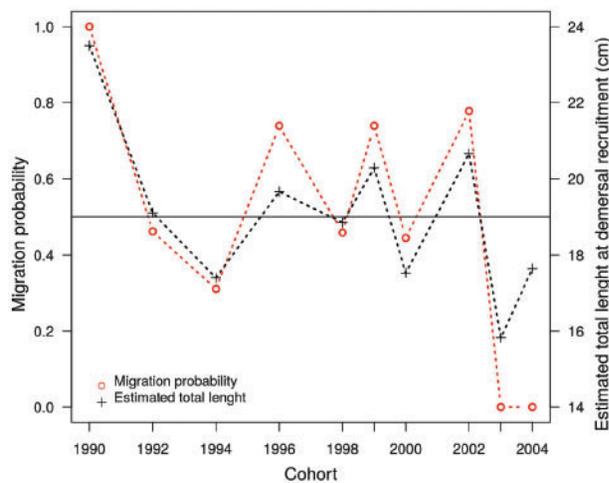


Figure 7. Mean estimates for migration probability and estimated total length at size of demersal recruitment by cohort in *M. australis* off NW Patagonia. Both sexes combined.

To reconcile a greater production and concentration of eggs and larvae in oceanic waters with a greater contribution of estuarine nursery habitats to the adult population, it would be necessary to assume that a large fraction of the juveniles from estuarine nursery habitats had been transported from oceanic spawning grounds. Considering unpublished results that show earlier spawning dates in ocean habitats, we can hypothesize that eggs/larvae advected from ocean spawning grounds into the estuarine nursery habitats should exhibit greater sizes at their demersal recruitment and, therefore, increased probabilities to migrate back into the ocean. Besides advection from oceanic spawning grounds, higher early survival rates could benefit eggs/larvae or early juveniles inhabiting estuarine waters. This idea is consistent

with the higher growth rates reported for *M. australis* larvae in estuarine waters by Landaeta et al. (2018). Exploring these two non-exclusive hypotheses, as well as investigating the degree of reproductive and genetic separation between life-cycle types would be required in order to understand the population dynamics of *M. australis* in this study area and elsewhere.

The close relationship we found between the probability of migration and size at demersal recruitment in fish of estuarine nursery origin match general patterns previously observed in other species. Although the probability of migration has been observed to increase with pre-migratory size and condition (Brodersen et al., 2008), migratory fish tend to present greater early growth rates than resident individuals (Kraus and Secor, 2004). Moreover, despite high inter-annual variability in early growth rates, the relationship we found was consistent across all analysed cohorts (1990–2005). Thus, high variability was also observed in the estimated proportion of individuals belonging to each life-cycle type and, therefore, in the hindcast contribution of estuarine nursery habitats to the stock inhabiting oceanic waters. Given the multiple intrinsic and extrinsic factors that can affect early growth, this rate could be either the actual triggering factor or just a reflection of other unobserved factor(s) that determine the migratory behaviour adopted by a given individual (Secor, 2015).

From a physiological point of view, migration is expected to be limited by the availability of energy reserves. Hence, fish exhibiting larger body sizes might also have larger energy reserves and, therefore, greater mobility to search for new and/or better feeding conditions. However, this is not necessarily the case as observed in *Anoplopoma fimbria* (Sogard and Spencer, 2004) and *Polyodon spathula* (Hemingway and Scarnecchia, 2017), which were found to allocate more energy to growth and less to lipid storage during their early stages. Even with sufficient energy resources to start the migration, the question is, what might be the adaptive advantage of doing so. It could be that a significant fraction of migratory fish find greater availability and/or quality of prey sufficient to support higher growth (Skov et al., 2010; Gillanders et al., 2015) and, therefore, higher survival rates (Houde, 1987) than their resident siblings. Greater growth and survival rates should lead to the enhanced fitness required to keep a dynamic equilibrium between resident and migratory life cycles (Gross, 1985).

In the case of *M. australis* and other coastal species from NW Patagonia, the adaptive advantages of migration are still unclear. Migration here commonly involves switching between two highly dissimilar habitats: the Patagonian Fjords Estuarine System, of smaller extent, but greater (although more variable) productivity, and the Coastal Ocean, much larger and stable, but less productive (on average) than the first (Iriarte et al., 2010; Niklitschek et al., 2014). It must also be considered that *M. australis* switches its diet early in life from pelagic invertebrates to myctophids and other small mesopelagic fishes (Payá, 1992; Dunn et al., 2010), whose total abundances are probably greater in the coastal ocean. Putting all the pieces together, we can assume that early emigration from estuarine to oceanic habitats might be beneficial if oceanic habitats provide less intense density-dependent interactions and increased availability of small mesopelagic fishes at the time these immigrants are switching to a more piscivorous diet (Dunn et al., 2010). Resident fish, on the other hand, would face greater density-dependent interactions, being forced to maintain a less piscivorous diet for a longer period. However, they could benefit later from the large availability of *M. magellanicus* sub-adults

(2–5 years of age) that enter the NW Patagonia Fjords and Channels System on mass each year (Niklitschek *et al.*, 2014). *M. australis* from oceanic nursery habitats, on the other hand, would have smaller incentives to perform an early emigration into estuarine waters. This speculation is supported by the larger size at demersal recruitment observed in this group and the low representation of the oceanic-migratory life cycle in our samples.

It should be noted that no otoliths of YOY/yearling fish were available from the time when sampled adults inhabited their corresponding nursery areas (1990–2006). YOY/yearling otolith samples available to produce EC and SI nursery baselines were, instead, captured between 2013 and 2015. This temporal mismatch, along with a limited sample size, could introduce some important bias to our nursery origin and/or nursery habitat contribution estimates. Such potential bias and related uncertainty must be considered if any quantitative use of our results is attempted. Nonetheless, observed variability in marginal sections from sub-adult and adult fish collected in the study area suggest that inter-annual variability within estuarine and nursery habitats tends to be much smaller than habitat variability over time.

Partial migration and diversity of life cycles in *M. australis* may have arisen in response to the great environmental variability existing along the western Patagonian coast (Acha *et al.*, 2004; Iriarte *et al.*, 2010). This could be a key feature in increasing the resilience of this species to the growing anthropogenic impacts (e.g. habitat modification, fishing, aquaculture, climate change) affecting this area (Molinet *et al.*, in press; Iriarte *et al.*, 2010). Given these threats and the overexploitation status of *M. australis* in the eastern Pacific Ocean (Quiroz *et al.*, 2014), there is an urgent need to evaluate the consequences that the observed diversity of life cycles and contribution of different nursery habitats might have upon the stock assessment and operative models being used for managing this species. It is also imperative to keep filling in the knowledge gaps indicated by our results concerning the life history and migratory ecology of *M. australis* in NW Patagonia and elsewhere, assessing the degree of reproductive isolation between nursery habitats and contingents, the transport mechanisms connecting nursery habitats, and the survival rates experienced by eggs and larvae in different nursery habitats.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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