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Evaluación de la estructura poblacional de la corvina blanca, *Atractoscion nobilis*, en la costa Pacífico de Norteamérica a través del análisis microquímico y del crecimiento de los otolitos

Tesis

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Resumen de la tesis que presenta Alfonsina Eugenia Romo Curiel como requisito parcial para la obtención del grado de Doctor en Ciencias en Ecología Marina.

Evaluación de la estructura poblacional de la corvina blanca, *Atractoscion nobilis*, en la costa Pacífico de Norteamérica a través del análisis microquímico y del crecimiento de los otolitos

Resumen elaborado por:

Alfonsina Eugenia Romo Curiel

La corvina blanca, *Atractoscion nobilis*, se distribuye desde bahía Magdalena en Baja California Sur, México, hasta la bahía de San Francisco en California, EUA, incluyendo el golfo de California. A pesar de ser una especie costera de importancia en la pesca comercial y deportiva por ambos países, se desconoce si son una o varias subpoblaciones las que son explotadas regionalmente. El objetivo de este estudio fue evaluar si la corvina blanca comprende una población o son varias subpoblaciones en el Pacífico Este. Para este fin se usaron dos aproximaciones complementarias: (1) se compararon las tasas de crecimiento a nivel poblacional e individual de corvinas capturadas a lo largo de su distribución, y (2) se midió la composición isotópica (δ^{13}C y δ^{18}O) del núcleo y anillos de crecimiento de los otolitos de corvinas adultas, para establecer si hay evidencia de diferencias en las condiciones de crianza, e inferir sobre el uso de hábitat y patrones de migración entre localidades. Como resultado se obtuvo que a nivel poblacional hay una similitud en las tasas de crecimiento, lo cual es un indicativo de la presencia de una sola población. Sin embargo, a nivel individual se encontraron diferencias significativas en el crecimiento durante el primer año de vida, lo cual sugiere que las corvinas capturadas al sur de Punta Eugenia crecieron bajo condiciones ambientales diferentes a las del norte (del sur de California hasta bahía Vizcaíno). La composición isotópica del núcleo (fase larvaria) de los otolitos de corvinas adultas capturadas al norte y sur de su distribución presentó un alto nivel de variación y no hubo diferencias significativas entre regiones. Por lo tanto, no se pudo diferenciar entre subpoblaciones potenciales de larvas criadas en cada región. Sin embargo, el valor del δ^{18}O del primer anillo de crecimiento, correspondiente al crecimiento de verano durante el primer año de vida, fue significativamente diferente entre la región sur y norte. Esto indica que corvinas adultas capturadas en estas dos regiones pueden pertenecer a subpoblaciones diferentes. Las diferencias encontradas en el crecimiento y la composición isotópica del oxígeno en el primero anillo de crecimiento estacional sugieren la presencia de dos subpoblaciones potenciales discretas divididas por Punta Eugenia. Estos resultados son cruciales para entender la estructura poblacional de la corvina blanca y podrían ser utilizados en una futura evaluación de la pesquería necesaria para el manejo sustentable de este recurso binacional.

Palabras Clave: **Corvina blanca, estructura poblacional, isótopos estables, tasas de crecimiento, otolitos, Pacífico de Norteamérica**

Abstract of the thesis presented by Alfonsina Eugenia Romo Curiel as a partial requirement to obtain the PhD in Science in Marine Ecology.

Evaluation of population structure of white seabass, *Atractoscion nobilis*, along the Pacific coast of North America based on the microchemistry and growth of the otoliths

Abstract by:

Alfonsina Eugenia Romo Curiel

The white seabass, *Atractoscion nobilis*, inhabits the Pacific North American coast and ranges from Magdalena Bay in Baja California Sur, Mexico, to San Francisco Bay in California, USA, including the Gulf of California. Although it is an important coastal resource for both commercial and sport operations of both countries, it is unknown if the white seabass population is comprised of multiple stocks. The aim of this study was to evaluate if white seabass subpopulations exist across its range in the eastern Pacific. In this study, two complementary approaches were used: (1) a comparison of regional growth rates, and (2) the isotopic composition (δ^{13}C and δ^{18}O) of otolith cores and seasonal growth rings representative of larval, juvenile and adult life stages. Isotopic composition data were used to identify larval rearing grounds, habitat use and migratory patterns between potential subpopulations. Results suggest similar growth rates across the distribution, however, significant differences were identified in the first year of growth. Findings suggest that different environmental conditions off southern Baja California contribute to higher growth rates in the first year of life when compared to those north of Punta Eugenia (in the Vizcaino bay and southern California). The isotopic composition of otolith cores (corresponding to the larval stage) from northern and southern areas revealed high variability with no significant differences among regions. However, the δ^{18}O values from the first seasonal growth ring were significantly different between the northern and southern regions, implying that subpopulations may exist. The differences in both growth rates and δ^{18}O isotopic composition of the first seasonal growth ring, suggests the presence of discrete subpopulations divided by Punta Eugenia. These findings are critical for understanding white seabass stock structure and may be useful in future stock assessments necessary for the sustainable management of this binational resource.

Keywords: **White seabass, population structure, stable isotope, growth rate, otoliths, Pacific of North America**

Dedication

A Nicolás y Cristóbal por ser la fuerza que me impulsa a seguir adelante...

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Executive abstract

I. Introducción

Las poblaciones son definidas como grupos de individuos de la misma especie que habitan un lugar específico en un tiempo determinado, comparten el mismo pool genético y presentan las mismas características en su historia de vida, la cual se ve reflejada en la dinámica poblacional. La conectividad poblacional es el intercambio de individuos entre grupos; como resultado de una conectividad limitada una población puede estar estructurada en subpoblaciones o pequeños grupos de individuos de la misma especie aislados entre sí; la alta conectividad típicamente resulta en una sola población. En muchas especies costeras marinas, la mayor dispersión entre grupos se lleva a cabo durante la etapa larvaria. El nivel de dispersión se lleva a cabo por medio de procesos físicos y biológicos, y depende del tiempo que las larvas se mantienen en la columna de agua antes del asentamiento o metamorfosis hacia el estadio juvenil. Sin embargo, la conectividad también puede darse a través de la migración de los adultos a diferentes áreas de desove. En poblaciones sometidas a una presión pesquera, con conectividad limitada, la caracterización de la estructura poblacional es crucial para establecer estrategias de manejo y conservación de los recursos.

La corvina blanca, *Atractoscion nobilis*, se distribuye desde San Francisco, USA hasta el sur de la península de Baja California, México incluyendo el golfo de California. La longitud total máxima registrada es de 1.6 m, más de 41 kg en peso y puede llegar a vivir hasta 28 años. Dado que alcanza tallas muy grandes y por la calidad de su carne, a lo largo de su distribución la corvina blanca es considerada una especie de gran importancia tanto en la pesca deportiva como la comercial.

Con el fin de evaluar la estructura poblacional de la corvina blanca, se han realizado diferentes aproximaciones entre las cuales están la definición de las potenciales áreas de desove a través de la evaluación de abundancia y distribución larval, la evaluación de poblaciones genéticas y el marcaje de juveniles y adultos. Sin embargo, no se ha logrado establecer con claridad si a lo largo de su distribución la corvina blanca comprende una población o son varias subpoblaciones. Es por ello que en el presente trabajo se usaron dos técnicas para evaluar la estructura poblacional de esta especie en la costa Pacífico de Norte América: (a) el análisis de las tasas de crecimiento y (b) la composición isotópica de los otolitos.

Los otolitos son estructuras duras de carbonato de calcio que se depositan continuamente a lo largo de la vida de los peces y su principal función es la audición y el equilibrio. El patrón de crecimiento continuo y la formación periódica de los anillos de crecimiento permiten que sean utilizados para la estimación de las tasas de crecimiento a nivel individual y poblacional. Cuando esta información es combinada con mediciones químicas de los otolitos (análisis de isótopos estables o elementos traza del carbonato), es posible hacer inferencias sobre las condiciones ambientales en las cuales han estado los peces, evaluar la estructura poblacional, reconstruir los patrones de migración y estimar la contribución de diferentes áreas de crianza a la población de los adultos. Las condiciones ambientales experimentadas por los peces adultos durante su etapa larvaria o juvenil pueden ser evaluadas a partir del análisis de la composición isotópica del núcleo o anillos de crecimiento, respectivamente. La presencia de diferencias en las tasas de crecimiento y la composición química de los otolitos de una determinada especie recolectada a lo largo de su distribución pueden ser utilizadas para diferenciar subpoblaciones.

Con base en el alto potencial de dispersión larval y la migración de juveniles y adultos de corvina blanca, se plantea la hipótesis de que la corvina blanca, *Atractosción nobilis*, localizada a lo largo de la costa Pacífico comprende una sola población (no se considera la población que se encuentra en el golfo de California). Este estudio provee información biológica importante que podrá ser utilizada en el desarrollo de estrategias de manejo efectivas para la corvina blanca como recurso.

II. Objetivos generales

El objetivo principal de este estudio es estimar las tasas de crecimiento y la composición isotópica de submuestras de los otolitos de corvina blanca capturada en la costa Pacífico en el sur de California y norte y sur de la península de Baja California para evaluar si hay evidencia de la presencia de estructura poblacional. Las preguntas específicas a contestar son:

1.- ¿Es posible diferenciar entre subpoblaciones potenciales a partir de los parámetros de crecimiento a nivel poblacional e individual estimados para diferentes regiones?

2.- ¿Se puede diferenciar entre peces capturados en diferentes regiones a partir de la composición isotópica (δ^{13}C y δ^{18}O) del núcleo de los otolitos de peces adultos? ¿Es posible usar la temperatura retrocalculada y las condiciones ambientales locales del periodo de crecimiento de las larvas para diferenciar entre peces de diferentes regiones?

3.- ¿Los valores de δ^{13}C y δ^{18}O obtenidos de los anillos de crecimiento de los estados juvenil (edad 1-2 años) y adulto (edad 8-10 años) pueden indicar diferencias en el uso de hábitat y patrones de migración entre subpoblaciones?

III. Metodología

Los ejemplares de corvina blanca fueron recolectados durante primavera y verano del 2009 al 2012 en la pesca comercial y recreativa del sur de California y a lo largo de la costa Pacífico de la península de Baja California. Se midió la longitud total (LT) y estándar de los peces, y se extrajeron los otolitos sagita para posteriormente ser procesados en el laboratorio.

Para el análisis de las tasas de crecimiento (a) se consideraron tres regiones de muestreo: el sur de California (SCB) en EUA y las regiones del norte (NBC) y sur (SBC) de la península de Baja California (Figura 1). Dado el tamaño de los otolitos, éstos fueron incluidos en resina y cortados, en la región central a lo largo del plano dorso-ventral, con una cortadora de baja velocidad para obtener secciones que incluyeran el núcleo del otolito. Cada sección fue pulida, montada en un portaobjeto y, con una cámara adaptada a un microscopio, se obtuvieron imágenes de cada una de las muestras. El conteo de los anillos de crecimiento se llevó a cabo a partir del núcleo hacia el margen exterior, usando como guía el sulcus (Figura 2). Cada otolito fue datado dos veces por dos lectores independientes sin contar con información del pez. En el análisis de los datos se calculó el porcentaje de acuerdo entre lectores (PA), el porcentaje de error promedio (APE) y el coeficiente de variación (CV). Se identificó el tipo de margen de cada otolito, opaco o translucido, se para evaluar la periodicidad del depósito de los anillos.

En la evaluación de las tasas de crecimiento a nivel poblacional se aplicó el modelo de crecimiento de von Bertalaffy. Con la prueba de análisis de suma de cuadrados de los residuales (ARSS) y la prueba de máxima verosimilitud (Likelihood Ratio Test) se evaluó si había diferencias entre los parámetros poblacionales estimados para cada región. El crecimiento individual se evaluó a partir del ancho de cada uno de los anillos de crecimiento. El crecimiento fue representado por proyecciones del radio en función de la edad, evaluadas a partir de un análisis de medidas repetidas (MANOVA). El ancho de los incrementos entre regiones se comparó por medio de un ANOVA de una vía. Por último, las diferencias en el crecimiento entre regiones fue examinada con un análisis de residuales; el ancho promedio a cada edad para cada región fue estimada a parir del ancho promedio a cada edad para todos los otolitos analizados.

En el análisis de la composición isotópica del núcleo y los anillos de crecimiento de los otolitos (b) se utilizaron algunas muestras de las procesadas en la sección anterior.

Las regiones de muestreo se clasificaron en Sur de California (SC), Bahía Vizcaíno (VB) y Golfo de Ulloa (GU; Figura 8). En general, las muestras de carbonato fueron extraídas con un micro-taládro de alta precisión y fueron enviadas para su análisis a la Universidad de California, en Santa Cruz, USA. El peso de las muestras fue entre 30 y 50 μg de carbonato del núcleo (alrededor de 30 muestras por región). Así mismo, de otro grupo de muestras se extrajeron el núcleo, los cuatro primeros anillos de crecimiento correspondientes a la edad 0.5-2 años de la etapa juvenil y de los anillos de crecimiento correspondientes a 8.5-10.5 años de la etapa adulta (Figura 9). El promedio mensual de la temperatura regional se obtuvo a partir del análisis de imágenes satelitales y la salinidad a partir de los reportes CalCOFI e IMECOCAL.

La composición isotópica del agua (δw) se calculó a partir de la salinidad regional con la ecuación (3) de Craig y Gordon (1965). Las temperaturas retrocalculadas se obtuvieron a partir de la ecuación (4) de Campana (1999). Los valores predichos del δ^{18}O del mapa isotópico se estimaron con base en el intervalo completo de salinidad (33-36 ups) y temperaturas regionales (10-30 T^oC) determinadas para el periodo de desove durante el verano.

IV. Resultados

Análisis de las tasas de crecimiento

De las 415 muestras obtenidas, 105 fueron del SC, 119 del NBC y 191 del SBC. El rango de tallas por región vario entre localidades (Figura 3). En el SC la LT fue de 35.6 a 147.3 cm (media 118.6 cm TL; Figura 3A). En el NBC las longitudes fueron de 40.6 a 156.0 cm LT (media=113.8 cm; Figura 3B). La longitud de las corvinas blancas capturadas en el SBC fueron entre 31.0 y 147.0 cm LT (media=81.5 cm LT; Figura 3C).

En el análisis del margen de los otolitos la proporción de individuos con margen opaco fue mayor durante febrero y noviembre, sin embargo el número de muestra para esos meses fue reducido. Las bandas translúcidas predominaron en muestras recolectadas durante abril a septiembre. Durante este periodo, 25 a 45% de los otolitos tuvieron bandas opacas en el margen (Figura 4). Las edades variaron entre 0 y 28 años. El APE y CV fue de 8.3% y 11.5% respectivamente considerando el total de los datos obtenidos en las tres regiones de muestreo. El porcentaje de acuerdo entre lectores fue de 96%, lo cual indica un nivel alto de consistencia.

En el modelo de crecimiento de von Bertalanffy se observó una alta variabilidad en la LT en función de la edad (Figura 5). Las tasas de crecimiento y la longitud infinita fueron muy similares en las tres regiones (de 0.18 a 0.19 año^{-1} y de 140.84 a 141.20 cm). La comparación entre curvas de crecimiento fueron diferentes entre regiones (ARSS; $F_{(3,373)}$ = 55.46, P$<$0.05), estas diferencias fueron significativas en el valor de t_o entre SC y SBC (Tabla 1).

A nivel individual, se observo una alta variabilidad en las mediciones del crecimiento en el plano transversal (Figura 6). El ancho promedio de los anillos a una determinada edad fue similar en las tres regiones; como era de esperarse, el ancho de los anillos se redujo con la edad (Figuras 6B, D and F). El incremento promedio entre localidades fue significativamente distinto (Wilks′s λ, F$_{(2,148)}$ = 1.754, P$<$0.05). Estas diferencias se encontraron entre el ancho de los otolitos de SC vs. SBC (Hotelling′s, t = 29.05, P$<$0.05) y NBC vs. SBC (t = 23.43, P$<$0.05), pero no hubo diferencias entre SC y NBC (t = 13.09, P$>$0.05). Específicamente, los otolitos recolectados en SBC fueron significativamente más largos en el ancho del primer anillo de crecimiento que los otolitos del SC y NBC (Tabla 2). Así mismo, en el análisis de residuales se encontró que las corvinas blancas recolectadas en el SC presentan un radio menor al promedio, y los otolitos recolectados en el SBC son en promedio más anchos que los de SC y NBC (Figura 7).

Análisis de la composición isotópica del núcleo

Los valores isotópicos se obtuvieron en un total de 100 otolitos de corvina blanca (Figura 10). Se identificaron dos valores extremos que fueron eliminados de los análisis. Se encontraron diferencias significativas en los valores de δ^{13}C entre regiones (ANOVA F$_{(2,95)} = 27.47, P < 0.001)$; la composición isotópica promedio de VB fue diferente a la del SC y GU (Scheffes test, MS=0.506, P <0.001). En contraste, no se observaron diferencias entre los valores promedio de $\delta^{18}O$ entre regiones (ANOVA F$_{(2,95)} = 1.41, P = 0.249)$. El rango de valores de δ^{13}C y $\delta^{18}O$ en función del año de desove mostró un alto nivel de variación, incluso cuando el número de individuos analizados por año fue reducido (Figura 11).

La comparación de la temperatura superficial del mar (SST) promedio mensual ente regiones mostró un gradiente latitudinal muy marcado (Figura 12), con un patrón similar durante el periodo de desove de 1999 a 2006. Las temperaturas más cálidas fueron observadas en GU (17.3-26.6^{o}C). Durante el verano, la SST fue 5.5^{o}C más alta en el GU y 5.0^{o}C que VB. Las salinidades regionales, a 10 m de profundidad, también mostraron un gradiente latitudinal muy marcado tanto en verano como en invierno durante los meses de 1999 a 2006 (Tabla 3). Dada la relación lineal entre la salinidad y el δw, la estimación de la composición isotópica del agua en el GU fue más ligera que en el SC y VB (Figura 13).

La temperatura retrocalculada a partir de la composición isotópica del núcleo de los otolitos ($\delta^{18}O_{oto}$) varió entre 14 y 23^{o}C (Figura 14). A pesar del traslape entre las temperaturas retrocalculadas para cada una de las regiones, la temperatura promedio para el GU fue significativamente más alta que la del SC y VB (Scheffe's test, MS=2.572, P=0.032).

El rango de valores predichos de δ^{18}O del carbonato calculados a partir del a SST y salinidades regionales presentó un rango más amplio para el GU que para el SC y VB (Tabla 3; Figura 15). La comparación entre el rango de valores predichos de δ^{18}O con respecto a los valores de δ^{18}O medidos indica que en general todos los valores medidos de δ^{18}O caen en los valores esperados para cada una de las regiones. Sin embargo, en el GU el rango de valores predichos de δ^{18}O fue mayor a los valores medidos; ninguna de las mediciones fue $<$-1.6‰.

Composición isotópica de los anillos de crecimiento de los estadios juvenil y adulto

Los valores individuales de δ^{13}C de los anillos de crecimiento de los estadios juvenil y adulto de corvina blanca recolectada en el SC y GU mostraron un incremento en la variabilidad en función de la edad; el rango de valores se incrementó de 2-3‰ durante el estadio juvenil a casi 4.5‰ en el estadio adulto (Figura 16A and C). En contraste, los valores de δ^{18}O de los anillos de crecimiento del estadio juvenil mostraron un patrón consistente entre los anillos opacos (crecimiento de verano, empobrecido en la razón isotópica) y hialina (crecimiento de invierno, enriquecido en la razón isotópica) y con un rango mucho más reducido que los valores de δ^{13}C. Sin embargo, no se observó un patrón estacional durante el estadio adulto (Figura 16B and D).

Los valores promedio de la razón isotópica del carbono y oxígeno de los anillos de crecimiento de los otolitos mostraron un patrón diferente entre estadios del ciclo de vida (Figura 17). La prueba de ANOVA de dos vías de medidas repetidas indicó que no hubo diferencias significativas en ambos isótopos entre regiones durante el estadio juvenil y adulto (Tabla 4). Sin embargo, si hubo diferencias significativas en ambos isótopos entre edades en peces muestreados en las dos regiones (Tabla 4). La prueba de comparaciones pareadas post-hoc de Holm-Sidak indica que hay diferencias significativas en los valores de δ^{18}O en los anillos de crecimiento de los juveniles entre verano (S) e invierno (W; Figura 17, Tabla 5). La única diferencia encontrada entre edades fue en $S_{0.5}$ que corresponde al crecimiento de verano del primer año de vida, con diferencias significativas entre regiones (RM ANOVA, t=2.663, P=0.010).

La temperatura retrocalculada del núcleo y los anillos de crecimiento del estadio juvenil mostraron un rango amplio y un traslape entre edades y estaciones del año (Figura 18). La poca variabilidad observada en la salinidad del agua de mar entre regiones (por ende los valores estimados de δw) dió como resultado una diferencia en la temperatura menor a los 2^{o}C por anillo de crecimiento individual. Las altas temperaturas coinciden con la precipitación de carbonato durante el verano y las bajas temperaturas corresponden a los anillos de crecimiento de invierno. Las temperaturas más altas se calcularon para otolitos del GU con una diferencia de 1^{o}C para la misma edad entre regiones. Sin embargo, la temperatura del primer anillo opaco correspondiente al verano $(S_{0.5})$ fue más alto en el GU que en el SC en promedio con 4.5^{o}C.

V. Discusión

El patrón de crecimiento continuo y periódico de los otolitos permitió su uso para la estimación de las tasas de crecimiento a nivel individual y poblacional. Dado que las estimaciones de crecimiento de la corvina blanca son limitadas (Thomas, 1968; CDFG, 2002; Williams *et al.*, 2007), este estudio fue capaz de proporcionar información valiosa sobre la edad-talla así como probar la hipótesis con respecto a las posibles diferencias en las tasas de crecimiento con base en las localidades. A parte de la estructura poblacional, este trabajo será utilizado en la gestión de la corvina blanca, ya que actualmente se está incorporando en la primera evaluación del stock de corvina blanca en Norte América.

Los resultados más significativos de esta aproximación, en el contexto de la estructura poblacional de la corvina blanca, fue la similitud en las tasas de crecimiento y longitudes asintóticas de peces capturados en el sur de California y el norte y sur de la península de Baja California. A nivel individual, el ancho promedio del primer anillo de crecimiento fue significativamente más grande en peces capturados en el sur de Baja California en comparación con los del sur de California y norte de Baja California, lo cual sugiere que los peces de la región más sureña crecieron bajo condiciones ambientales diferentes (posiblemente a temperaturas más altas y con mayor disponibilidad de alimento).

Las condiciones ambientales bajo las cuales crecieron las corvinas fueron estimadas a partir de la composición isotópica (δ^{13}C and δ^{18}O) de los otolitos usados en la estimación del crecimiento. A partir de la presencia de un gradiente latitudinal en la temperatura superficial del mar y la salinidad a lo largo de la distribución de la corvina blanca (Lynn and Simpson, 1987; Durazo *et al.*, 2010), así como la premisa de que los otolitos formados bajo condiciones ambientales diferentes tendrán diferente composición isotópica (Campana, 2005); en este capítulo se tomaron submuestras de carbonato de los estadios larval, juvenil y adulto para inferir sobre el hábitat de crianza y el nivel de mezcla y conectividad poblacional. La composición isotópica del núcleo de los otolitos de corvinas blancas capturadas en el sur de California, bahía Vizcaíno y golfo de Ulloa varió sustancialmente pero no fue lo suficientemente distinta como para discriminar entre larvas crecidas en diferentes subpoblaciones potenciales. Sin embargo, durante el estadio juvenil las variaciones estacionales de la composición isotópica del carbono y oxígeno de corvinas del sur de California y golfo de Ulloa fueron muy evidentes. Adicionalmente, hubo diferencias significativas en la composición isotópica del oxígeno y temperaturas retrocalculadas obtenidas en el primer anillo de crecimiento estacional de peces capturados en cada región. Considerando que estos resultados corresponden al estadio juvenil, esto sugiere la presencia de dos subpoblaciones potenciales discretas divididas por Punta Eugenia en la parte central de Baja California.

En conjunto, estos resultados sugieren que los peces del sur de California y del golfo de Ulloa pasan parte de su vida bajo condiciones ambientales diferentes y esto ocurre consistentemente a lo largo de los años. La presencia de dos subpoblaciones potenciales de corvina blanca a lo largo de la costa Pacífico implica la necesidad de implementar, a nivel regional, estrategias de manejo pesquero dirigidas al uso sustentable de cada stock. Sin embargo, si futuras investigaciones indican un nivel de conectividad entre corvinas blancas adultas capturadas a lo largo de California y Baja California, entonces deberá implementarse una estrategia de manejo binacional basada en la presencia de un solo stock. De cualquier manera, la información acerca de la talla poblacional de la corvina blanca, población capturable, regiones de desove estacionales y la mortalidad natural aún se desconoce, principalmente en las regiones del sur de Punta Eugenia.

Dada la importancia de la corvina blanca en la pesca comercial y recreativa de Norteamérica, principalmente durante el periodo de desove, y su susceptibilidad a la sobreexplotación demostrada a lo largo de la historia de esta pesquería en California, los estudios sobre la estructura poblacional son críticos para un efectivo plan de manejo a largo plazo y para el uso sustentable de este recurso.

VI. Conclusión

Las diferencias encontradas en el crecimiento a nivel individual de la corvina blanca, así como la composición isotópica y las temperaturas retrocalculadas correspondientes al primer anillo de crecimiento estacional de peces capturados en el sur de California y golfo de Ulloa, sugieren la presencia de dos subpoblaciones potenciales discretas divididas por Punta Eugenia en la parte central de la península de Baja California.

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Chapter 1. General Introduction

1.1. Problem statement

A population can be defined as a group of individuals of the same species inhabiting a specific place at a specific time, which has the same gene pool, it is self-perpetuating and also has similar life history characteristics that are reflected in the population dynamics (King, 1995; Begg *et al.*, 2005; Waldman, 2005). Considering the concept of population connectivity as the exchange of individuals among groups, a population can be structured into subpopulations or small groups of individuals of the same species as a result of reduced connectivity or isolation between them; high connectivity typically results in a single population (King, 1995; Waldman, 2005). For most of the coastal marine species, the larval phase is the dominant dispersive stage between groups and it is driven by the interplay between biological and physical processes, and also depends of the amount of time that larvae remain in the water column prior to settlement or metamorphosis into a juveniles (Largier, 2003; Herzka, 2005; Levin, 2006; Cowen and Sponaugle, 2009). However, connectivity may also occur through the migration of adults to different spawning grounds (Harden, 1968; Cowen and Sponaugle, 2009). In populations subject to fishing pressure, with limited connectivity, the characterization of population structure is critical for effective management strategies and resource conservation.

The white seabass, *Atractoscion nobilis*, is the largest sciaenid member found along the Pacific coast of North America. Its distribution ranges from the southern part of the Baja California peninsula, Mexico, to northern California, USA, and includes the Gulf of California (Thomas, 1968; Allen and Franklin, 1992). The maximum recorded length is 1.6 m total length, more than 41 kg and they can live as long as 28 years (Miller and Lea, 1972; Eschmeyer *et al.*, 1983; Romo-Curiel *et al.*, 2015). Because white seabass reach large sizes and its meat is of very good quality it is considered an important target species in commercial and recreational fishing operations along its distribution (Thomas, 1968; Allen and Franklin, 1992).

The commercial fishery targeting white seabass started in the XIX century along the coast of California. In the 70s there was a marked decrease in landings and estimated population size, which was attributed to several factors including the increase in fishing effort, fluctuations in oceanographic conditions and the degradation of the nursery areas (Vojkovich, 1992). Recreational fishery has been important in terms of revenue, which comprised more than 25% of the commercial landings during 2008-2011 (CDFG, 2012). The first attempts to regulate the catches of white seabass in USA waters started in 1931, when several regulations were implemented including a commercial closure period from May 1 to June 30, a minimum catch size of 71 cm of total length, and restrictions regarding the types of fishing gear that can be used (Thomas, 1968). Based on the peak of the reproductive period, currently the fishery closure season is from March 15 to June 15 (Vojkovich, 1992; Hervas *et al.*, 2010). Allen *et al.* (2007) reported that there has been an important increase in the commercial catch per unit effort (CPUE) and a general increase in the recreational landings in California. They attributed this pattern to the positive effect of the management plans and suggested the increase in CPUE might indicate that the population has undergone a recovery process.

In Mexico, white seabass are caught primarily by the artisanal fisheries using small vessels ($<$10 m length) and by medium size vessels (10-27 m in length). Off the west coast of Baja California peninsula the white seabass is considered a target species of several artisanal operations (Cartamil *et al.*, 2011). However, currently there is no specific management plan for the exploitation of this source, and species-specific statistics on the commercial and recreational landings are unavailable (SAGARPA, 2006).

Different approaches have been used to infer the population structure of this species throughout its distribution, including evaluating the spawning areas through the evaluation of larval abundance and distribution, evaluation of population genetics and tagging of juveniles and adults fishes. Moser *et al.* (1983) based on the analysis of 104 plankton samples collected from Point Conception, Ca, USA, to Magdalena Bay, Baja California Sur, Mexico, found that the highest larval abundance occurred in southern California waters (15%) and off the central Baja California peninsula (85%). Donohoe (1997) determined that the shallow waters along the open coast and just beyond the breaking waves appeared to be the primary nursery area for early juveniles in southern California waters, and proposed that recruits were derived from local larvae. Allen and Franklin (1992) used patterns of abundance, distribution and settlement of young-of-the-year (YOY) to propose that larval transport from northern Baja California to southern California was a major source of YOY for this region, and that adults caught in southern California could be a minor source of larvae for local recruitment. However, neither of these studies assessed potential larval transport or recruitment directly, and the level of connectivity between the southern and northern spawning areas remains unknown.

Studies that have assessed white seabass genetics suggest the absence of population structure. Bartley and Kent (1990) assessed the level and distribution of genetic variability based on starch-gel electrophoresis of samples collected throughout the Southern California Bight, and found a low level of genetic variability and did not detect evidence supporting the presence of population structure. Franklin (1997) analyzed microsatellite DNA of fish collected from Point Conception, CA to Magdalena Bay, off the southern Baja California peninsula and the central Gulf of California, and suggested the existence of a single population along the Pacific coast and a genetically distinct population in the Gulf of California. Similarly, Coykendall (2005) used mitochondrial DNA sequences from 6 localities including the Mexican Pacific coast, and did not found evidence of clear population structure. However, most of these studies used a small number of samples or had a limited spatial sampling effort, which greatly weaken the strength of the inferences that can be made regarding the presence of absence of population structure throughout their distribution.

Tagging studies of juveniles and adults white seabass suggest their capacity for movement and migration along the California and Baja California coastlines. Hervas *et al.* (2010) evaluated the dispersal level of cultured juveniles (162-224 mm standard length, SL) tagged with a coded wire and released in the SCB between 1999 and 2004. They found that 50% of recaptures occurred within 47 km and 95% within 135 km from the release site. More recently, Aalbers and Sepulveda (2015) tagged adult white seabass along the southern coastline of California, including Santa Catalina Island, during spring and summer months of 2008-2011. They proposed that adults migrate north during the spawning season coincident with the seasonal increase in surface temperatures in southern California. However, multiple individuals also travelled in a southern direction and were recaptured in Mexican waters as far south as La Salina, BC, Mexico, supporting a high level of exchange across a broad geographic range. The recapture of tagged adult white seabass in Mexican waters suggests that southern California and nothern Baja California peninsula fisheries are harvesting of the same stock. Although this resource is shared between both countries, different management approaches are currently in use among countries, and binational management efforts are lacking.

Two methods that have been used extensively for evaluating population structure of marine coastal fishes include the analysis of otolith growth rates and their chemical composition. The continuous growth pattern and periodic ring formation of fish otoliths allows them to be used for generating estimates of growth rates at the individual and population levels. When that information is combined with chemical measurements (stable isotope analysis of the carbonate or elemental analysis) of the otoliths, it is possible to infer the environmental conditions experienced by fishes, evaluate population structure, reconstruct migration patterns and estimate the contribution of specific nursery areas to adult fish production (see reviews by Campana and Neilson, 1985; Campana, 1999; Campana and Thorrold, 2001). Whole otoliths or specific regions of otoliths may show different chemical compositions that can also be used to infer population structure, natal origin, and migration patterns (Campana, 1999; Elsdon *et al.*, 2008). Importantly, the environmental conditions experienced by adult fishes during the larval or juvenile periods can be assessed by analyzing the isotopic composition of the portion of the otoliths that correspond specifically to those life stages (Tanner *et al.*, 2013). The presence of differences in the growth rates and chemical composition of the otoliths of a given species sampled throughout its distribution can also be used to differentiate subpopulations (MacNair *et al.*, 2001; Begg *et al.*, 2005).

Considering that the white seabass is an important resource in Mexico and the USA, and that there is uncertainty regarding whether the fish that inhabit the western coast of North America comprise one or more subpopulations, the present study sought to assess population structure. Given the high potential for larval dispersal and migration of juveniles and adults, it was hypothesized that white seabass, Atractoscion nobilis, found along the Pacific coast compose a single population (the population found in the Gulf of California was not examined). This study provides important biological information that can be used in the development of effective, long-term management strategies for the white seabass resource.

1.2. General objectives

The aim of this study is to estimate growth rates and the isotopic composition (δ^{13}C and δ^{18}O) of subsamples from the otoliths of white seabass (*Atractoscion nobilis*) captured in Pacific waters off southern California and northern and southern Baja California to evaluate whether there is evidence for the presence of population structure. The specific questions to be answered are:

1.- Do individual and population-level growth parameters of potential subpopulations differ between sampling regions?

2.- Does the isotopic composition (δ^{13}C and δ^{18}O) of adult otolith cores (corresponding to the carbonate precipitated during the larval rearing stage) differ between fish captured in different regions? Do back-calculated temperatures and local environmental conditions during the larval rearing period differ between regions?

3.- Do δ^{13}C and δ^{18}O values obtained from annual growth rings corresponding to juvenile (ages 1-2 yr) and adult stages (ages 8-10 yr) indicate differences in habitat use and migration patterns between subpopulations?

Chapter 2. Otolith-based growth estimates and insights into population structure of white seabass, *Atractoscion nobilis*, off the Pacific coast of North America

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2.1. Introduction

The sciaenid *Atractoscion nobilis*, or white seabass, is distributed along the Pacific coast of North America from northern California, USA, to southern Baja California, Mexico and within the Gulf of California. White seabass are considered an important commercial and recreational fish species in both countries (Thomas, 1968). Although landings have fluctuated widely over time, U.S. management regimes have been in effect since 1930 and have included different gear restrictions, bag limits, closed seasons and minimum size limits (Vojkovich and Reed, 1983; Pondella and Allen, 2008). Fishing by the US fleet was permitted in Mexican waters until 1982 and comprised as much as 89% of the annual catch landed by the US commercial fleet (CalCOFI, 2009).

In Mexican waters the white seabass fishery existed before the 1950s (Vojkovich and Reed, 1983; Erisman *et al.*, 2010). During late spring and summer, white seabass are considered a target fishery species along the western coast of the Baja California peninsula (Cartamil *et al.*, 2011). In the northern Gulf of California, (Moreno-Báez *et al.*, 2012) identified white seabass as one of 40 target fishery species. Little is known about the white seabass population in the Gulf of California. However, (Franklin, 1997) provided evidence of a genetically distinct group from that found in the Pacific coast. Mexico does not have a specific regulatory strategy for this fishery resource such as minimum size limits, landing quotas for different fishing areas or a total allowable catch. The fishery is managed through non species-specific commercial fishing permits, and white seabass are included in the broad category of coastal finfish species (Escama; SAGARPA, 2013).

Species-specific catch statistics are unavailable for white seabass. SAGARPA (2013) reported a total commercial catch for all croaker species in the Pacific off Baja California were ca. 1,800 metric ton (mt) for 2012, and white seabass likely represent most of the catch. Data for recreational catches in Mexico are unavailable.

Studies on the biology of *A. nobilis* have been performed only in the northern portion of their range. Along the Pacific, the spawning period is from March to August with a peak in May or June (Allen and Franklin, 1992; Donohoe, 1997). White seabass form seasonal spawning aggregations within shallow coastal waters and around nearshore islands (Thomas, 1968; Donohoe, 1997; Aalbers and Sepulveda, 2012) estimated the daily growth rate of recently settled white seabass and calculated that early juveniles remain in shallow nursery areas for two or three months. Older juveniles are concentrated in shallow areas close to the surf zone and their abundance decreases as a function of depth and distance from shore. Adults are found in schools and also as solitary individuals from the surf zone to a depth of 120 m and in habitats including sandy banks, rocky areas, kelp beds and artificial reefs (Vojkovich and Reed, 1983; Allen and Franklin, 1988; Donohoe, 1997).

Although the white seabass is an important commercial resource of the US and Mexico, there are few growth estimates for this species with no studies assessing growth parameters across their range in the Pacific. The studies published to date are based on both otolith and scale analyses of fish captured in southern California waters. Clark (1930) generated the first estimates of age based on length frequency information from a limited number of individuals. Thomas (1968) conducted the first comprehensive age determination work based on the analysis of scales, but those estimates were later shown to underestimate age (CDFG, 2002; Williams *et al.*, 2007). Based on unpublished data, the CDFG (2002) generated population-level growth rate parameters based on otolith ageing, and found that the maximum age and size were 27 years of age and 136.6 cm total length

(TL). Fish of 71.1 cm TL (the current minimum size limit in California) were estimated to be three years old and the growth rate during the first few years was estimated to be 0.156 mm yr^{-1}. The CDFG (2002) data was based on primarily smaller individuals and examined a limited number of samples from age classes seven and older.

Williams *et al.* (2007) suggested that white seabass growth rates vary annually relative to temperature; growth rates of juvenile white seabass (1 to 4 years of age) were positively correlated with the higher sea-surface temperatures (SST) that are characteristic of El Niño Southern Oscillation (ENSO) conditions. This was observed despite the lower overall productivity of the region under ENSO conditions (Chavez *et al.*, 2002). Temperature and food availability are among the most important environmental factors influencing growth rate in fishes. Within physiological limits, higher temperatures are reflected in fast growth rates, particularly in young fishes if food is not limiting (e.g. Brett, 1979; Otterlei *et al.*, 2002; Folkvord *et al.*, 2004; Neat *et al.*, 2008). Somatic and otolith growth are highly correlated, and temperature has also been shown to have a strong influence on incremental ring widths and an otolith's growth rate (Brett, 1979; Mossegard *et al.*, 1988; Arnason *et al.*, 2009). Otolith-based age estimates and incremental (seasonal) ring width measurements have long been shown to provide a good approach for reconstructing the growth of fishes at the population (Campana and Neilson, 1985) and individual levels (Wilson and Larkin, 1980; Chambers and Miller, 1995). Consequently regional variations in growth could be an indicative of separate populations (Begg *et al.*, 2001; MacNair *et al.*, 2001; Yamaguchi *et al.*, 2004).

Biogeographical breaks along the Pacific coast of North America have been shown to play an important role in determining population structure of coastal fish and invertebrate species. Punta Eugenia, located in the central part of the Baja California peninsula, is considered a transitional area in the California Current System (CCS) due to seasonal and latitudinal shifts in upwelling intensity and regional variation in the direction and intensity of coastal currents. There is also a well-documented latitudinal pattern in sea surface temperature (SST) along the Pacific coast of North America (Lynn and Simpson, 1987; Durazo *et al.*, 2010). Some studies have documented the presence of biogeographical breaks in fish and invertebrate species north and south of Punta Eugenia (Horn *et al.*, 2006; Kelly and Eernisse, 2007; Selkoe *et al.*, 2007; Blanchette *et al.*, 2008). To date, there are no studies that investigate the growth rate of this economically valuable species across their range, despite the oceanographic differences along the distribution of white seabass in the Pacific.

The widths of otolith growth increments (daily rings and annuli) have been used to determine the somatic response to variations in habitat quality (Molony and Choat, 1990; Jones, 1992). The average values of the internal measurements of otoliths can vary significantly when comparing individuals of different stocks, although individual measurements do not necessarily allow individuals to be assigned to a particular stock (Pawson and Jennings, 1996); this tool has been used to help discriminate between stocks (Campana and Casselman, 1993; Begg *et al.*, 2001). This study used otolith-based techniques to estimate age and growth in white seabass sampled off southern California and the northern and southern Baja California peninsula.

2.1.1. Hypothesis

White seabass collected along the Pacific coast may exhibit different growth rates throughout their distribution, particularly during their first year when is the biggest growth. If that's, could be and indicative of the presence of separate populations.

2.1.2. Objectives

- Strengthen the age estimates for this species by examining a large range of adult sizes.
- Compare the population level growth rates among southern California, U.S.A., northern and southern Baja California peninsula, Mexico.
- Assess individual growth trajectories through measurements of the width of annual growth rings.

2.2. Methods

2.2.1. Sample collection

White seabass were sampled between 2009 and 2012 from commercial and recreational fisheries in southern California (SC) and along the Pacific side of the Baja California peninsula (Figure 1). Samples collected off Baja California were subdivided in two regions separated by Punta Eugenia (northern and southern Baja California, or NBC and SBC, respectively). Samples were primarily collected during the spring and summer months, which is when the fisheries operate in the US and Mexico. The SC samples were obtained from recreational fisheries that have a minimum size limit of 70 cm TL (CDFG, 2002). In NBC white seabass were caught by gill nets as well as by hook and line, which yielded a broader size range than for SC. In SBC commercial fishermen used gill nets and smaller fishes were caught than in SC and NBC. Fish total length and standard length (SL) were measured to the nearest cm (n = 415). Sagittal otoliths were extracted, cleaned and stored dry. For southern Baja California only SL measurements were taken, and a linear regression between TL and SL was generated to convert to total lengths (TL = (SL + 2.54) / 0.93; r^2 = 0.99; n = 135).

2.2.2. Otolith ageing

Sagittal otoliths of white seabass are very large, as in other sciaenids, and are unreadable if not sectioned. Whole otoliths were embedded in epoxy resin and two or three transverse sections 1 mm thick were cut through the central region along the dorso-ventral plane with a slow-speed circular saw (Buehler, ISOMETTM) to obtain a section that included the otolith core. Sections that included the core were polished using decreasing

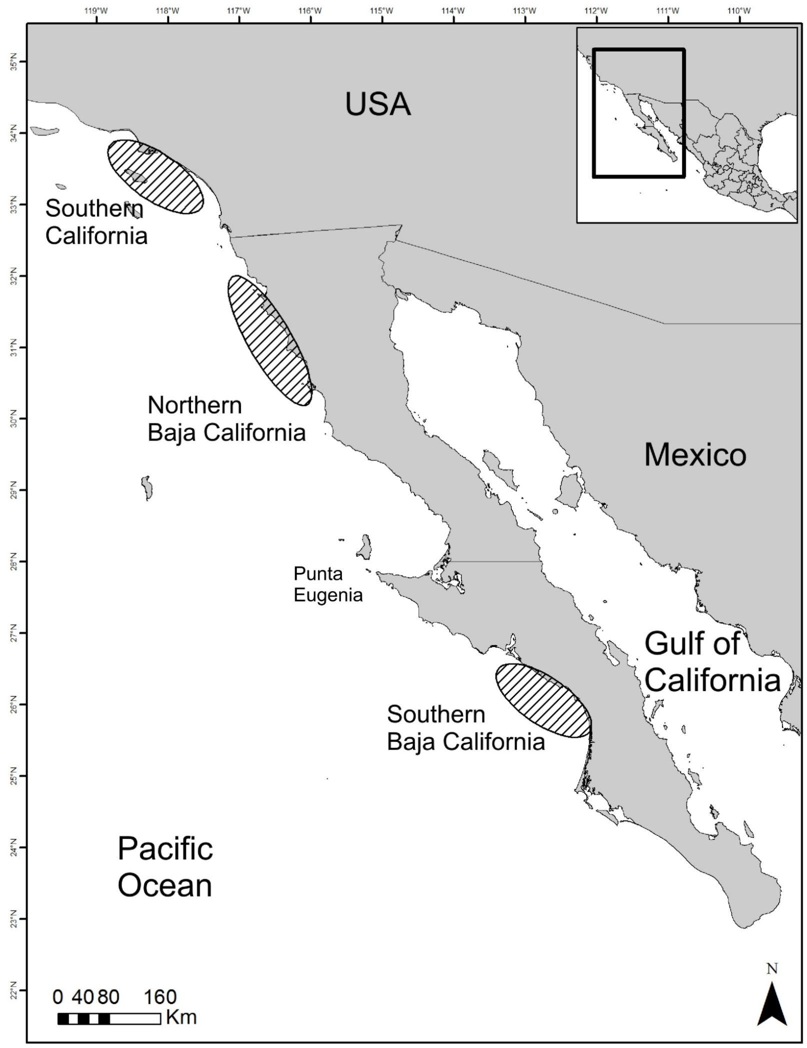

Figure 1. White seabass, *Atractoscion nobilis*, sampling regions along the Pacific coast of North America. The presence of population structure was evaluated by estimating population and individual-level growth rates based on otolith ageing of White Seabass captured off southern California, U.S.A. and on the Pacific side of the northern and southern Baja California peninsula, Mexico between 2009 and 2012.

Figura 1. Regiones de muestreo de corvina blanca, *Atractoscion nobilis*, a lo largo de la costa Pacífico de Norteamérica. Se evaluó la estructura poblacional a partir de la estimación de la tasa de crecimiento a nivel poblacional e individual con base en el análisis de la edad en otolitos de corvina blanca capturada en el sur de California, E.U., y en la costa Pacífico del norte y sur de la península de Baja California, México entre 2009 y 2012.

grit abrasive paper. A final polish with micro-cloth and 0.3-micron alumina powder was performed. Otolith sections (0.7-0.8 mm width) were mounted on a glass slide and viewed with a stereoscope (Olympus SZX7) at magnifications between 1.2 and 3.6 X and photographed with a digital camera (Olympus U-CMAD3). Under transmitted light the core and opaque bands appear as dark rings, and the wider translucent bands as clear or hyaline rings (Figure 2).

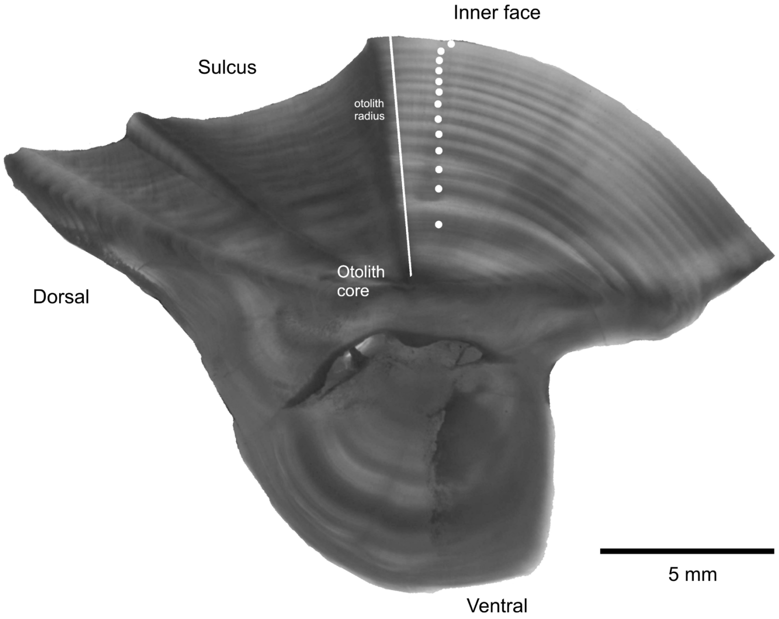

Figure 2. Transverse section cut through a sagittal otolith of white seabass (*Atractoscion nobilis*) showing the annuli in a 13 year old fish. Dots indicate annuli and the white line indicates the axis along which otolith radius measurements were taken.

Figura 2. Corte transversal del otolito sagita de la corvina blanca (*Atractoscion nobilis*) mostrando los anillos de crecimiento en un pez de 13 años de edad. Los puntos indícan la edad y la línea blanca el eje por el cuál se hicieron las mediciones del radio.

The count path of the annuli was from the nucleus towards the tip of the inner face next to the sulcus, where the deposition of seasonal rings appeared clearly defined (Figure 2). For each otolith, age was estimated twice by two independent readers in the absence of information on fish size or sampling date. The agreement between readings and readers were evaluated by calculating the percent agreement (PA). Disagreements in age estimates $>$4 years were resolved by both readers examining the otoliths simultaneously. The index of average percent error (APE; Beamish and Fournier (1981) and the mean coefficient of variation (CV; Chang, 1982) were calculated to estimate the relative precision of age estimates between readers. A total of 33 otoliths (8%) were excluded from age determinations because they were crystallized or if the growth rings were difficult to interpret and a consensus between readers could not be achieved.

To assess the yearly pattern of deposition of otolith annuli, the appearance of each otolith margin was recorded as opaque or translucent. Only fishes 5-15 years of age were included in this analysis because the type of otolith margin was clearly discernible. The timing of annulus formation was examined by plotting the percent occurrence of otoliths with a peripheral opaque band as a function of the sampling month (Okamura and Semba, 2009). The winter months were not well represented and were therefore excluded from the analysis.

2.2.3. Population-level growth rate

To estimate population-level growth rates, age-at-length estimates were fitted with the von Bertalanffy growth model using non-linear regression (Nielsen and Johnson, 1985). The model is described by the equation:

$$LT = L_{\infty}(1 - exp^{-K(t-t_o)}) \tag{1}$$

were (L_{∞}) is mean asymptotic total length (cm), K is the growth coefficient (yr^{-1}), t is age (years) and t_o is the theoretical age (yr) at zero length. The growth function was fitted using a nonlinear least square in a SOLVER routine of Excel software (Haddon, 2001). The differences in the von Bertalanffy growth parameters among the three localities were compared through an analysis of residual sum of squares (ARSS) and the likelihood ratio test (Chen *et al.*, 1992; Haddon, 2001). In order to compare the growth curves among localities the mean TL at each age was also plotted.

2.2.4. Individual-level otolith growth

Individual otolith growth along the transverse plane was measured as the distance from the core to the distal edge of each opaque ring using the *Image J* software package. Only fishes between 9-26 years of age were included to generate time series of comparable lengths (at least 10 years). Growth was represented as the projection of the radii of each opaque ring as a function of age; those projections were evaluated within and among localities with repeated-measures MANOVA (Chambers and Miller, 1995). In addition, the mean radius of each annuli at age was calculated for each region for fishes $<$10 years of age; older fish exhibit slower growth rates and the width of the area did not vary greatly. In order to test for differences in the increment width among ages, a one-way ANOVA was applied (Chambers and Miller, 1995). Both statistical analyses were performed with the SYSTAT 13.0 software package.

Lastly, growth differences between regions were examined using residual analysis; the average width-at-age for each region was subtracted from the average width-at-age for all the otoliths analyzed (Haddon, 2001). Only fish $<$10 years of age were considered because growth differences were more evident during the first years of life.

2.3. Results

2.3.1. Lenght frequency distributions

Of the 415 fish sampled, 105 were from SC, 119 from NBC and 191 from SBC. The size range of the fish sampled varied between locations (Figure 3). In SC the TL of the white seabass sampled ranged from 35.6 to 147.3 cm, with a mean of 118.6 cm (Figure 3A). The NBC sample was dominated by fish between 40.6 and 156.0 cm TL (mean = 113.8 cm; Figure 3B). The size range of white seabass caught off SBC was 31.0 to 147.0 cm TL (mean = 81.5 cm TL; Figure 3C).

2.3.2. Analysis of otolith margins

The proportion of individuals with an opaque otolith margin was highest during February and November, although the sample size for those months was limited. Translucent bands predominated in samples collected from April to September. During this period, 25-45% of otoliths had opaque bands along their margin (Figure 4).

2.3.3. Otolith ageing

Ages ranged from 0 to 28 years. The APE and CV were 8.3% and 11.5%, respectively for the data in all localities. After eliminating the otoliths that were hard to read or for which agreement could not be reached between readers, there was a 96% agreement between readers, indicating a high level consistency. Disagreements in age estimates between readers were more frequent for fish $<$ 4 yr and $>$ 16 yr.

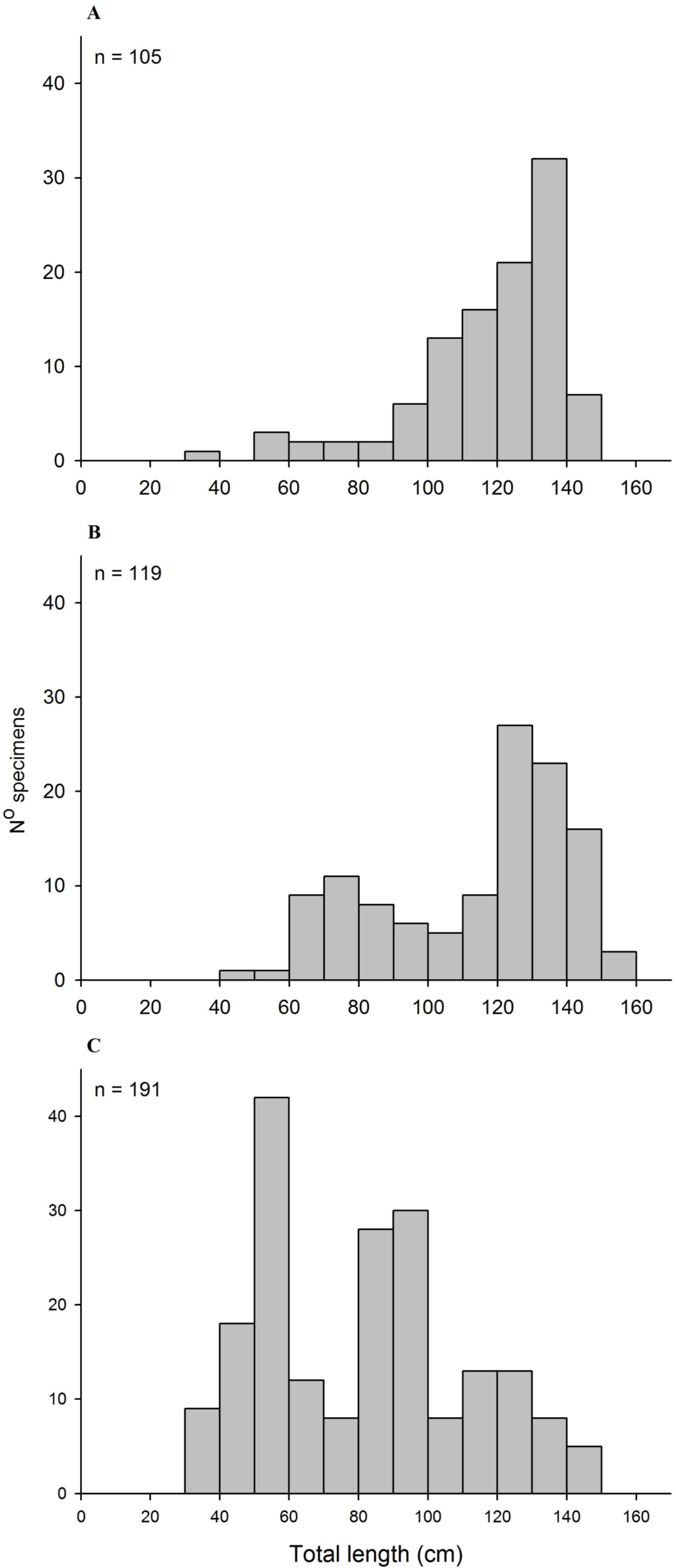

Figure 3. Length-frequency distributions of white seabass, *Atractoscion nobilis*, sampled from 2009 to 2012 off southern California (A), northern Baja California (B) and southern Baja California (C). n, sample size.

Figura 3. Distribución de frecuencias de la longitud total de la corvina blanca, *Atractoscion nobilis*, recolectada del 2009 al 2012 en el sur de California (A), norte de Baja California (B) y sur de Baja California (C). n, tamaño de la muestra.

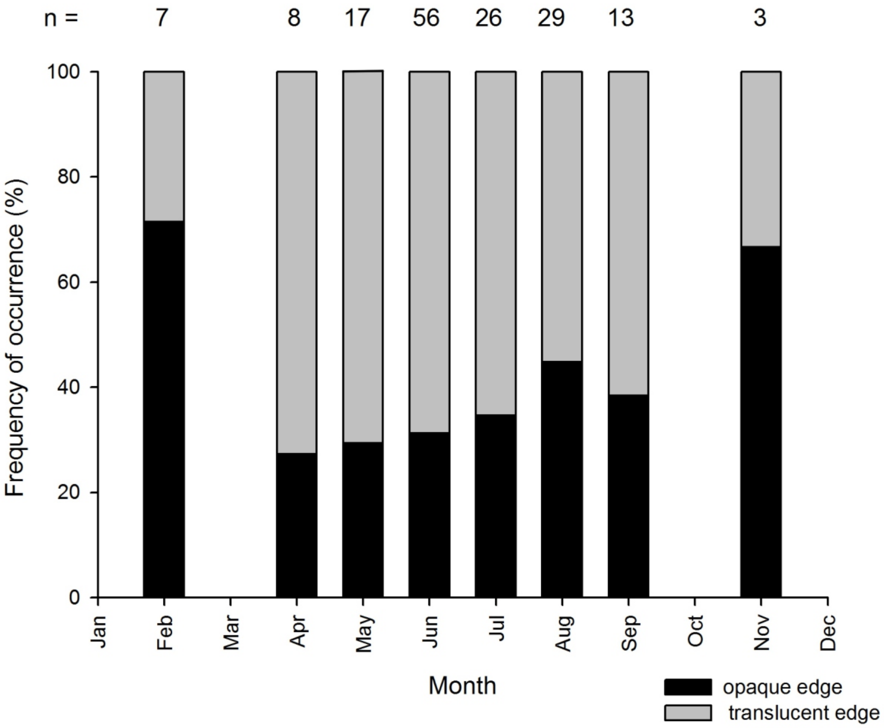

Figure 4. Percentage of occurrence of opaque and translucent margin of sectioned sagittal otoliths of *Atractoscion nobilis* collected off Southern California and in the Pacific off the Baja California peninsula. Only the otoliths of fish aged 5-15 yr were selected and analyzed. n, number of otoliths analyzed for each month.

Figura 4. Porcentaje de ocurrencia del margen opaco y translucido en una sección del otolito sagita de la corvina blanca *Atractoscion nobilis* recolectada en el sur de California y la costa Pacífico de la península de Baja California. Para este análisis sólo fueron seleccionados otolitos de peces entre 5 y 15 años. n, numero de otolitos analizados por mes.

2.3.4. Population-level growth rates

The von Bertalanffy growth model showed that the TL of white seabass varied as a function of age class (Figure 5). All fish showed a rapid increase in size during the first eight years of life. There were similar growth rates and asymptotic lengths in the three regions (0.18 to 0.19 year^{-1} and 140.84 to 141.20 cm, respectively). Residual sum of square analysis (ARSS) indicated that the von Bertalanffy growth curves varied among areas (ARSS, $F_{(3,373)}$ = 55.46, P$<$0.05). However, results of the Likelihood Ratio Test indicated that the growth rates and asymptotic length parameters from the von Bertalanffy function were not significantly differed between SC, NBC and SBC (Table 1). Significant differences were evident in t_o values between SC and SBC (-0.67 cm and -1.78 cm, respectively), notably in fish younger than 4 years sampled in SBC providing an explanation for the statistical differences between locations found with the ARSS analysis.

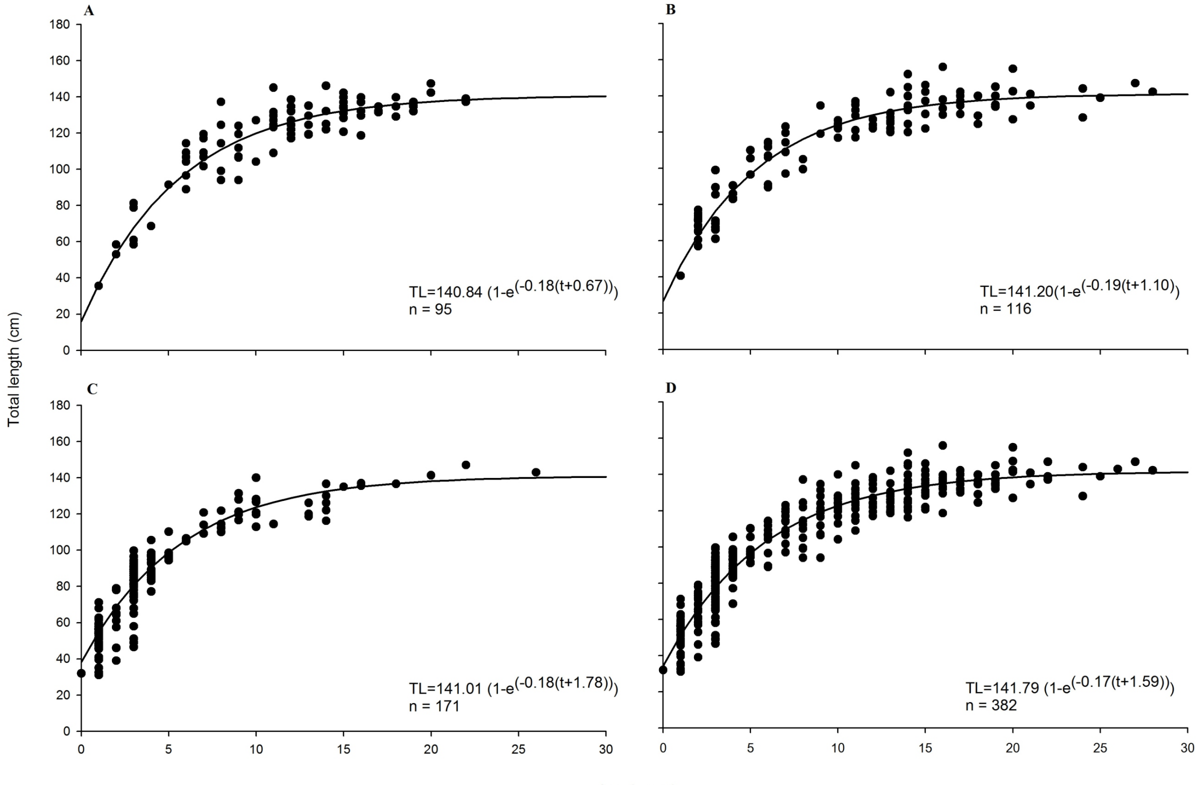

Figure 5. Plots of age-length data for white seabass, *Atractoscion nobilis*, sampled between 2009 and 2012. Otolith aging was conducted on samples from fish caught off southern California (A), northern Baja California (B) and southern Baja California (C). The pooled data are also presented (D). The data were fitted with the von Bertalanffy growth model. Note that a single point could denote several overlapping data points and n is sample size.

Figura 5. Datos de edad-longitud de corvina blanca, *Atractoscion nobilis*, recolectada entre 2009 y 2012. El datado de los otolitos se hizo en otolitos de peces capturados en el sur de California (A), norte (B) y sur de Baja California (C). También se obtuvo un modelo para el total de los datos (D). Los datos fueron ajustados con el modelo de crecimiento de von Bertalanffy. Notar que en los puntos puede haber un traslape de valores individuales, n es el tamaño de muestra.

2.3.5. Individual-level otolith growth

Otolith growth measured along the transverse plane showed high variability between individuals for the three regions (Figure 6). The average width of age-specific annuli was similar for the 3 regions; as expected, annuli width decreased with age, particularly for fish 1-4 years of age (Figures 6B, D and F). The average width increments among localities were significantly different (Wilks's λ, F$_{(2,148)}$ = 1.754, $P<0.05$). Those differences were found in the otolith width comparison between SC vs. SBC (Hotelling's, t = 29.05, $P<0.05$)

Table 1. Results of the likelihood ratio tests comparing von Bertalanffy parameter estimates for white seabass, *Atractoscion nobilis*, collected off southern California, northern Baja California and southern Baja California between 2009 and 2012. Statistical results represent the null hypotheses that parameter estimates do not differ between regions. RSS = residual sum of squares; $*$ significant at α = 0.05: $**$ significant at α = 0.001; ns = not significant.

Tabla 1. Resultados de la prueba de máxima verosimilitud en la cual se comparan los parámetros estimados para la corvina blanca, *Atractoscion nobilis*, recolectada en el sur de California, norte y sur de la península de Baja California entre 2009 y 2012. Los resultados estadísticos representan la hipótesis nula de que los parámetros estimados no difieren entre regiones. RSS = suma de cuadrados de los residuales; $*$ significativo a α = 0.05: $**$ significativo a α = 0.001; ns = no significativo.

Hypothesis	RSS	X^2	P	
Southern California - Northern Baja California				
H$_o = L_\infty$	835.384	0.032	0.858	*ns*
H$_o = K$	838.244	0.189	0.664	*ns*
H$_o = t_o$	854.918	1.095	0.295	*ns*
Southern California - Southern Baja California				
H$_o = L_\infty$	918.437	0.002	0.965	*ns*
H$_o = K$	918.399	0.000	0.988	*ns*
H$_o = t_o$	1049.441	5.469	0.019	*
Northern Baja California - Southern Baja California				
H$_o = L_\infty$	1065.718	0.012	0.914	*ns*
H$_o = K$	1068.984	0.149	0.699	*ns*
H$_o = t_o$	1111.085	1.888	0.169	*ns*

and NBC vs. SBC (t = 23.43, P$<$0.05), but no significant difference was found in otolith width measurements between SC and NBC (t = 13.09, P$>$0.05). At a specific age, otoliths collected off SBC had significantly larger increment annuli for the first year of life than those from SC and NBC. There were significant differences in the average increment width for age 3 and 8 (Table 2). Growth rate declined at 8 years of age, and was followed by an extended period over which little change in size occurred.

The residual analysis of the average radii indicated white seabass otoliths collected off NBC were similar to the average for the pooled data in the 10 years analyzed. White

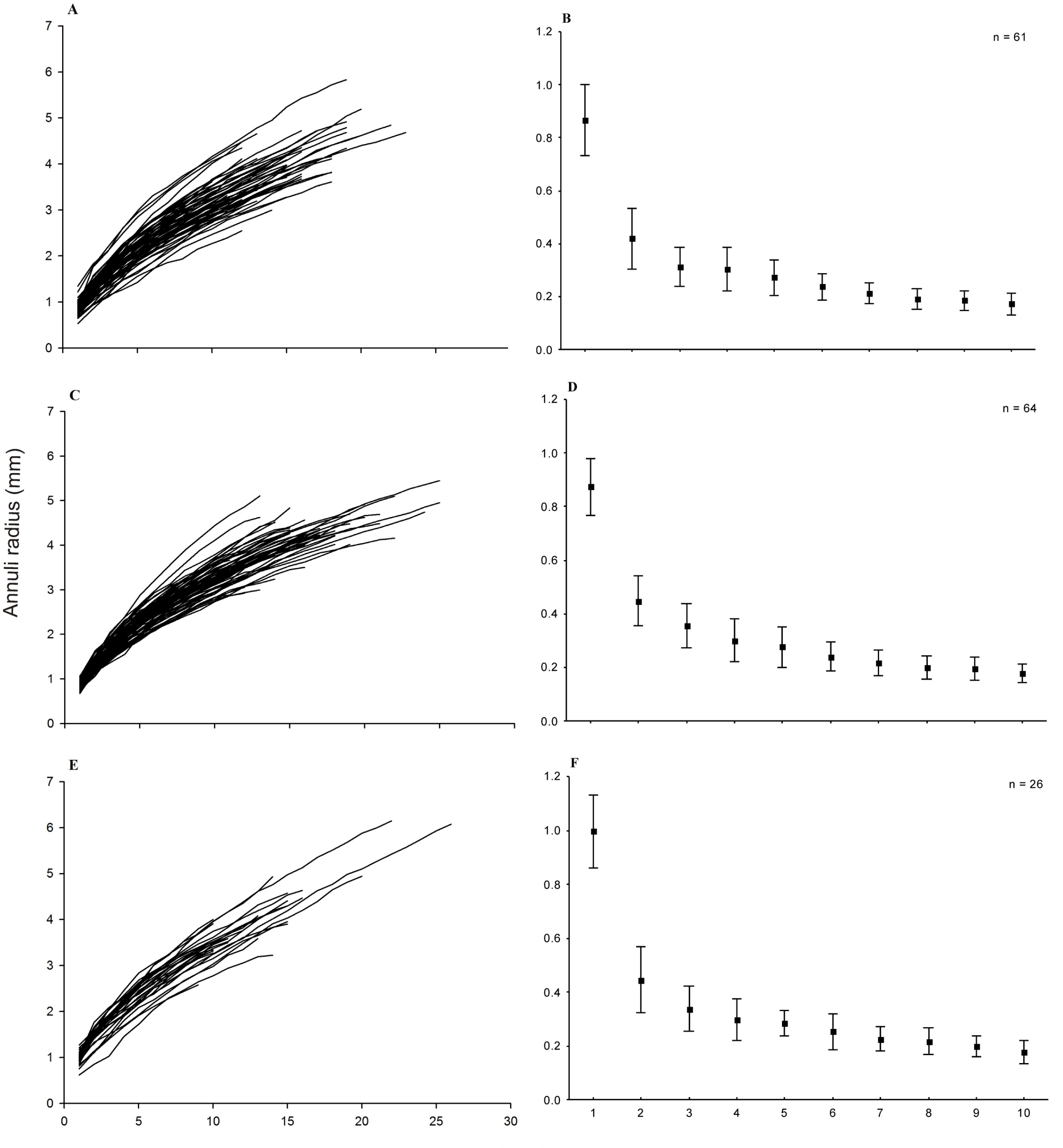

Figure 6. Individual growth trajectories of white seabass, *Atractoscion nobilis*. White seabass were collected off southern California (A and B), northern Baja California (C and D) and southern Baja California (E and F). Measurements were performed along the transverse plane of otoliths that were cut, mounted and polished. The individual growth tracks (A, C and E) were determined from measurements of the distance from the core to the distal edge of each opaque ring (radius-at-age). The average width of age-specific annuli (±SD) was also calculated (B, D and F).

Figura 6. Trayectorias del crecimiento individual de la corvina blanca, *Atractoscion nobilis*, recolectada en el sur de California (A y B), norte (C y D) y sur de Baja California (E y F). Las mediciones se hicieron a lo largo del plano transversal de otolitos previamente cortados, montados y pulidos. Las trayectorias del crecimiento individual (A, C, y E) fueron determinadas a partir de la medición de la distancia desde el núcleo hasta el margen distal de cada anillo opaco (radio-edad). Así mismo, se calculó el ancho promedio de los anillos de determinada edad (±DE; B, D y F).

Table 2. Results of the repeated measures MANOVA comparing the average annuli radius (±SD) of white seabass, *Atractoscion nobilis*, collected between 2009 and 2012 off Southern California (SC), northern (NBC) and southern (SBC) Baja California peninsula. Statistical results represent comparison for each annuli radius among localities. $*$ significant at α = 0.05; $**$ significant at α = 0.001; ns = not significant. Overall MANOVA results indicated a significant interaction between location-and-width at age.

Tabla 2. Resultados de la prueba de medidas repetidas MANOVA comparando el radio promedio de cada annuli (±DE) de la corvina blanca, *Atractoscion nobilis*, recolectada entre 2009 y 2012 en el sur de California (SC), norte (NBC) y sur (SBC) de la península de Baja California. Los resultados estadísticos representan la comparación entre el radio de cada uno de los anillos de crecimiento entre localidades. $*$ significativo a α = 0.05; $**$ significativo a α = 0.001; ns = no significativo. Todos los resultados del MANOVA indicaron una interacción significativa entre localidad-ancho en cada edad.

Annuli	SC	NBC	SBC	*F*	P	
1	0.87 ± 0.14	0.87 ± 0.11	1.00 ± 0.14	11.503	0.000	**
2	0.42 ± 0.12	0.45 ± 0.10	0.44 ± 0.13	1.143	0.322	*ns*
3	0.31 ± 0.08	0.36 ± 0.09	0.34 ± 0.09	4.337	0.015	*
4	0.30 ± 0.09	0.30 ± 0.08	0.30 ± 0.08	0.027	0.973	*ns*
5	0.27 ± 0.07	0.28 ± 0.08	0.28 ± 0.05	0.296	0.744	*ns*
6	0.24 ± 0.05	0.24 ± 0.06	0.25 ± 0.07	0.922	0.400	*ns*
7	0.21 ± 0.04	0.22 ± 0.05	0.23 ± 0.05	0.880	0.417	*
8	0.19 ± 0.04	0.20 ± 0.04	0.22 ± 0.05	3.604	0.030	*ns*
9	0.19 ± 0.04	0.20 ± 0.04	0.20 ± 0.04	1.299	0.276	*ns*
10	0.17 ± 0.04	0.18 ± 0.04	0.18 ± 0.04	0.223	0.800	*ns*

seabass sampled off SC had a smaller radius at age and measurements of otoliths collected off SBC were higher than those from SC and NBC (Figure 7).

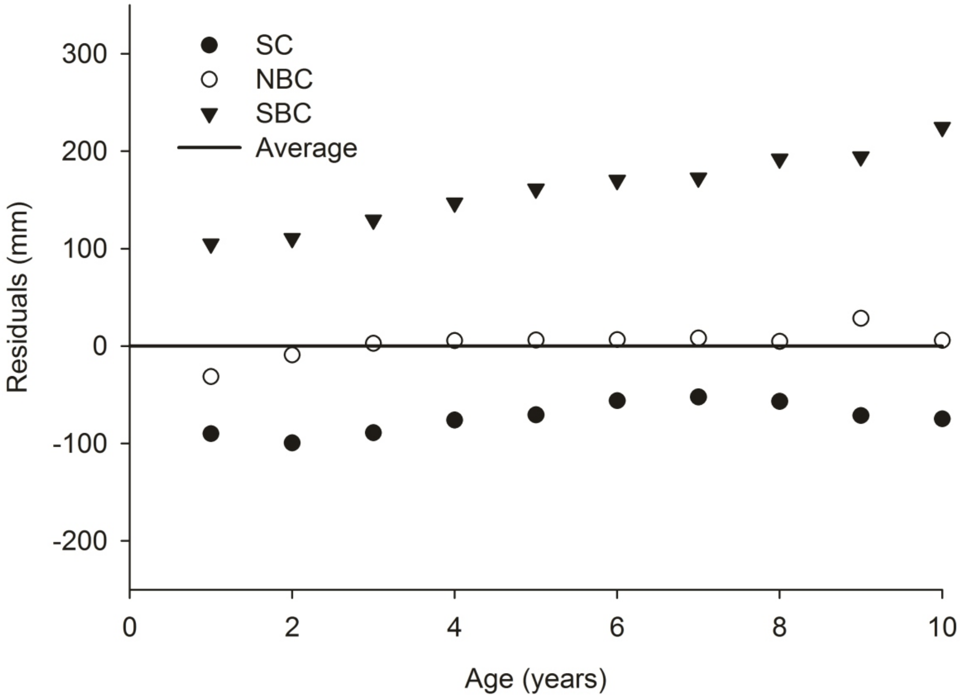

Figure 7. Residuals analysis of mean individual annulus widths-at-age of white seabass, *Atractoscion nobilis*, from southern California (SC), northern Baja California (NBC) and southern Baja California (SBC).

Figura 7. Análisis de residuales del ancho de los anillos de crecimiento por edad de la corvina blanca, *Atractoscion nobilis*, del sur de California (SC), norte de Baja California (NBC) y sur de Baja California (SBC).

2.4. Discussion

This study used two complimentary approaches, the generation of population and individual-level growth estimates, for evaluating whether there were differences in the growth rates of white seabass along the Pacific coast of North America. This work updates growth estimates for this species and suggests the presence of a single population of white seabass over their distribution in the Pacific. Also, identifies differences at the individual growth level during the first years of life between the northern (SC and NBC) and southern regions (SBC).

2.4.1. Validation of age determinations and otolith analysis

Generating estimates of age and growth based on the analysis of fish otoliths relies on a systematic interpretation of the optical appearance of internal structures, the assumption that periodic features are formed with constant frequency and that the distance between consecutive features such as annuli are proportional to fish growth (Campana and Neilson, 1985). Those features can be described at a population or individual level. At the population level, fish growth represents the average of many individual characteristics of fish inhabiting a region. On the other hand the growth pattern at the individual level is a direct reflection of the environmental conditions in which an individual fish grew and its integrated response to food availability and temperature, among other factors (Weatherley, 1972; Persson and De Roos, 2006; Zhang *et al.*, 2014). Fisheries-dependent collections run the risk of being too irregular or geographically imprecise to provide adequate samples for the evaluation of stock separation (Hilborn and Walters, 1992). Ideally, the analysis of otoliths for ageing studies should include a good representation of fish from broad range of sizes (Baggenal and Tesch, 1978).

This study targeted the local coastal fisheries and we were able to obtain otolith samples from a relatively broad size range of white seabass (e.g. 30-150 cm TL for all locations). However, the length-frequency distributions of white seabass sampled in the Pacific varied between regions. The distribution was unimodal for SC and bimodal for NBC and SBC. A greater proportion of relatively small fish ($<$60 cm TL) were sampled in SBC. During the first collections in NBC (2009 and 2010) and SBC (2010) most of the fish caught measured around 100 cm TL. In 2011 and 2012, a large number of smaller ($<$70 cm TL) white weabass were caught by the fishery in SBC. Despite the limitations associated with our fisheries-dependent sampling and the differences in fishing gear used in SC, NBC and SBC, we consider that the sampling is reasonably representative of white seabass of all sizes.

There are no published studies that fully validate the yearly deposition of annuli in white seabass otoliths. Previous studies have estimated the age of white seabass based on non-validated otolith ring deposition and assuming yearly annuli formation (Clark, 1930; CDFG, 2002). Williams *et al.* (2007) estimated the age of juveniles based on the morphological characteristics of the second primordia of the otoliths and documented that young white seabass appear to form four increments each year (bipartite annuli) that can be observed as pairs of opaque and translucent bands in the ventral otolith face. However, in other sciaenid species, annulus counts typically start at the core and proceed toward the outer edge next to the sulcus (VanderKooy, 2009). Since the objective of this study was to perform age determinations of fishes of all sizes and not only juveniles, we selected a methodology that was consistent with that used for fish with similar otolith morphology (Barbieri and Chittenden, 1994; Román-Rodríguez and Hammann, 1997; La Mesa *et al.*, 2008).

We were unable to fully validate the temporal periodicity of annuli formation due to difficulties in obtaining samples throughout the year because of the seasonal nature of the fishery. Nevertheless, our data indicates that during the spring and summer months 60-75% of otolith margins were translucent, which is consistent with the season of rapid growth. Beckman *et al.* (1988) found that the translucent zones in red drum (*Sciaenops ocellatus*; Sciaenidae) were deposited during summer and fall months and the opaque zones were during winter and spring months. Our data suggest an annual pattern but is not conclusive due the lack of sampling during the winter months.

Annual increment ring formation has been validated in other members of the family Sciaenidae, including red drum *Sciaenops ocellatus* (Murphy and Taylor, 1991), atlantic croaker (*Micropogonias undulatus*; Barbieri and Chittenden, 1994), totoaba (*Totoaba macdonaldi*; Román-Rodríguez and Hammann, 1997), and brown meager (*Sciaena umbra*; La Mesa *et al.*, 2008). Consistent growth increment patterns within the otoliths of white seabass, the previous validation of annual ring deposition in other members of the family, and the predominance of transparent growth rings during the spring and summer support the hypothesis of annual ring deposition for this species.

Long-lived species often have large, robust otoliths that require sectioning in order to accurately enumerate annuli for age estimation (VanderKooy, 2009). Transverse otolith sections of White Seabass generally provided clear zones that could be used for age determinations. The otolith of fish $>$4 years of age showed a clear pattern of deposition of annuli, while the growth bands of some younger white seabass were difficult to differentiate and frequently showed what could be false annual rings. For fish $>$16 years of age, rings were often narrow and sometimes difficult to differentiate. However, the values of precision obtained for APE, CV and PA (8.3%, 11.5% and 96%, respectively) can be considered adequate based on the reference points indicated by Campana (2001; 5.5% APE and 7.6% CV).

2.4.2. Population and individual-based growth rates

Size-at-age was highly variable. For example, white seabass from SBC that were estimated to be 3 years of age had a range of about 50 cm between the largest and smallest individuals, and the same level of variability was observed in fish from SC at 8 years of age. Williams *et al.* (2007) documented that cohorts of juveniles white seabass grow at different rates in relation to water temperature, with faster growth during warm periods or throughout the southern extent of their distribution. Similar to what we found, a considerable level of variation in size-at-age between individuals has been observed in other species of Sciaenidae (e.g. Griffiths and Hecht, 1995; Román-Rodríguez and Hammann, 1997; La Mesa *et al.*, 2008). For example, Barbieri and Chittenden (1994) suggested that high variability in size-at-age observed in atlantic croaker was due the fast growth rate during the first year and the fact that spawning lasts several months. Thus, fish hatch at different periods of the spawning season and display different growth rates. However, unlike white seabass, atlantic croaker reaches their asymptotic length at about 2 years of age. We suggest that the wide range of size-at-ages observed in white seabass otoliths could be attributed to (1) field sampling variability, since length measurements of some fish were performed after processing by fishermen (i.e., removing of the gills and gut); (2) the prolonged spawning period that characterizes this species and (3) local and inter-annual variation in temperature and food availability. The causes underlying the variability warrant further study.

The results of the von Bertalanffy growth models indicated that in all three regions white seabass exhibited a pattern of rapid growth until approximately 8 years of age, after which asymptotic TL of 141 cm was reached and the growth rate decreased. In previous collections from the southern California Bight, white seabass had a slightly lower asymptotic length and a lower growth rate (L_∞ = 139.1 $cm\,TL$, K = 0.156 $year^{-1};$ CDFG, 2002) than those found in this study (L_∞ = 140.84 $cm\,TL$, K = 0.18-0.19 $year^{\ -1})$. The maximum age estimated of 28 years (for an individual with 142.2 cm TL from the NBC) was similar to that reported by CDFG (2002), which was 27 years of age. The growth coefficient values that were estimated for the 3 areas of the Pacific coast of North America were higher than those reported for white seabass in previous studies published to date (Thomas, 1968; CDFG, 2002).

There were no significant differences between the asymptotic lengths and growth rates of white seabass sampled in southern California, northern Baja California and southern Baja California, representing a distance of over 1,000 km along the coastline. The results of the maximum likelihood test indicated that there were only significant differences in the length at age 0 (t_o) between SC and SBC. These differences may be due to the smaller number of fish sampled at the lower end of the size range in SC and NBC. The parameter to represents the hypothetical age at zero length and can affect the steepness of the curve Haddon (2001). The results suggest similar growth rates and asymptotic lengths between white seabass captured in this study at the population level.

Measurement of annulus radii of individual fishes showed a high variability among individuals as a function of age in all regions. This is consistent with the variability in length-at-age observed in the population-level analysis. There were significant differences in the mean widths of the first radius (corresponding to the growth accrued during the first year of life); White seabass from SBC had wider ring widths than those from SC and NBC. The residual analysis also showed consistent albeit slightly larger ring widths in white seabass from SBC until about 10 years of age. Williams *et al.* (2007) found that higher temperatures appeared to have a positive effect on growth rates of white seabass juveniles from the Southern California Bight, and noted that the growth rates during the first 3 years of life were significantly and positively correlated with mean SST. The difference in the width of the first annuli and in the mean width until age 10 found in SBC fishes compared with SC and NBC suggest that those fish grew under different environmental conditions. This could be in response to coastal SSTs that are about 4 - 5°C higher south of Punta Eugenia during the summer than in more northern locations (Durazo *et al.*, 2010).

Franklin (1997) assessed the population structure of white seabass based on microsatellite DNA analysis, comparing specimens collected from Point Conception, CA to Magdalena Bay, off the southern Baja California peninsula and the central Gulf of California. Their samples included young of the year, older juveniles and adults. Their results support the existence of a single panmictic breeding population of White Seabass along their distribution in the Pacific coast, and a genetically distinct population in the Gulf of California. The results of the individual and population growth rates presented here are consistent with the absence of subpopulation structure for this species, which is consistent with the results reported by Franklin (1997) for the Pacific coast.

2.5. Conclusions

Size-at-age measurements indicate similar growth rates and asymptotic lengths between white seabass captured in southern California, northern and southern Baja California peninsula. These findings are suggestive of a single population of white seabass along the Pacific coast of North America. Individual growth trajectories and the width of the annual growth increments suggest that the white seabass from SBC grew under different environmental conditions during their first year of life than fish from the northern regions. However, additional studies that focus on movement patterns, otolith microchemistry and population genetics are necessary to better determine the stock structure of white seabass in the Pacific.

Chapter 3. Recostruction of rearing conditions and habitat use of white seabass, *Atractoscion nobilis*, in the Northeastern Pacific from the isotopic composition (δ^{13}C and δ^{18}O) of otoliths

3.1. Introduction

Assessing the role of dispersion, migration and the level of population connectivity is important for managing coastal fish populations and identifying ecologically important habitats (Gillanders, 2005; Cowen and Sponaugle, 2009). The early life stages of fish species of the family Sciaenidae are found in various habitat types typical of coastal waters and shallow estuaries and lagoons, including eelgrass, kelp forests and river mouths (Cowan and Birdsong, 1985; Gray and McDonall, 1993; Rowe and Epifanio, 1994; Luczkovich *et al.*, 1999). Some sciaenid species have been shown to have distinct spawning and nursery areas within their distribution that can contribute differentially to the recruitment of juveniles to adult populations (Griffiths and Hecht, 1995; Jones and Wells, 1998). Estimating the relative contribution of different habitats types and areas to juvenile production and recruitment to adult populations is fundamental to understanding population structure and dynamics (Beck *et al.*, 2001; Fodrie and Levin, 2008).

In marine fish species with pelagic larvae, such as sciaenids, the larval phase is the dominant dispersive stage. Larval drift distance is driven by the interplay between a host of biological and physical processes, and depends in part on the amount of time that larvae remain in the water column prior to settlement or metamorphosis into juveniles (Largier, 2003; Cowen and Sponaugle, 2009). Sciaenids can spend months to years in juvenile habitats (Griffiths and Hecht, 1995), and adults have the potential to migrate tens to hundreds of kilometers, including seasonal migrations to coastal spawning grounds (Aalbers and Sepulveda, 2015). After the spawning period, sciaenids tend to migrate offshore

(Overstreet, 1983; Jones and Wells, 1998; Aalbers and Sepulveda, 2015). Hence, the population structure of sciaenids may reflect the processes influencing larval dispersion, the contribution of nursery areas to the recruitment of adults, as well as migration patterns during the adult stage.

3.1.1. White seabass biology and distribution

White seabass, *Atractoscion nobilis*, is one of the largest members of the family Sciaenidae, reaching 160 cm total length (TL) and more than 41 kg (Vojkovich and Crooke, 2001). It is an important species for both the recreational and local commercial fisheries along their distribution in the northeast Pacific coast of the USA and Mexico (Allen and Franklin, 1992; Allen *et al.*, 2007; Cartamil *et al.*, 2011). Few studies have provided information regarding their spawning behavior and distribution, as well as their larval and juvenile ecology. The white seabass spawning period is during the spring and summer months, and spawning aggregations may be found in the interface between the sandy areas and shallow rocky reefs that support kelp forest (Thomas, 1968; Donohoe, 1997; Aalbers and Sepulveda, 2012). Moser *et al.* (1983) analyzed 104 plankton samples collected from Point Conception, CA, USA, to Magdalena Bay, Baja California Sur, Mexico, by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) monthly cruises held between 1950 and 1978. Only 15% of white seabass larvae were sampled in southern California waters, and the remaining 85% were captured off the Baja California peninsula. Of those caught in Mexican waters, 50% were collected in San Sebastian Vizcaino Bay and 35% in the Gulf of Ulloa (also known as San Juanico Bay; Figure 8). Most larvae were caught in the inshore zone ($<$50 km from the surf zone) from May to August, with a peak in relative abundance during July.

Allen and Franklin (1992) studied the pattern of abundance, distribution and settlement of young-of-the-year (Y-O-Y) white seabass along the coast of southern California during the summer 1988 and 1989. They proposed that larvae transported from northern Baja California to southern California were a major source Y-O-Y for this region, and that adults caught in southern California were only a minor source of larvae for local recruitment. Donohoe (1997) characterized the distribution of recently settled white seabass based on monthly tow surveys conducted in two bays and the open coast of San Diego County in southern California. He found that the shallow waters along the open coast and those just beyond the breaking waves appeared to be the primary nursery area for early juveniles, and suggested that recruits were derived from local larvae. Donohoe (1997) rejected Allen and Franklin (1992) hypothesis that younger larvae (4-5 mm SL) caught in the Southern California Bight (SCB) were transported from Mexican waters northward to southern California. He argued that the velocity of poleward-flowing undercurrent and equatorward-flowing surface current were less than 20 cm/s during spring and early summer. At this speed, larvae would only be transported 200-300 km during the 12-21 day period that larvae spend in the pelagic habitat; hence it was unlikely that newly-settled larvae caught in the SCB were spawned along the Mexican coast. Both studies were conducted during periods of peak low abundance of white seabass in southern California, and the adult population size has increased since 1999 (Allen *et al.*, 2007). The potential for local recruitment has therefore increased over the past 15 years off southern California, and the level of population connectivity between potential subpopulations along the Pacific remains in need of evaluation.

3.1.2. Genetic studies

Limited efforts to characterize the population structure of white seabass have suggested a high level of genetic diversity among potentially continous spawning population in the eastern Pacific. Bartley and Kent (1990) used starch-gel electrophoresis to assess the level and distribution of genetic variability in nine areas within the SCB (n = 470). They found low levels of variability and suggested the absence of population structure within the region. Franklin (1997) performed microsatellite DNA analysis and compared fish collected from Point Conception, CA to Magdalena Bay, off the southern Baja California peninsula, as well as the central Gulf of California. The samples included YOY, older juveniles and adults. Their results support the existence of a single panmictic breeding population of white seabass along their distribution in the Pacific coast, and a genetically distinct population in the Gulf of California. Coykendall (2005) analyzed mitochondrial DNA sequences (n = 594 from 6 localities, including the Mexican Pacific coast), but did not find evidence for clear population structure. Given that the studies of Bartley and Kent (1990) and Coykendall (2005) covered a limited geographical range and differ from the findings of Franklin (1997), the population structure of white seabass remains uncertain throughout their distribution.

3.1.3. Tagging studies

Tagging studies of hatchery-reared juvenile white seabass suggest limited seasonal migrations along the California coastline. Hervas *et al.* (2010) evaluated the dispersal level of cultured juveniles (162-224 mm standard length, SL) tagged with a coded wire and released in the SCB between 1999 and 2004. They found that 50% of recaptures occurred within 47 km and 95% within 135 km from the release site.

Studies on wild, adult white seabass have documented seasonal movements based on recapture information for fish tagged in southern California (Aalbers and Sepulveda, 2015). Mean point to point displacement was shown to be 229 km and the maximum observed movements were reported to be over 600 km from the initial tagging location(Aalbers and Sepulveda, 2015). The majority of adults tagged in the SCB moved in a north and westerly direction from July through September as SST increased throughout southern California. However, some individuals also travelled across the USA-Mexico border in a south and easterly direction. Extensive movements observed in adult white seabass provide evidence of mixing in the northern range, specifically from northern Baja California to the USA, however additional tagging studies off Baja California are necessary to further text hypotheses on population structure.

3.1.4. Otolith-based studies

Regional differences in otolith-based growth rate of age 1 fish have been found between southern California and southern Baja California that may be due to variations in environmental conditions (Romo-Curiel *et al.*, 2015). Findings are suggestive to the presence of discrete populations, at least during the first year of life. Despite the recent work on movements and growth of this species, a clear understanding of population structure and spawning dynamics remain lacking for this valuable bi-national resource.

The isotopic composition of otolith carbonate (δ^{18}O and δ^{13}C) has been used as a natural tracer to evaluate habitat use, population structure, migration, connectivity and mixing of fish populations, and for reconstructing their temperature and salinity history (Petterson *et al.*, 1993; Edmonds *et al.*, 1999; Thresher, 1999; Thorrold *et al.*, 2001; Campana, 2005; Valle and Herzka, 2008). Due to their metabolic inertness, continuous growth, and periodic ring deposition, otoliths are calcified structures that serve as environmental recorders through the entire life of a fish (Campana and Neilson, 1985; Campana, 1999). The δ^{18}O and δ^{13}C values are permanently imprinted in the otolith carbonate, recording ambient conditions experienced by an individual fish at the time of carbonate precipitation (Campana, 1999). The stable isotopes of oxygen (^{18}O/^{16}O) in otolith carbonate (typically aragonite) are deposited near isotopic equilibrium with the isotopic composition of the ambient water (δ^{18}Ow). During the precipitation of calcium carbonate, there is isotope discrimination against ^{18}O as a function of temperature, resulting in a negative relationship between δ^{18}O values and temperature (Epstein *et al.*, 1953; Iacumin *et al.*, 1992; Petterson *et al.*, 1993; Radtke *et al.*, 1996; Thorrold *et al.*, 1997; Weidman and Millner, 2000; Hoie *et al.*, 2004). After accounting for local variation in δ^{18}Ow, oxygen isotope ratios enriched in ^{18}O can be related to the high temperatures typically of summer periods, while isotopic values depleted in ^{18}O are associated with colder temperatures (Petterson *et al.*, 1993; Weidman and Millner, 2000; Campana, 2005). It is possible to estimate the temperature of the water at the time of carbonate deposition using δ^{18}O values, and to thereby discriminate between fish living under different environmental conditions (Kalish, 1991; Iacumin *et al.*, 1992; Thorrold *et al.*, 1997; Radtke *et al.*, 1996).

In contrast, carbon isotopes (^{13}C/^{12}C) are not deposited in strict equilibrium with the dissolved inorganic carbon (DIC) in the water. The isotopic composition of the carbon in the otoliths reflects both dietary sources via metabolic processes as well as the DIC pool (Kalish, 1991; Radtke *et al.*, 1996; Thorrold *et al.*, 1997; Schwarcz *et al.*, 1998; Hoie *et al.*, 2003; Gao *et al.*, 2013). The contribution of carbon deposited in the otoliths from metabolic sources has been estimated at 20-30% of the total (Kalish, 1991; Weidman and Millner, 2000), and the remainder would presumably reflect the isotopic composition of the DIC pool (Campana, 1999). However, the relative contribution of these two sources of carbon to the isotopic composition of the otolith carbonate varies among species, and even among individuals of the same species (Iacumin *et al.*, 1992). Nevertheless, geographic variations in carbon and oxygen isotope ratios of the otolith carbonate have been successfully used as natural tags to differentiate between fish stocks or subpopulations (Newman *et al.*, 2010; Steer *et al.*, 2010; Correia *et al.*, 2011).

Otolith isotope analysis can encompass different periods within the life of a fish.

Whole otoliths integrate the entire life history of a fish, and may reflect the range of environmental conditions that an individual was exposed to over the course of its life (Campana, 1999; Newman *et al.*, 2000; Valle and Herzka, 2008). By analyzing select portions of an otolith, the isotopic composition of the carbonate can be associated with conditions prevalent during particular growth stages. Data from the otolith nuclei (the central portion of otoliths that is deposited during early life) can provide information regarding natal origin and spawning areas, while data corresponding to specific ages may indicate changes in fish habitat over time (Begg *et al.*, 1999; Gao *et al.*, 2004; Steer *et al.*, 2010; Gao *et al.*, 2013). For example, Gao *et al.* (2004) measured the isotopic composition of the otolith nuclei and the first 4-5 annual growth rings of juvenile and adult sablefish (*Anoplopoma fimbria*). They were able to identify three different spawning stocks in the waters between British Columbia, Canada, to southern Oregon, USA. Steer *et al.* (2010) sampled southern garfish (*Hyporhamphus melanochir*) in South Australia, and analyzed the nuclei and first two otolith annuli. Their results indicated differences between sites as well as differences between some of the sampling regions and suggested the presence of population structure at least during the first two years of life. However, in the canary rockfish (*Sebastes pinniger*) the analysis of isotopic values from the otolith nuclei and the 5th annual ring suggested the presence of a single spawning stock or population along the Washington and Oregon coasts, USA (Gao *et al.*, 2013). Overall, the isotopic analysis of subsamples from specific sections of adult otoliths corresponding to specific time periods enables the reconstruction of each individual's environmental history as a function of age, date and other life history considerations (Gillanders, 2005; Weidman and Millner, 2000).

In this study, we analyzed the isotopic composition of the otolith nuclei and seasonal growth rings of white seabass collected from three regions of the northeastern Pacific to evaluate whether δ^{18}O and δ^{13}C values can be used for identifying larval rearing grounds, habitat use and population structure.

3.1.5. Hypothesis

Differences in the oxygen and carbon isotopes values in otolith nuclei and growth rings of adult white seabass from different locations would indicate that adult fish were reared under different environmental conditions, and would suggest limited connectivity between subpopulations.

3.1.6. Objectives

- Evaluate whether δ^{18}O and δ^{13}C values from the otolith core can be used to identify larval rearing habitats.
- Analyze the δ^{18}O and δ^{13}C values of annual otolith growth rings corresponding to the juvenile (age 0.5-2 yr) and adult (age 8-10 yr) stages to infer ontogenetic movement patterns and the level of mixing between different life stages.

3.2. Methods

3.2.1. Sample collection

Otoliths were obtained opportunistically from commercial and recreational catches of white seabass from April through August of 2009 and 2011. A total of 117 samples were collected in three regions: southern California (SC; n = 40), USA, San Sebastian Vizcaino Bay (VB; n = 36) and the Gulf of Ulloa (GU; n = 41) off the central and southern Baja California peninsula, Mexico, respectively (Figure 8).

3.2.2. Isotopic analysis

One sagittal otolith from each fish was embedded in epoxy resin and sectioned transversely using a low speed diamond saw (Buehler, ISOMET^{TM}) to cut through the otolith core. The section containing the nucleus was mounted on a microscope slide using epoxy resin and polished using abrasive paper of decreasing grit size. To select the otoliths for sampling of the annual growth rings, the spawning year for each fish was calculated based on the age estimate and catch date. The ages for the same set of otoliths were estimated in a previous study by counting annual increment growth rings (Romo-Curiel *et al.*, 2015). White seabass born between 1999 and 2006 (age range 4-12 yrs; n = 32 for SC, n = 36 for VB and n = 32 for GU) were selected for isotopic analysis of the otolith nuclei. This period excludes El Niño years, which has been shown to influence the isotopic composition of fish otoliths in the California Current region due to the abnormally high water temperatures (Dorval *et al.*, 2011).

Carbonate was extracted from three different regions along the otolith surface with a high precision microdrill (ESI New Wave Micromill) at the Marine Science Institute, U-

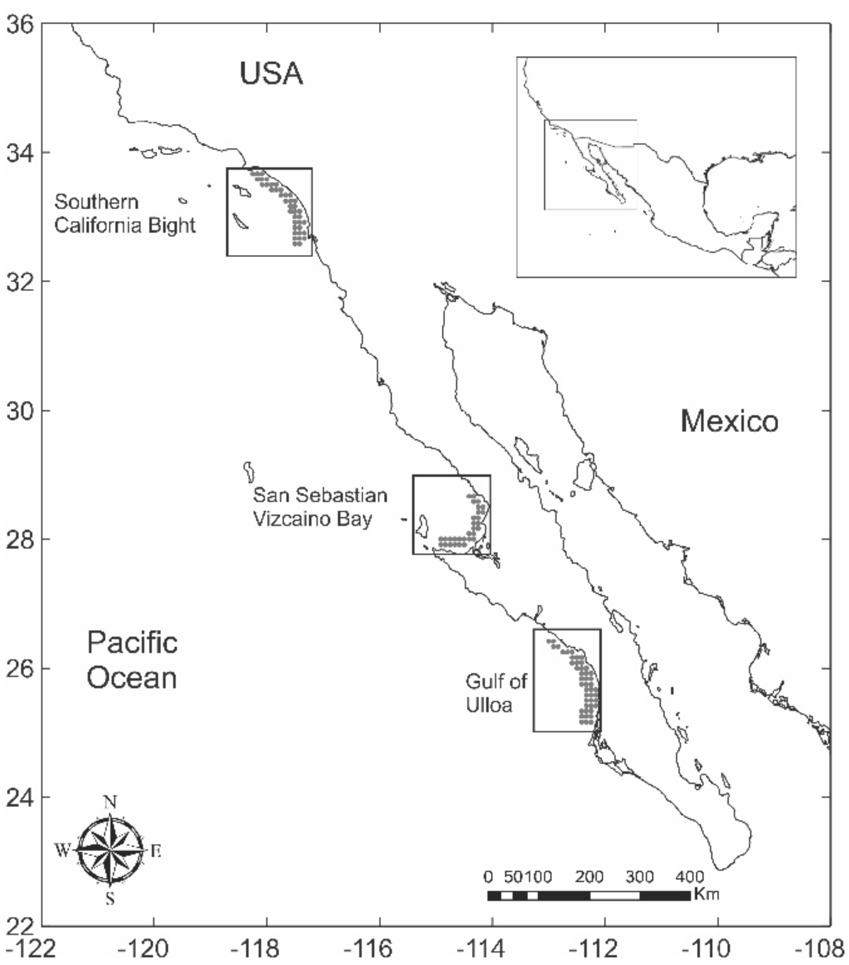

Figure 8. Sampling areas of white seabass, *Atractoscion nobilis*, off southern California (SC), San Sebastian Vizcaino Bay (VB) and the Gulf of Ulloa (GU) in the Baja California peninsula. Dots indicate the pixels considered to calculate the average monthly sea surface temperature (SST) using high-resolution estimates generated by the Scripps Photobiology Group at Scripps Institution of Oceanography.

Figura 8. Áreas de muestreo de corvina blanca, *Atractoscion nobilis*, en el sur de California (SC), Bahía San Sebastián Vizcaíno (VB) y el golfo de Ulloa (GU) en la península de Baja California. Los puntos indícan los pixeles considerados en el cálculo del promedio mensual de la temperatura superficial del mar (SST) utilizando estimaciones de alta resolución generadas por Scripps Photobiology Group en Scripps Institution of Oceanography.

niversity of Texas in Austin and at CICESE. Each otolith core sample was obtained from a 300x300 μm square centered on the nucleus using a raster pattern with parallel lines separated by 100 m and with a depth setting of 100 μm. The raster area was designed to coincide with the dimensions of the otolith core (Figure 9). Fishes of at least 10 years of age (mean age of 13 yrs.) were selected for isotopic analysis of annual growth rings. Only white seabass from SC and GU were selected for this analysis because these populations are located furthest from each other and hence are subject to the most contrasting environmental conditions. Five growth rings corresponding to the juvenile stage were sampled: the first and second summer growth seasons (opaque rings corresponding to the first and second year of life, hereafter referred to as 0.5 and 1.5 yrs) and the first and second winters (hyaline rings, hereafter age 1 and 2 yrs). Likewise, five growth rings corresponding to the adult stage were sampled (8.5, 9.5, and 10.5 yrs, corresponding the summer opaque growth rings and 9 and 10 yr, corresponding to the winter hyaline rings). Each growth ring was sampled using a single curve 100 μm in length and a depth of 80 μm (Figure 9). After the collection of each sample, the microdrill bit and work surface were cleaned with compressed air.

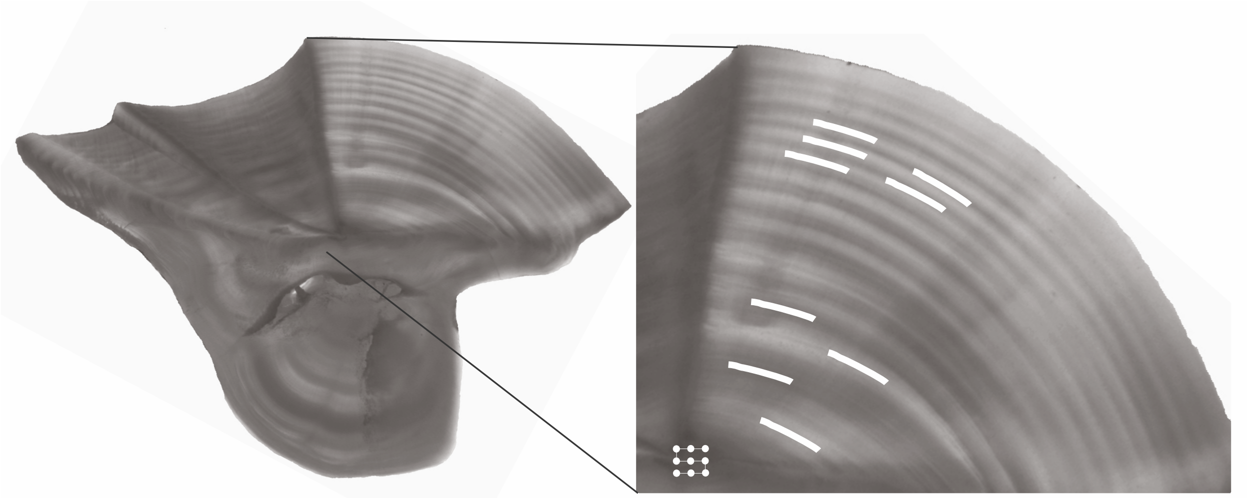

Figure 9. Image of a transverse section of an adult white seabass (*Atractoscion nobilis*) otolith. The core is at the center with the raster sampling pattern of the automated micro-milling (dotted lines). White lines represent the single curve for each sampled growth ring of the juvenile and adult stages.

Figura 9. Imagen de un corte transversal de otolito de corvina blanca adulta (*Atractoscion nobilis*). El núcleo se localiza en el centro con el patrón de muestreo del microtaládro (lineas punteadas). Las líneas blancas representan las curvas individuales de cada anillo de crecimiento muestreado para la etapa juvenil y adulta.

Between 30 and 60 μg of carbonate were weighed on a microbalance. Analysis of otolith powder was performed in the Stable Isotope Laboratory of the University of California at Santa Cruz using a Kiel IV carbonate device coupled to a Thermo Scientific MAT253 Isotope Ratio Mass Spectrometer. The laboratory routinely analyzes certified standards during sample runs (CM12, Atlantis II, NBS-18 and NBS-19). Precision measurements (SD) of δ^{18}O values were 0.03‰ for CM12, and 0.02‰ for Atlantis II, NBS-18 and NBS-

19. For δ^{13}C, the precision was 0.06‰ for CM12 and Atlantis II, 0.02‰ for NBS-18 and 0.05‰ for NBS-19. All isotopic analysis and measurements are reported in standard δ notation (‰) using VPDB (Vienna Peedee Belemnite) as the international standard:

$$\delta = ((R_{sample} - R_{standard}) - R_{standard}) * 1000 \tag{2}$$

The time period integrated by each core sample was estimated based on the analysis of the otoliths of juveniles 4 to 12 cm TL that were collected during a trawl survey along the coast off Camp Pendleton, California on July 19-21, 2010. Each sagittal otolith was mounted sulcus-side up on a glass slide using Krazy Glue. The daily increments were not easily visible, and it was necessary to polish the otoliths using abrasive paper of decreasing grit and 0.05-micron alumina. Polished otoliths were viewed with a microscope (Leica DMLS) at magnifications between 10X and 40X and photographed with a digital camera (Leica DFC 450). Daily growth increments were counted twice for each individual, starting from the focus to the edge of the core where what appears to be a settlement mark can be observed. After the settlement mark, the depositional pattern of the daily growth ring changes due the presence of secondary primordia. Measurements of the core diameter were conducted in the same direction in which the rings were counted using the Image J software package (National Institutes of Health, Bethesda, MD, USA). Assuming daily growth deposition (Donohoe, 1997), the length of the period integrated by the carbonate sampled from the otolith core ranged between 18 and 25 days. The average diameter of the otolith core was 350 μm (n=14).

3.2.3. Regional SST and salinity

White seabass larvae inhabit the upper 10 m of the water column Donohoe (1997) and are found in higher abundance $<$50 km from the coast (Moser *et al.*, 1983). To obtain temperature estimates representative of white seabass larval habitat, sea surface temperatures (SST) during the spawning season (April-September) were obtained by downloading oceanographic data through the Scripps Photobiology Group of Scripps Institute of Oceanography, University of California San Diego (*http://spg.ucsd.edu/Satellite_data/California_Current/* viewed on October 2014). The SSTs represent an integration of data generated with the AquaMODIS, Terra and SeaWiFS satellites processed by Mati Kahru. The SST estimates are available with high resolution (approx. 1 km^2). Monthly average temperatures were compiled for the period of April 2000-September 2006. The SST data that were available as near as possible to the coast were selected (around 5 km offshore; Figure 8). Salinities at 10 m were obtained from reports and publications derived from in situ measurements conducted during CalCOFI cruises and the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) cruises off the coast of the Baja California peninsula (Hayward *et al.*, 1999; Bograd *et al.*, 2000; Durazo *et al.*, 2001; Scwing *et al.*, 2002; Venrick *et al.*, 2003; Georicke *et al.*, 2004; CalCOFI, 2005; Petterson *et al.*, 2006). Both sets of surveys are conducted quarterly. Salinities were obtained for two periods: summer (April to September) and winter (October to March), and considering the same regions used for estimating mean monthly SSTs. To evaluate the degree of similarity between monthly average SSTs and salinity very near the coast, the sea surface temperature and salinity records were compared with in situ measurements at the Scripps Institution of Oceanography Pier in southern California (*http://www.sccoos.org/data/piers*). For the waters off the Baja California peninsula regions, the comparisons were made with the seasonal climatology provided by Durazo *et al.* (2010).

3.2.4. Isotopic composition of seawater (δw) and back-calculated temperature

The isotopic composition of seawater (δw) was calculated from regional salinity estimates using the Craig and Gordon (1965) equation for north Pacific surface waters:

$$\delta w = -18.5 + 0.54\ Salinity \tag{3}$$

The slope of Craig and Gordon's (1965) equation is similar to the one reported by Paul *et al.* (1999) for mid-latitudes and that was derived from GEOSECS data (δw = -17.95 + 0.50 Salinity; see Valle and Herzka, 2008). Since δw values are expressed relative to Standard Mean Ocean Water (SMOW), the isotopic composition of the water was corrected (-0.22‰) to account for the difference in the standards used to report oxygen isotope ratios of water and biogenic carbonates (Epstein *et al.*, 1953; Sharp, 2007).

Back-calculated temperatures were estimated from oxygen isotope ratios (δ^{18}O$_{oto}$) at the otolith core and along juvenile growth rings by applying the aragonite equation proposed by Campana (1999):

$$\delta^{18}O_{oto} = +3.71 - 0.206\ T^{o}C \tag{4}$$

where $\delta^{18}O_{oto}$ is the isotopic composition measured from otolith subsamples. Subsamples of juvenile growth rings from both sites (SC, GU) were used in the back-calculated temperature analysis to compare $\delta^{18}O_{oto}$ values and temperatures between seasonal growth ring depositions.

Predicted $\delta^{18}O_{oto}$ values for aragonite used in the isotopic map were estimated based on the observed full range of salinity (range 33 - 36 psu) and SSTs (from 10 to 30°C) during the white seabass summer spawning season. values (isotopic composition of seawater) were calculated for each 0.5 salinity values using the Craig and Gordon (1965) equation, before applying the (Campana, 1999) equation to determine the predicted $\delta^{18}O_{oto}$ at each 1°C SSTs value.

3.2.5. Statistical analysis

Using the Quartile Method based on median distribution values (Zar, 1999), outliers of all isotopic values were identified and excluded from statistical analyses. One-way analysis of variance (ANOVA) was used to test whether the $\delta^{13}C$ y $\delta^{18}O$ values of otolith cores differed between sampling regions. The non-parametric Kolmogorov-Smirnov test (K-S) was used to compare the distribution of isotopic values among regions. Back-calculated temperatures were compared between regions using a one-way ANOVA. The post-hoc multiple comparisons between isotopic values among regions were performed using Scheffe's test. Age-specific $\delta^{13}C$ and $\delta^{18}O$ values from juvenile and adult growth rings were compared between regions and with a two-way repeated measures analysis of variance (RM ANOVA); the data corresponding to juvenile and adult growth rings were treated separately. Holm-Sidak post-hoc tests for pairwise comparison were used to identify whether there were differences in isotopic values between ages and regions. All data were complied with parametric assumptions of normality (Shapiro-Wilks test) and homoscedacity (Levene's test). Data were analyzed using the Systat 13 and Sigma Plot 12.5 software packages.

3.3. Results

3.3.1. Isotopic analysis of otolith nuclei

Stable isotope values were obtained for 100 white seabass otolith cores (Figure 10). Based on analysis of upper and lower quartiles, two outliers were identified in two different GU samples with values of -5.37‰ for δ^{13}C and -1.88‰ for $\delta^{18}O$; both fish were excluded from further analysis. The average δ^{13}C value was -2.66 ± 0.60 for SC (mean ± SD; range -3.73 to -1.54‰), -3.75 ± 0.78‰ for VB (-4.74 to -1.92‰) and -2.81 ± 0.64 for the GU (range -4.17 to -1.28‰). The $\delta^{18}O$ values were also variable, ranging from -1.52 to -0.02‰ for SC (mean ± SD = -0.61 ± 0.31‰), -1.57 to 0.01‰ for VB (-0.75 ± 0.35‰) and -1.49‰ to -0.09 (-0.71 ± 0.34) for the GU.

There was a significant difference in δ^{13}C values between regions (ANOVA F$_{(2,95)} = 27.47, P < 0.001)$; the mean carbon isotope composition of VB differed from SC and GU (Scheffeś test, MS=0.506, P <0.001). The frequency distribution of δ^{13}C values between localities differed significantly between VB and the northern and southern regions (K-S, P <0.001). In contrast, average $\delta^{18}O$ values were not significantly different between regions (ANOVA F$_{(2,95)} = 1.41, P = 0.249)$, nor were there differences in the frequency distribution of isotopic values (K-S, P >0.05). The range of δ^{13}C and δ^{18}O values as a function of spawning year showed a high level of dispersal, even when the number of individuals analyzed for a particular year was limited (Figure 11).

3.3.2. Regional SST and salinity

Comparison of mean monthly SSTs between regions indicated a marked latitudinal gradient (Figure 12), and there was a similar pattern in SSTs during the spawning pe-

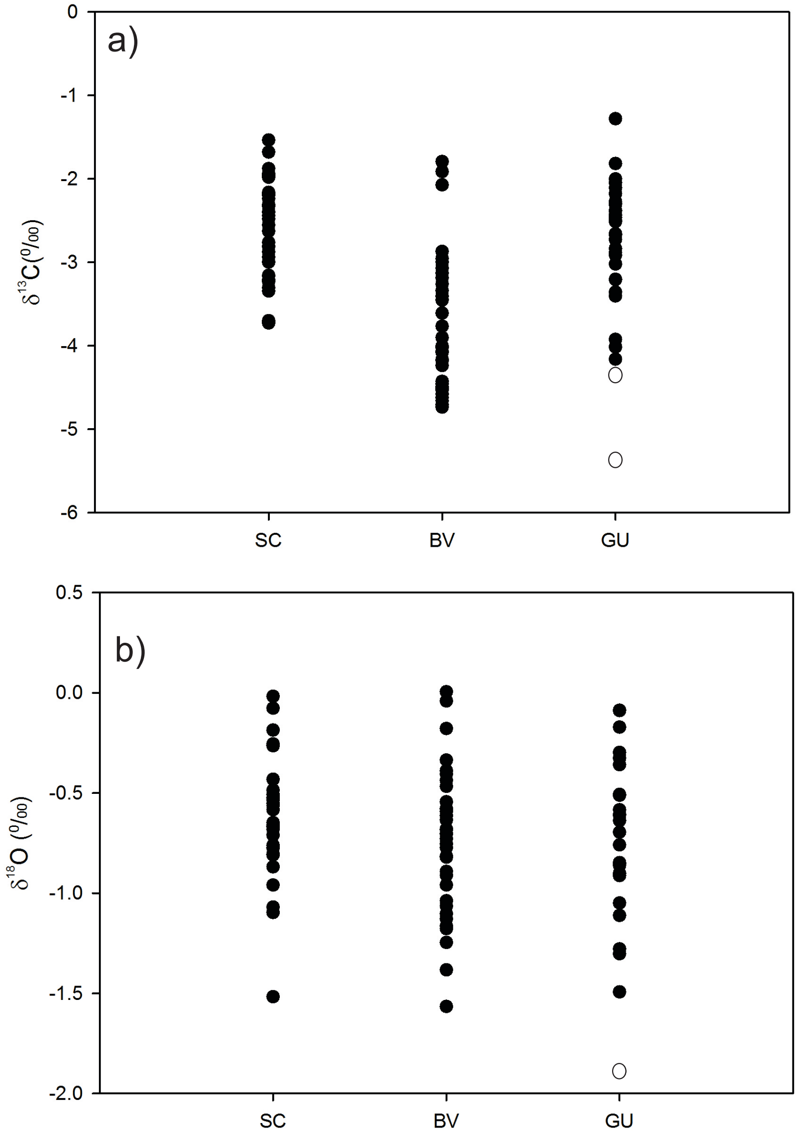

Figure 10. Carbon and oxygen isotope ratios measured in the otolith cores (n=100) of white seabass (*Atractoscion nobilis*) sampled off Southern California (SC), Vizcaino Bay (VB) and the Gulf of Ulloa (GU). White dot indicate outliers that were excluded from statistical analyses.

Figura 10. Razón isotópica del carbono y oxígeno medidos en el núcleo de otolitos (n=100) de covina blanca (*Atractoscion nobilis*) recolectada en el Sur de California (SC), Bahía Vizcaíno (VB) y Golfo de Ulloa (GU). Los puntos blancos indican puntos extremos que fueron excluídos del análisis estadístico.

riod (April-September) from 1999 to 2006. Monthly average temperatures from April to September were similar between SC and VB (ranging from 15.8 to 21.0°C and 16.3 to 21.8°C, respectively). Higher temperatures were observed for GU (17.3-26.6°C). During the summer, SSTs were about 5.5°C higher in GU than the SC and 5.0°C than VB. In SC and VB the highest monthly SST was observed during August (21.0°C and 21.8°C, respectively). In the southern region the highest SST occurred during September (26.6°C).

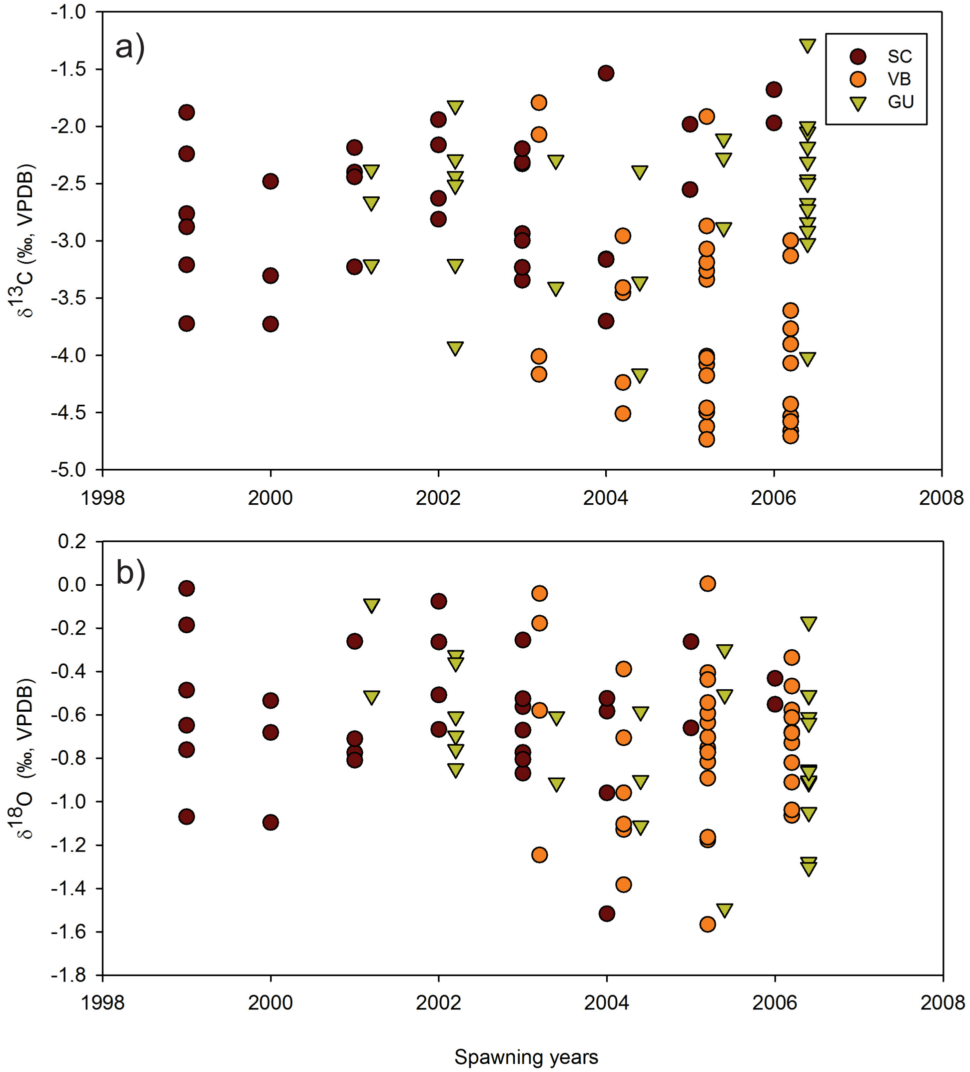

Figure 11. Isotopic signature values of δ^{13}C (a) and δ^{18}O (b) of core otoliths of white seabass for each spawning year and by sampled region: Southern California (SC), Vizcaino Bay (VB) and Gulf of Ulloa (GU).

Figura 11. Valores de la señal isotópica del δ^{13}C (a) y δ^{18}O (b) del núcleo de los otolitos de corvina blanca de cada año de desove y región muestreada: Sur de California (SC), Bahía Vizcaíno (VB) y Golfo de Ulloa (GU).

Regional salinity at 10 m depth during the spawning season (April-September) and winter (October-March) months during 1999-2006 period also showed a latitudinal gradient (Table 3). Given the linear relationship between salinity and δw, estimates of the isotopic composition of seawater in GU exhibited lighter values than that from SC and VB (Figure 13). Average values, considering all years, in SC and VB varied $<0.02‰$ between seasons, in the GU this difference was 0.12‰.

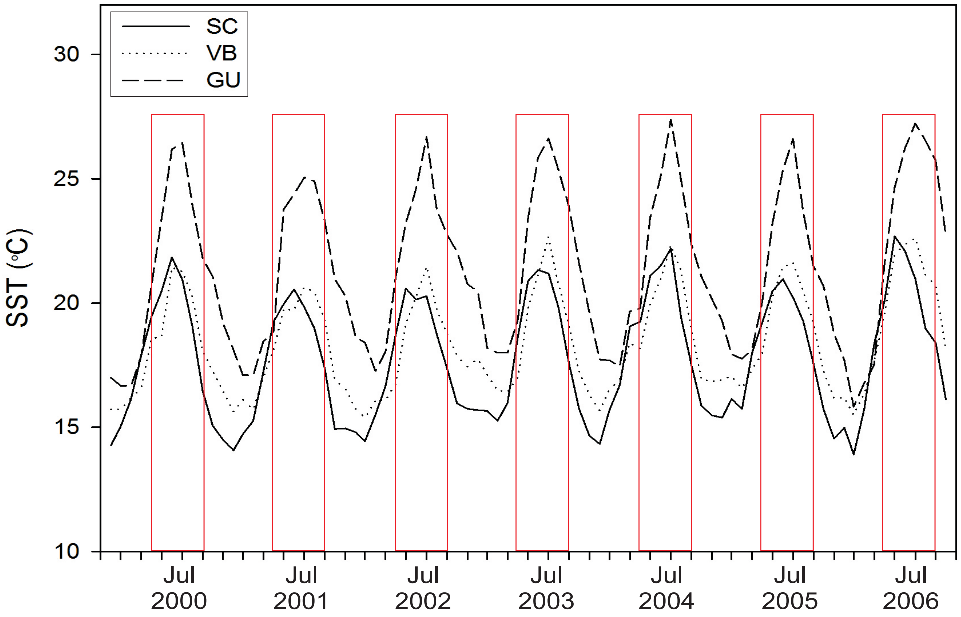

Figure 12. Average monthly of Sea Surface Temperature (SST) at 5 to 35 km approximately from the coast of Southern California (SC), Vizcaino Bay (VB) and the Gulf of Ulloa (GU) along the Pacific coast of North America. Red rectangles represent the spawning season of white seabass (April to September) of each year.

Figura 12. Promedio mensual de la temperatura superfical del mar (SST) entre los 5 a 35 km, aproximadamente, de la costa del Sur de California (SC), Bahía Viscaíno (VB) y Golfo de Ulloa (GU) a lo largo de la costa Pacífico de Norteamérica. Los rectángulos rojos representan la temporada de desove de la corvina blanca (abril-septiembre) de cada año.

3.3.3. Back-calculated temperature of otolith nuclei

The back-calculated temperatures derived from $\delta^{18}O_{oto}$ values of the otolith cores of white seabass ranged from 14^{o}C to 23^{o}C (Figure 14). The back-calculated temperatures for fish captured in each region were highly variable, reflecting the variability in $\delta^{18}O_{oto}$ values. For SC, the average back-calculated temperature was 17.8^{o}C (range 15.3 -21.9^{o}C), 18.6^{o}C for VB (range 14.9 - 22.5^{o}C) and 18.9^{o}C for GU (range 16.0 - 22.2^{o}C). Despite the overlapping back-calculated temperatures between regions, there were significant differences among regions (F$_{(2,95)} = 3.797, P = 0.026)$; the mean back-calculated temperature in GU was significantly higher than SC and VB (Scheffe's test, MS = 2.572, P = 0.032).

Table 3. Regional salinities values (minimum, maximum and mean), estimated oxygen isotopic composition of the water (δw), and summer SSTs obtained from satellite images for Southern California (SC), Vizcaino Bay (VB) and Gulf of Ulloa (GU).

Tabla 3. Valores de salinidad regional (mínimo, máximo y promedio), valores estimados de la composición isotópica del oxígeno del agua (δw), y SSTs estimadas para el verano a partir de las imagenes de satélite para el Sur de California (SC), Bahía Vizcaíno (VB) y Golfo de Ulloa (GU).

	Salinity (psu)						δw (‰)				T (°C)	
	Summer			Winter			Summer		Winter		Summer	
	min	max	mean	min	max	mean	min	max	min	max	min	max
SC	33.2	33.6	33.4	33.2	33.9	33.6	-0.79	-0.58	-0.79	-0.41	15.76	21.06
VB	33.3	33.7	33.6	33.3	33.6	33.5	-0.74	-0.52	-0.74	-0.58	16.32	21.81
GU	33.6	34.1	33.9	33.7	34.5	34.1	-0.58	-0.31	-0.52	-0.09	17.28	26.58

3.3.4. Comparison of predicted vs. measured $\delta^{18}O$ values

The range of predicted carbonate δ^{18}O values obtained by considering regional summer SSTs and salinities had a broader range for the GU than SC and VB, and showed overlap between regions (Table 3; Figure 15). For SC the predicted δ^{18}O values ranged from -0.10‰ and -1.40‰; the range for VB was similar (from -0.15‰ to -1.50‰). In contrast, the range of predicted $\delta^{18}O$ values was greatest for GU (-0.17‰ to -2.30‰). Comparison of the range of predicted $\delta^{18}O$ values with $\delta^{18}O_{oto}$ measurements indicated that almost all $\delta^{18}O_{oto}$ measures were within the range of the predicted isotopic values for a given region. For SC and VB, the range of predicted $\delta^{18}O$ values (rectangles) is almost the same as the measured $\delta^{18}O_{oto}$. For GU, the range of predicted $\delta^{18}O$ values was greater than the measured $\delta^{18}O_{oto}$ values; none of the otolith cores has isotope ratios $<$-1.6‰.

3.3.5. Isotopic analysis of juvenile and adult growth rings

The δ^{13}C values of individual juvenile and adult white seabass otolith growth rings collected in SC and GU exhibited an increasing level of variability as a function of age; the

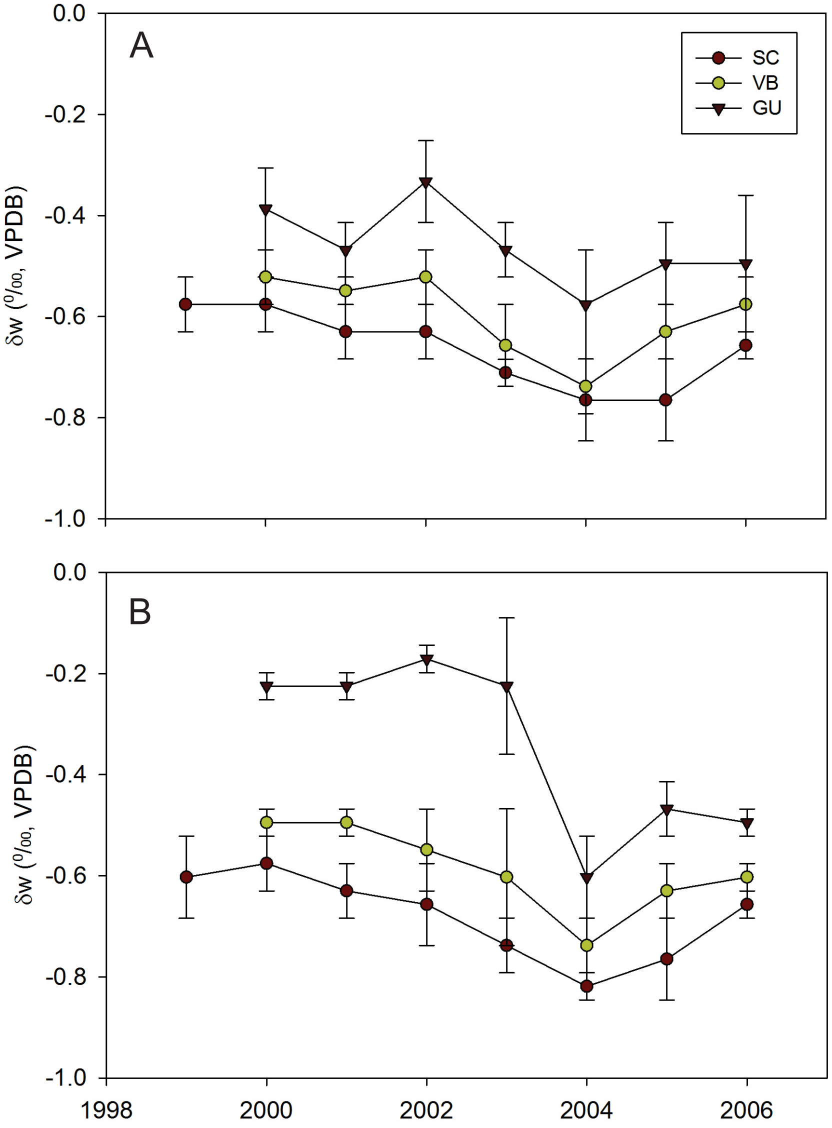

Figure 13. Mean (± min, max) oxygen isotopic composition of seawater (δw) calculated from salinity at a depth of 10 m for summer (April-September; A) and winter (October-March; B) months in waters of Southern California (SC), Vizcaino Bay (VB) and Gulf of Ulloa (GU) between April 1999 to September 2006.

Figura 13. Promedio (± mín, máx) de la composición isotópica del agua (δw) calculada a partir de la salinidad a 10 m de profundidad para los meses de verano (abril-septiembre;A) e invierno (octubre-marzo;B) en aguas del Sur de California (SC), Bahía Vizcaíno (BV) y Golfo de Ulloa (GU) entre abril de 1999 y septiembre del 2006.

range of values increased from 2-3‰ during the juvenile stage to ca 4.5‰ for the adult stage (Figure 16A and C). In contrast, the δ^{18}O values of juvenile growth rings showed a consistent pattern between opaque (summer growth, more depleted isotope ratios) and hyaline (winter growth, more enriched isotope ratios) rings and a much narrower range than δ^{13}C values. However, the seasonal pattern was no longer observed during the adult

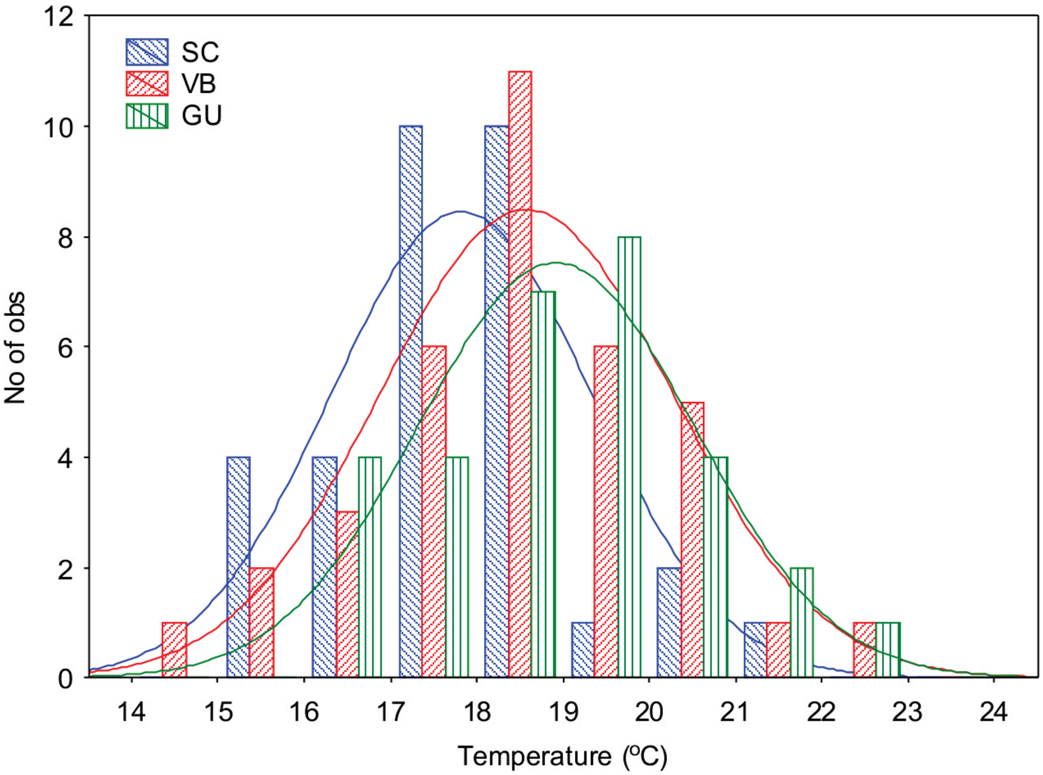

Figure 14. Derived temperatures from δ^{18}O of otolith core of white seabass, *Atractoscion nobilis*, for each sampled region Southern California (SC), Vizcaino Bay (VB) and Gulf of Ulloa (GU).

Figura 14. Temperaturas calculadas a partir del δ^{18}O del núcleo de los otolitos de corvina blanca, *Atractoscion nobilis*, para cada una de las regiones muestreadas Sur de California (SC), Bahía Viszcaíno (VB) y Golfo de Ulloa (GU).

stage (Figure 16B and D).

The mean carbon and oxygen isotope ratios for white seabass otolith growth rings showed distinct patterns when comparing the juvenile and adult life stages (Figure 17). While mean isotope ratios showed distinct seasonal shifts during the juvenile stage, these were not evident during the adult stage. Two-way repeated measures ANOVA indicated that there were no significant differences in mean δ^{13}C and δ^{18}O values between regions during either the juvenile or adult stage (Table 4). However, for the juvenile stage, mean δ^{13}C and δ^{18}O values differed significantly between ages for fishes sampled in both regions (Table 4). The Holm-Sidak post-hoc pairwise comparison test indicated significant differences in δ^{18}O values between summer (S) and winter (W) growth rings of juveniles

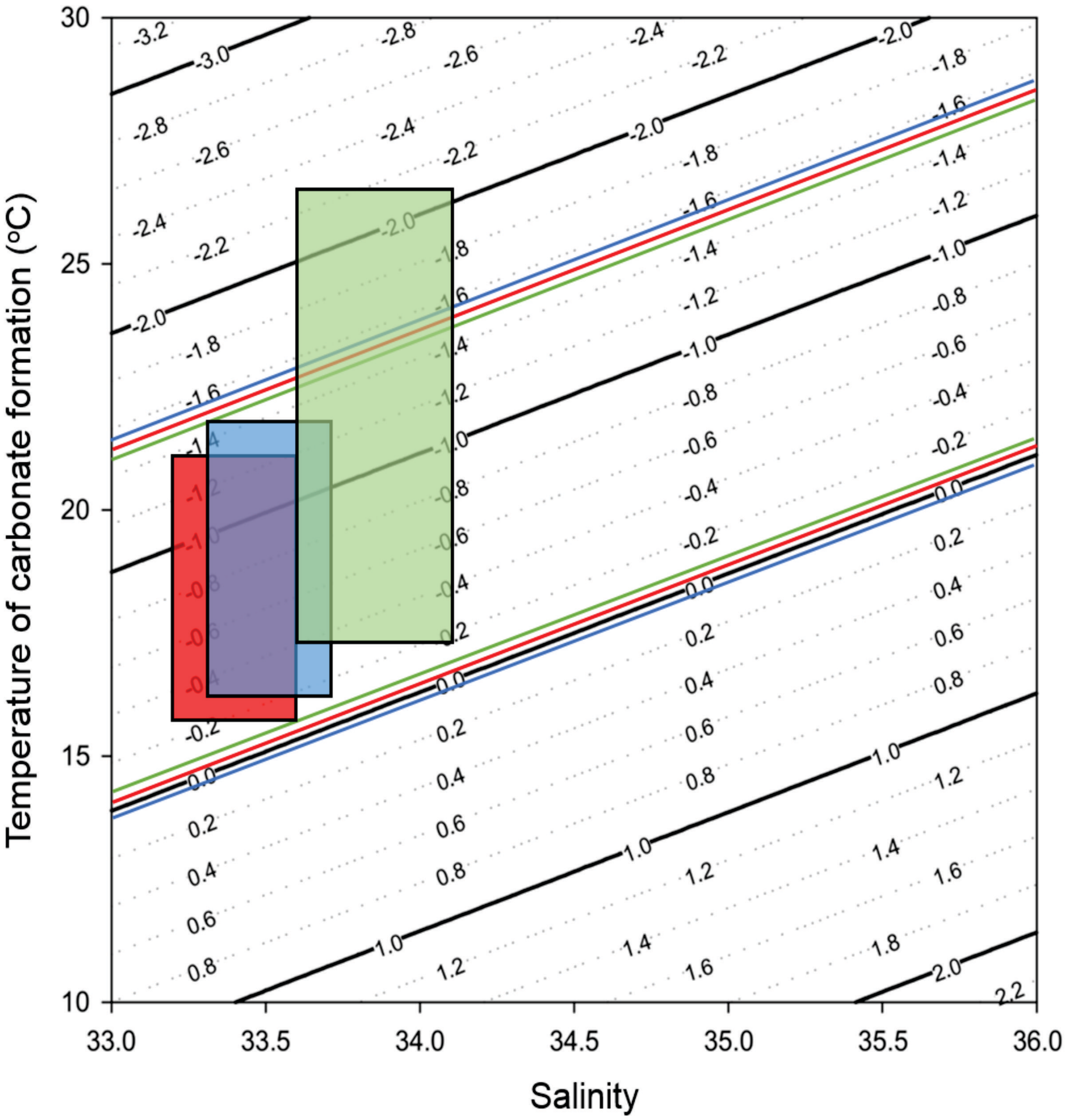

Figure 15. Isotopic map of predicted δ^{18}O values for aragonite as a function of salinity and temperature. Rectangles represent the range of predicted δ^{18}O values for three regions of the California Current System based on regional sea surface temperature and salinities during the white seabass summer spawning season. Diagonal colored lines indicate the full range of isotopic values measured in otolith cores for each region: Southern California (red), Vizcaino Bay (blue) and Gulf of Ulloa (green).

Figura 15. Mapa isotópico de valores predichos de δ^{18}O para aragonita en función de la salinidad y temperatura. Los rectángulos representan el intervalo de valores predichos de δ^{18}O para las tres regiones del Sistema de la Corriente de California, con base en la temperatura superficial del mar y salinidades regionales durante la temporada de desove de la corvina blanca. Las líneas diagonáles de colores indican el intervalo de todos los valores isotópicos medidos en el núcleo de los otolitos para cada una de las regiones: Sur de California (rojo), Bahía Vizcaíno (azúl) y Golfo de Ulloa (verde).

(Figure 17, Table 5). The only significant differences in δ^{18}O values between ages was for $S_{0.5}$, which corresponds to summer growth during the first year of life (the difference between mean isotope ratios was 0.65‰), with significant differences at that age among regions (RM ANOVA, t = 2.663, P = 0.010).

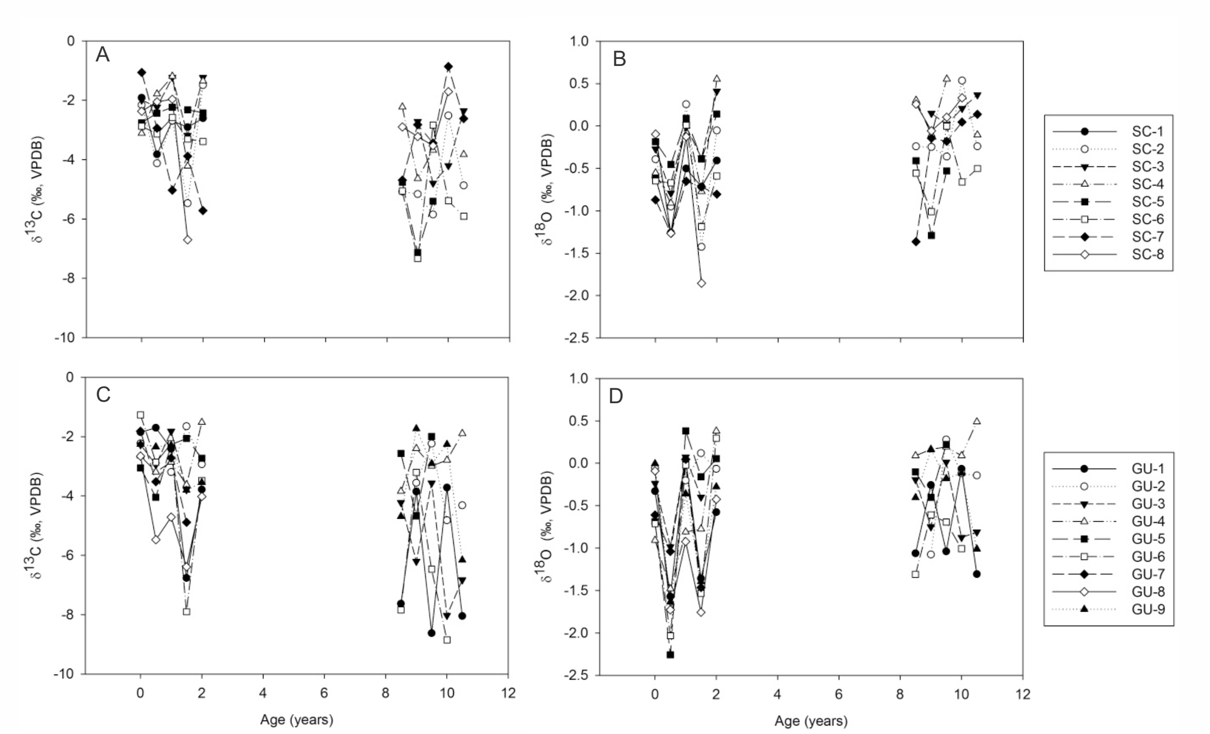

Figure 16. Age-specific δ^{13}C and δ^{18}O values measured in the otolith cores (0) and individual opaque and hyaline otolith growth rings of white seabass, *Atractoscion nobilis*, captured off Southern California (A, B) and Gulf of Ulloa (C, D).

Figura 16. Valores de δ^{13}C y δ^{18}O de cada edad medidos en el núcleo de los otolitos (edad 0) y los anillos opacos y hialinos individuales de otolitos de corvina blanca, *Atractoscion nobilis*, capturadas en el Sur de California (A, B) y del Golfo de Ulloa (C, D).

3.3.6. Back-calculated temperature for nuclei and seasonal growth rings of juvenile stage

The back-calculated temperatures for the seasonal growth rings sampled during the juvenile stage showed a broad range and overlapped between ages and seasons (Figure 18). The limited variability in salinity (and hence δw estimates) led to temperature differences of $<$ 2^{o}C for individual growth rings. Higher temperatures coincided with the summer precipitation of the carbonate and lower temperatures corresponded to the winter rings. Back-calculated temperatures were higher in fish captured in the GU than those from SC, with a difference around 1^{o}C for the same age among regions. However, the temperature of the first summer opaque ring ($S_{0.5}$) was higher in the GU than SC by about 4.5^{o}C on average.

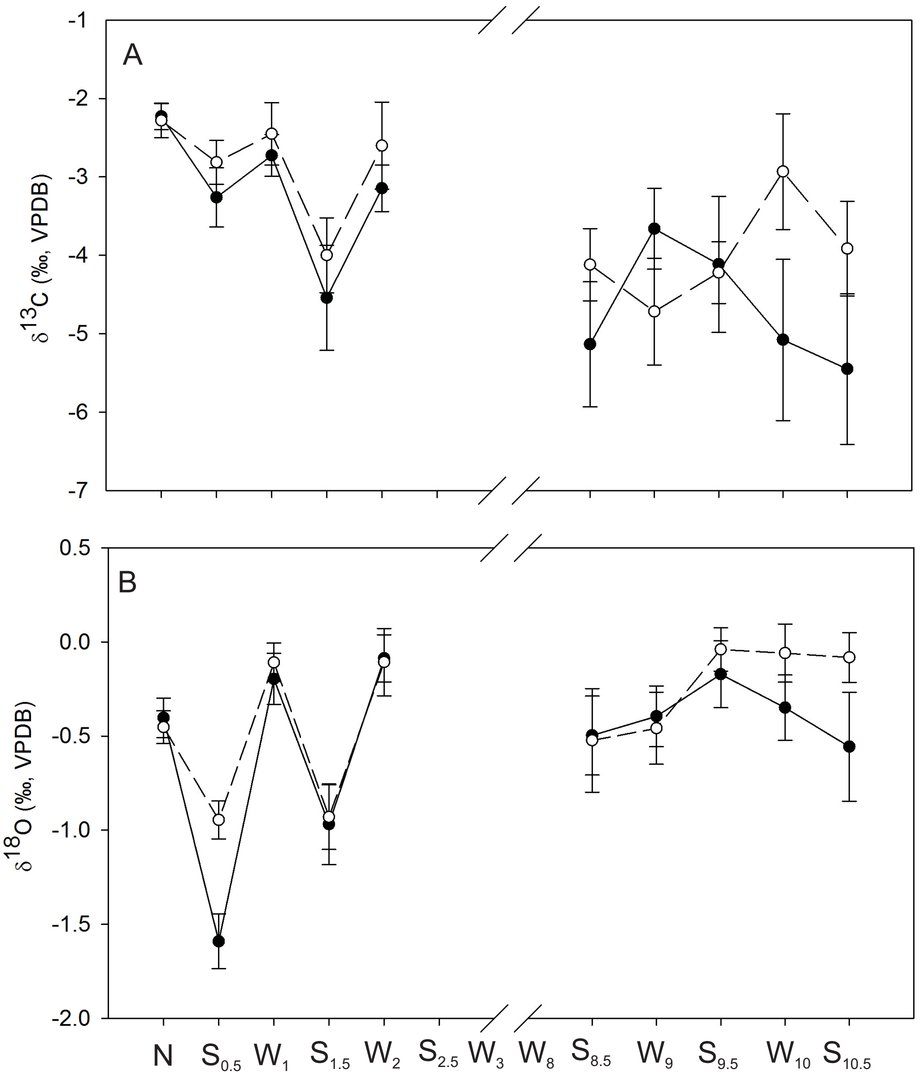

Figure 17. Mean $\delta^{13}C$ and $\delta^{18}O$ values (± standard error) measured in seasonal otolith growth rings of juvenile and adult of white seabass, *Atractoscion nobilis*. Samples were collected in Southern California (SC; white circles dots) and Gulf of Ulloa (GU; black circles). N = nuclei; S = summer; W = winter; subscript corresponds to the estimated age represented by each growth ring.

Figura 17. Valores promedio del $\delta^{13}C$ y $\delta^{18}O$ (± error estandar) medidos en los anillos de crecimiento estacionales de corvinas blancas, *Atractoscion nobilis*, juveniles y adultas. Las muestras fueron recolectadas en el Sur de California (SC; círculos blancos) y el Golfo de Ulloa; círculos negros). N = núcleo; S = verano; W = invierno; el subíndice indíca la edad estimada para cada anillo de crecimiento.

3.4. Discussion

The aims of this study were to reconstruct larval rearing temperatures and infer the population structure of white seabass collected in Southern California (SC), Vizcaino Bay (VB) and the Gulf of Ulloa (GU) using the isotopic composition (δ^{13}C and δ^{18}O) of carbonate extracted from otolith nuclei and seasonal growth rings of both juvenile and adult-stage

Table 4. Results of the two way repeated-measures analysis of variance testing for the effect of capture region and age on δ^{13}C and δ^{18}O values from juvenile and adult growth ring of white seabass, *Atractoscion nobilis*, collected in the Southern Califronia (SC) and Gulf of Ulloa (GU).

Tabla 4. Resultados del análisis de varianza de medidas repetidas de dos vías en la cuál se comparan los efectos de la captura por región y la edad en δ^{13}C y δ^{18}O de los anillos de crecimiento de corvinas blancas juveniles y adultas, *Atractoscion nobilis*, recolectadas en el Sur de California (SC) y el Golfo de Ulloa (GU).

		δ^{13}C			δ^{18}O		
Source	df	*MS*	*F*	*P*	*MS*	*F*	*P*
Juvenile stage							
Region	1	1.95	1.07	0.310	0.27	0.87	0.366
Age	4	9.96	7.15	<**0.001**	3.96	25.15	<**0.001**
Region*Age	4	0.21	0.15	0.961	0.29	1.82	0.137
Adult stage							
Region	1	7.19	0.84	0.378	0.97	1.32	0.272
Age	4	1.53	0.66	0.623	0.34	1.68	0.175
Region*age	4	4.87	2.10	0.098	0.32	1.59	0.197

white seabass. Given the complex life cycles that characterizes fish species such as the white seabass, examining different life stages and time scales simultaneously provides a much more powerful approach to the study of fish natal origin, movement and migration than the chemical analysis of whole otoliths (Begg *et al.*, 1999; Gao *et al.*, 2004; Elsdon *et al.*, 2008; Steer *et al.*, 2010; Gao *et al.*, 2013). In this study, otolith samples were collected from adults of various ages captured throughout the distribution of white seabass in the eastern Pacific, including potential spawning regions as off southern California and the central Baja California peninsula (Moser *et al.*, 1983). The sampling strategy encompassed a great part of the distribution of white seabass in Pacific waters. Central to the robust interpretation of the isotopic composition of biogenic carbonates and the calculation of robust temperature estimates based on δ^{18}O values is the explicit consideration of the processes that underlie its variability (Thorrold *et al.*, 1997; Campana, 1999; Elsdon and Gillanders, 2002). Thus, oceanographic data were incorporated in the analysis and

Table 5. Results of Holm-Sidak pairwise comparisons of δ^{13}C and δ^{18}O values of white seabass juvenile growth rings; W = winter, S = summer, subscript = estimated age represented by the otolith growth ring. Only significant differences are shown.

Tabla 5. Resultados de la prueba de comparaciones pareadas Holm-Sidak de los valores de δ^{13}C y δ^{18}O de los anillos de crecimiento de corvina blanca juveniles; W = invierno, S = verano, subíndice = edad estimada representada por los anillos de crecimiento en los otolitos.

	δ^{13}C		δ^{18}O	
Comparison	t	P	t	P
Among age				
N - S$_{0.5}$			5.831	$<$**0.001**
N - S$_{1.5}$	4.970	$<$**0.001**	3.826	**0.002**
W$_1$ - S$_{0.5}$			7.814	$<$**0.001**
W$_2$ - S$_{0.5}$			7.705	$<$**0.001**
W$_1$ - S$_{1.5}$	4.149	**0.001**		$<$**0.001**
W$_2$ - S$_{1.5}$	3.242	**0.016**		$<$**0.001**
S$_{0.5}$ - S$_{1.5}$	3.0883	**0.022**		
Age within SC				
W$_1$ - S$_{0.5}$			4.218	$<$**0.001**
W$_1$ - S$_{1.5}$			4.141	**0.001**
W$_2$ - S$_{0.5}$			3.892	**0.002**
W$_2$ - S$_{1.5}$			0.790	**0.002**
Age within GU				
N - S$_{0.5}$			5.795	$<$**0.001**
N - S$_{1.5}$	4.158	**0.001**	3.025	**0.019**
W$_1$ - S$_{0.5}$			6.858	$<$**0.001**
W$_1$ - S$_{1.5}$	3.264	**0.017**	4.131	$<$**0.001**
W$_2$ - S$_{0.5}$			6.979	$<$**0.001**
W$_2$ - S$_{1.5}$			4.457	$<$**0.001**
S$_{1.5}$ - S$_{0.5}$			2.889	**0.022**
Among regions				
S$_{0.5}$ - S$_{0.5}$			2.663	**0.010**

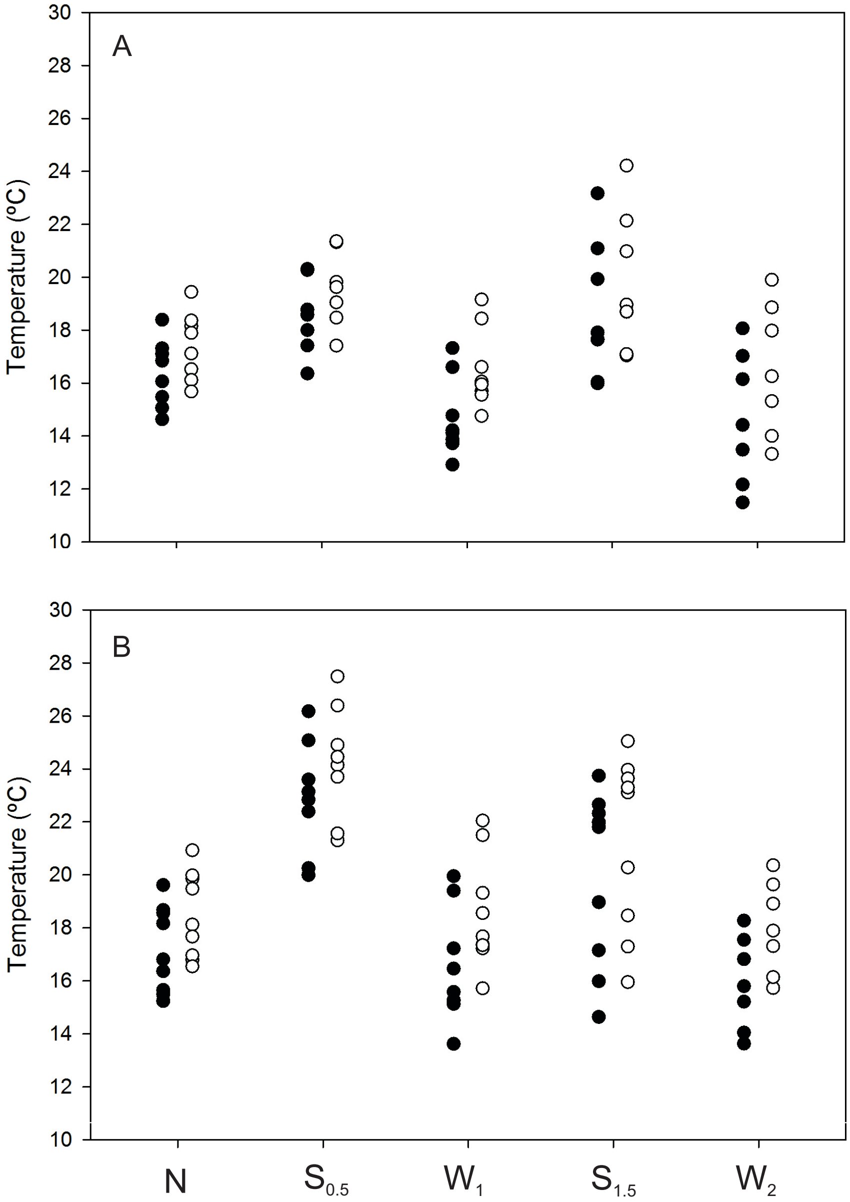

Figure 18. Back-calculated temperatures for the nuclei and seasonal growth rings of white seabass sampled off southern Califronia (A) and the Gulf of Ulloa (B). Mínimum (black circles) and maximum temperatures (white circles) were calculated using mínimum and maximum regional salinity estimates. In X axis W = winter, S = summer, subscript = age of fishes in years.

Figura 18. Temperaturas retrocalculadas del núcleo y anillos de crecimiento estacionales de la corvina blanca muestrada en el sur de California (A) y el Golfo de Ulloa (B). Las temperaturas mínimas (círculos negros) y máximas (círculos blancos) fueron calculados usando las salinidades regionales mínimas y máximas. En el eje X, W = invierno, S = verano, subíndice = edad de los peces en años.

interpretation of isotope ratios.

In this study, the isotopic composition of the otolith nuclei of adult white seabass varied substantially but did not differ sufficiently to discriminate between potential sub-populations of larvae reared in each region. However, there were differences between the oxygen isotopic composition and back-calculated temperature of the first seasonal growth ring of fish captured in SC and GU, suggesting the presence of two potentially discrete subpopulations divided by Punta Eugenia along the central Baja California peninsula (27°N).

3.4.1. Isotopic composition of otolith cores

The limited dimensions of the area from which carbonate was extracted in the otolith nuclei was designed to reduce the potential for contamination with carbonate precipitated during other life stages (Begg *et al.*, 1999; Campana, 1999; Steer *et al.*, 2010; Gao *et al.*, 2013). Given that there are few studies reporting larval age ranges and growth rates for white seabass, as a first approximation the number of daily growth rings in the otolith nuclei was estimated by analyzing the microstructure of a limited number of otoliths of wild-caught juveniles. The estimated time interval represented by the region of the otolith nuclei from which the carbonate subsamples were obtained ranged from 18-25 days. This is consistent with the duration of the white seabass larval period reported by Donohoe (1997), who found that larval white seabass caught in the Southern California Bight have a short pelagic life of 2-3 weeks. That study also validated the daily formation of otolith increments based on laboratory reared larvae. Hence, the time interval represented by the carbonate subsamples of the otolith nuclei integrate a time period of less than one month.

The δ^{13}C and δ^{18}O values of the otolith cores of adult white seabass captured within each sampling region were highly variable (up to 2‰; Figure 10). This high level of variability was also observed when considering specific spawning years or when the sample size for a given age class was limited. This implies that the variability in isotopic ratios was persistent through time and representative of the white seabass population, thus allowing for robust inferences into its population structure.

Carbon isotopic composition of otolith cores (δ^{13}C)

In sagittal otoliths, the bicarbonate in the saccular endolymph reacts with calcium ions and carbonate is precipitated under saturating conditions (Payan *et al.*, 2004). The δ^{13}C values of the carbon precipitated in fish otoliths is a function of the isotopic composition of the dissolved inorganic carbon (DIC) of the water as well as the byproducts of an individual's metabolism (Kalish, 1991; Campana, 1999; Weidman and Millner, 2000; Elsdon *et al.*, 2010; McMahon *et al.*, 2013). The δ^{13}C value of the DIC in the surface waters of the Pacific off North America is approximately 0.8 to 0.9‰ as a result of upwelling events along the coast, and those values do not change substantially at spatial scales dominated by isolated physical processes (Kroopnick, 1985; McMahon *et al.*, 2013). In contrast, the relative contribution of metabolically derived carbon to the δ^{13}C values of otolith carbonate varies between species and even among individuals of the same species (Iacumin *et al.*, 1992). For example, in cod (*Gadus morhua*) collected from different regions of the eastern North Atlantic, about 80% of otolith carbon was found to come from the DIC pool and 20% from metabolic sources; the relative contribution of each source depended on the isotopic composition of the diet as well as the temperature and physiology of the fish (Weidman and Millner, 2000). Tohse and Mugiya (2008) experimentally determined that in goldfish (*Carassius auratus*) the carbon derived from metabolism corresponded to about 25% of the isotopic composition of otolith carbonate, and the remaining 75% was from the ambient DIC. Likewise, Nelson et al., (2011) used laboratory experiments to calculate the contribution of food sources and the DIC pool to the δ^{13}C values of the otoliths of juvenile red drum (*Sciaenops ocellatus*) and found that the contribution of DIC was 85 to 95%. Only 8 to 15% of the isotopic composition was attributed to metabolically derived carbon.

The relative contribution of DIC and metabolically derived carbon to the isotopic composition of fish otoliths is therefore variable. Estimating the percent contribution of each source of carbon to the δ^{13}C values of white seabass otoliths would require laboratory experiments, which were beyond the scope of this study. However, the δ^{13}C values measured in otolith nuclei of white seabass from each sampled region were highly variable and lighter (ca -1.5 to -5‰) than regional DIC values (ca. 1‰; Figure 10a), suggesting that the contribution of metabolic carbon is likely important, albeit variable. The difference in average δ^{13}C in VB relative to those from SC and GU suggests that larval white seabass from VB probably relied on a different food source, or that the relative contribution of food-based carbon varied between regions.

Isotopic composition of the seawater (δw)

There is an absence of detailed regional data on the isotopic composition of seawater which is required for back-calculating the temperature of carbonate precipitation, particularly for the waters off central and southern California. Hence, δw was estimated using Craig and Gordon's (1965) salinity-δw relationship based on in situ salinity measurements (e.g. Valle and Herzka, 2008). The processes that contribute to changes in the salinity and δw of surface waters are rainfall, freshwater inflow, melting ice, evaporation and freezing, as well as vertical mixing and horizontal advection (Schmidt, 1998; Sharp, 2007). However, the waters off southern California and Baja California are not subject to freezing and are limited in freshwater inflow due to the region's arid nature (Wilkinson et al., 2009). The primary factors driving variations in salinity in the coastal waters inhabited by white seabass are therefore upwelling events and the mixing of different water masses. Considering both the annual variation in water masses currents and the latitudinal gradient, there was limited variation in regional salinity in the study area ($<$1 psu). By using regional salinity measurements to calculate the δw it was possible to characterize and account for seasonal variation in δw among regions and reduce the uncertainty level in back-calculated temperatures. Limited variability in regional salinity indicates that temperature is the most important factor influencing δ^{18}O values observed in white seabass otoliths.

The isotopic composition of seawater (δw) varied seasonally between regions, mirroring regional shifts in surface salinities. Craig and Gordon (1965) reported δw values between -0.5 and -0.4‰ for the northeastern Pacific surface waters based on samples taken between 20°N, 130°W and 32°N, 120°W. For the summer season during which white seabass spawn, the range of δw values reported by Craig and Gordon (1965) is only 0.12 and 0.19‰ more enriched in ^{18}O than the mean values applied to back-calculated temperature estimates of fish caught in SC and VB, respectively, and similar to the estimates for the GU (-0.58 to -0.31‰). Regional differences may be attributed to the latitudinal mixing of the California Current System water, subpolar water depleted in ^{18}O and with relatively low δw values, with the upwelled water of higher salinity and higher δw values (Craig and Gordon, 1965; Durazo *et al.*, 2010).

Oxygen isotopic composition of otolith cores (δ^{18}O)

The high variability in δ^{18}O values measured in otolith nuclei (range of 2‰) was reflected in a wide range of back-calculated temperatures for each sampling region, with overlapped. Aalbers (2008) reported an ambient water temperature of 11.3 to 21.7°C in coastal waters off southern California during spawning events of wild white seabass recorded. The highest frequency of spawning activity was recorded between 15 and 18°C, which is similar to the back-calculated temperatures estimated for the larval period of adult caught in SC waters. The broad range of back-calculated temperatures might reflect seasonal changes in the environmental conditions (and hence larval rearing period) prevalent during the long spawning period of white seabass, which ranges from March through August and peaks in May or June (Thomas, 1968; Aalbers, 2008). The average back-calculated temperature differed significantly between SC and GU. This likely reflects the well-documented latitudinal temperature gradient found along the southern California and Baja California peninsula during summer months (Lynn and Simpson, 1987; Durazo *et al.*, 2010). In particular, seasonal SSTs varied by at least 5°C in the SC and VB and by almost 10°C in the GU.

In contrast, the predicted range of δ^{18}O values for each region was calculated based on the full range of local salinity and SSTs estimates for the summer months (i.e., the larval rearing period). A broader range of potential aragonite precipitation temperatures (lighter δ^{18}O values) was predicted for GU than SC and VB; however, there was a high degree of overlap between regions. Even though the predicted δ^{18}O values for GU included lighter isotope ratios, the oxygen isotope ratios measured for GU covered roughly the same range as those of SC and VB. The similarity in measured δ^{18}O values, coupled with the overlap in predicted δ^{18}O values for each region, suggest that larvae were reared under similar sea surface temperatures and/or salinities, and a clear discrimination between regions was not possible.

Connectivity among fish subpopulations can occur during larval, juvenile or adult stage by larval drift or fish migration (Cowen and Sponaugle, 2009). The migration of juvenile and adult fishes to feeding areas or spawning grounds can congregate fish from different regions, reared under different environmental conditions (Harden, 1968). The variability in δ^{18}O values measured in the otolith core of adult white seabass collected in SC, VB and GU could be attributed to different causes including: (1) the mixing of larvae reared at different times during spawning season, (2) the mixing of larvae reared at the same time at different latitudes, (3) variation inshore/offshore temperatures, and (4) larval behavior.

(1) Mixing of larvae reared at different times during the spawning season

Off southern California, white seabass have a long spawning season that extends from March to August (Thomas, 1968; Aalbers, 2008). The sea surface temperature from the beginning to the end of the spawning season increases by around 5°C in SC waters, 6°C in VB and 10°C in the GU. Therefore, eggs spawned at the beginning of the spawning season (early spring) would have an otolith core with the highest δ^{18}O values, and otolith cores from eggs spawned at the end of the season (high SSTs) would have the lowest δ^{18}O values.

(2) Mixing of larvae reared at the same time at different latitudes

As suggested by Allen and Franklin (1992), larvae spawned in Mexican waters off northern Baja California can be transported by surface currents northward into southern California during the summer. However, as in other sciaenid species, adult white seabass can also migrate relatively long distances to feeding and spawning grounds, a scenario that increases vulnerability to local fisheries (Aalbers and Sepulveda, 2015). When otolith samples are collected opportunistically from local fishing vessels, as was done in this study, it is possible that samples were collected from different rearing grounds, contributing to the variability in the isotopic composition of otolith cores.

(3) Variation in inshore-offshore temperatures

The abundance of white seabass larvae off Baja California and southern California decreases from the coastal zone toward offshore waters (larvae are found up to 100 km offshore; Moser *et al.*, 1983). Along protected coastline of the Southern California Bight and Baja California, including semi-enclosed closed bays and coastal lagoons, during the spring and summer the sea surface temperature is higher in shallower waters than offshore. In contrast, along exposed coastlines and in areas prone to local intense upwelling, temperatures very close to the coast can be very lower than offshore (Graham and Largier, 1997; Marín *et al.*, 2003; Tapia *et al.*, 2009). Given that the local temperature regime near the coast is highly dynamic and variable, it could generate high variability in the oxygen isotope composition of larval otoliths.

(3) Larval behavior

During the late larval stage, fish can actively select suitable environmental conditions upon developing swimming abilities and the capacity to move independently in the water column (Armsworth, 2001; Morgan and Fisher, 2010). However, white seabass larvae are epipelagic during the late larval phase in nearshore southern California waters, which may be related with seeking preferential temperatures or their predator-avoidance capabilities (Margulies, 1989). In addition, white seabass larvae change from a pelagic distribution to a demersal environment following the 12-21 d larval period (Margulies, 1989; Donohoe, 1997). Ontogenetic habitat changes could lead to differences in temperature and salinity (and hence δw), generating variability in δ^{18}O values of otolith cores.

In summary, the results of this study do not clearly explain the high variability in δ^{18}O from otolith cores of adult white seabass. Therefore, even though SSTs vary substantially between regions, the rearing conditions of larval white seabass did not differ enough to discriminate between fish reared off southern California, central and southern Baja California. Given the high degree of overlap in δ^{18}O values between regions and the potential for larval dispersion and adult migration, the connectivity among potential subpopulations could occur during the adult stage.

3.4.2. Isotopic composition of juvenile otolith growth rings

The seasonal variation in δ^{13}C values of juvenile growth rings may be explained by variations in the isotopic composition of food sources as well as changes in metabolic rate as a function of water temperature; the latter is considered the most important factor (Kalish, 1991; Gauldie *et al.*, 1994). White seabass vary substantially in size-at-age (Romo-Curiel *et al.*, 2015), suggesting that individuals of the same age may have different food sources due to size-related feeding preferences, as has been documented for other sciaenid species (Stickney *et al.*, 1975; Peters and McMichael, 1987). Hence, at least part of the variation in δ^{13}C values may be attributed to size-specific differences in diet. The most depleted δ^{13}C values were measured in the growth rings laid down during the summer, when growth rates, water temperature, and respiration rates are higher, while the most enriched values corresponded to the winter growth rings, when growth and metabolic rates are reduced (Gauldie, 1996; Hoie *et al.*, 2003; Portner *et al.*, 2008). This suggests that the relative contribution of metabolically derived carbon to the carbon isotope ratios of the otoliths may be higher during the summer, a period of increased growth.

The linear relationship between carbonate δ^{18}O values and temperature has been used to validate the seasonality of ring deposition in otoliths (e.g. Weidmand and Millner, 2000). Samples taken from the translucent rings (summer growth season) of juvenile white seabass had the lightest δ^{18}O values. Opaque growth rings had more enriched δ^{18}O values, consistent with the lower temperatures of the winter season. Similar to other sciaenids, previous age and growth studies of white seabass suggest that this species has an annual ring deposition rate (Romo-Curiel *et al.*, 2015); however, a rigorous validation of the deposition of annuli remained lacking. The clearly seasonal pattern in δ^{18}O values found in juveniles implies that one opaque and one translucent growth ring is deposited every year, further validating the yearly deposition hypothesis of Romo-Curiel *et al.* (2015).

In this study there was a significant difference between SC and GU of the first summer growth ring (S$_{0.5}$). The absolute difference in mean δ^{18}O values of 0.65‰is equivalent to a 4°C back-calculated temperature difference. Southern California and the Gulf of Ulloa are located toward the northernmost and southernmost extent of the distribution of white seabass in Pacific waters, along a well-documented latitudinal temperature gradient. Given that in this study the otoliths came from fish collected in SC and GU over the course of several years and belonged to different age groups, the significant difference in the δ^{18}O values of the first summer growth ring indicates that there is likely limited mixing between the northernmost and southernmost sampled populations.

3.4.3. Isotopic composition of adult growth rings

While seasonal variations in the carbon and oxygen isotopic composition were evident during the juvenile stage, this was less evident for the growth rings corresponding to the adult stage. There were no significant differences in the δ^{13}C and δ^{18}O values of the seasonal rings of adults 8-10 years old, either between opaque and transparent growth rings or between SC and GU. In the case of adult white seabass, Aalbers and Sepulveda (2015) reported that adults tagged in southern California were found at a mean depth of 30 m during the winter, at average temperatures between 13 and 14°C. During the spring and summer months, these same fish were primarily found in surface waters at depths of less than 10.5 m, and at mean temperatures between 16 and 18°C. Hence, white seabass, like many other pelagic species, actively select their thermal distribution throughout the year, which is consistent with the more limited range of isotopic values that were measured during the adult stage.

3.4.4. Population structure of white seabass relative to oceanographic conditions

Species of fish that have a long (i.e., several months) larval period have an increased probability of passive dispersal, which can lead to high gene flow, high connectivity and the absence of population genetic structure (Wersing and Toonen, 2009). Dispersal distance has also been correlated with the duration of the larval period (see review by Levin 2006 and references therein). Based on a larval period of 12-21 days, Donohoe (1997) estimated that larvae from the Southern California Bight could be transported a maximum of 200-360 km (considering a current velocity of 20 cm/s of the northward flowing countercurrent that prevails during spring and early summer). The mean distance between SC and GU is approximately 1,000 km. The limited larval dispersal of white seabass could contribute to a low level of connectivity throughout the eastern Pacific, at least between the northern and southern boundaries of their distribution.

3.4.5. Oceanography, biogeography and climate

The potential level of connectivity between populations north and south of Punta Eugenia appears to be limited by seasonal oceanographic conditions. During late summer and fall the southernmost intrusion of the California Current (CC) decreases, while the coastal undercurrent (CCC) intensifies and transports water from the tropics northward to the southern region of the Baja California peninsula, significantly heating the area (Lynn and Simpson, 1987; Durazo, 2015). Over the continental shelf there is a narrow surface countercurrent (10-20 km) with poleward flow (Soto-Mardones *et al.*, 2004a), which interacts with small gyres (20-50 km in diameter; Durazo et al., 2005). The Southern California Bight and the Gulf of Ulloa are cyclonic gyres, while the circulation within Vizcaino Bay is largely anticyclonic (Lynn and Simpson, 1987; Durazo, 2015). During the summer and autumn, the presence of anticyclonic and cyclonic gyres to the north and south of Punta Eugenia, respectively, generate a divergence area that may limit larval connectivity. Hence, eggs spawned in SC and GU produce larvae and juveniles that may be limited to those regions. This scenario is consistent with the observed differences in the first summer-autumn growth of otolith rings reported by Romo-Curiel *et al.* (2015), which suggests that juvenile white seabass from the waters below Punta Eugenia grew faster than those reared in the northern region. Differential growth rates along with differences in the oxygen isotopic composition and back-calculated temperature of the first summer growth ring ($S_{0.5}$) of fish captured in SC and GU provide further evidence for the presence of two potentially discrete subpopulations divided by Punta Eugenia.

Along central Baja California, the regions north and south of Punta Eugenia are considered to be different biogeographic provinces (Durazo, 2015). Punta Eugenia is the southern limit of distribution for a variety of temperate species, as well as the northern limit of distribution for tropical species characteristic of the subtropical equatorial Pacific (Hubbs, 1960; Bernardi *et al.*, 2003; Lluch Belda *et al.*, 2003; Blanchette *et al.*, 2008; Durazo *et al.*, 2010). The seasonality of oceanographic conditions, the combination of coastal upwelling, mixing of various water masses and the presence of gyres appear to foster high productivity and favorable spawning conditions, considering VB and GU as a center of high biological activity (Lynn and Simpson, 1987; Parrish *et al.*, 1981; Lluch Belda, 1999; Horn *et al.*, 2006; Checkley Jr and Barth, 2009; Durazo *et al.*, 2010).

Despite the support for two discrete sub-populations, this work, it is possible that El Niño events could lead to increased connectivity between VB and GU. Under El Niño conditions, there are significant changes in the California Current System which include an alteration of the current direction and coastal upwelling intensities, an increase in salinity and SSTs, as well as a significant variation in the primary productivity and larval abundance (Moser *et al.*, 2001, 2002; McGowan *et al.*, 2003; Durazo and Baumgartner, 2002; Perez-Brunius *et al.*, 2006; Checkley Jr and Barth, 2009; Funes-Rodríguez *et al.*, 2011). During this oceanographic condition the northernmost distribution of white seabass extends further north, from San Francisco, CA, to Juneau, Alaska (Vojkovich and Reed, 1983). Based on the migration of adult white seabass from the Southern California Bight (mean distance of 229 km; Aalbers and Sepulveda, 2015), there could be a regional level of connectivity between potential subpopulations from GU and VB. For this reason it may be that the genetic studies conducted to date have not found evidence of population structure (Franklin, 1997).

3.5. Conlcusions

The isotopic composition (δ^{13}C and δ^{18}O) of carbonate from the otolith nuclei of adult white seabass caught in southern California, Vizcaino Bay and the Gulf of Ulloa varied substantially and did not differ sufficiently to discriminate between potential subpopulations. However, there were differences between the oxygen isotopic composition and the back-calculated temperature of the first seasonal growth ring of fish captured in the southern California and Gulf of Ulloa. This finding suggests the presence of two potentially discrete subpopulations divided by Punta Eugenia in the central Baja California peninsula. Given the importance of stock structure in the management of binational resources, this work provides managers with insight into population dynamics and biological information necessary for seek and apply the most appropriate strategies management of this natural resource which is susceptible to overexploitation.

Chapter 4. General discussion

The white seabass, *Atractoscion nobilis*, is considered an important target specie in commercial and recreational fishing operations along the western coast of North America (Thomas, 1968; Allen and Franklin, 1992). Given the importance of understanding population structure for the development of fishery management strategies, several approaches have been used to infer the stock structure of white seabass across its distribution. However, it is still uncertain whether white seabass comprise one or more subpopulations. The collective aim of this thesis was to investigate the population structure of white seabass along the Pacific coast of North America. To accomplish this goal, two complementary approaches were used based on (1) estimates of growth rates at the individual and population levels and (2) measurements of the isotopic composition (δ^{13}C and δ^{18}O) of adult white seabass otoliths subsamples corresponding to specific life stages.

4.0.1. Growth parameters

Continuous growth and periodic ring formation of fish otoliths allows them to be used for generating estimates of age and offer a means to differentiate growth at both individual and population level. Given that growth estimates for white seabass are limited (Thomas, 1968; CDFG, 2002; Williams *et al.*, 2007), this study was able to provide valuable age at size information as well as test hypotheses regarding potential differences in growth rates based on location. Aside from population structure, this work will be used in the management of the white seabass resource as it is currently being incorporated into the first white seabass stock assessment in North America.

In the context of white seabass population structure this work identified similar growth rates and asymptotic lengths of fish sampled within the three study regions, southern

California (SC), Vizcaino Bay (VB) and the Gulf of Ulloa (GU). In the growth analysis at the individual level, average ring width measured from the first annuli of otoliths sampled off southern Baja California (GU) was significantly greater compared with those from SC and VB. This difference suggested that fish from GU grew under different environmental conditions (i.e. temperature and food availability). This findings suggest the presence of separate subgroups of white seabass at least during the first year of life.

4.0.2. Isotopic analysis

Environmental conditions under which white seabass grew were inferred from the isotopic composition (δ^{13}C and δ^{18}O) of otolith pairs used in the growth analyses. Based on the sea surface temperature and salinity latitudinal gradients among their distribution (Lynn and Simpson, 1987; Durazo *et al.*, 2010) as well as the premise that the otoliths formed in waters with different environmental conditions may exhibit different δ^{13}C and δ^{18}O composition (Campana, 2005); in this chapter carbonate subsamples from the larval, juvenile and adult stages were used to infer habitat use, level of mixing, and population connectivity. The isotopic composition of otolith nuclei samples from all regions varied substantially and did not differ sufficiently to discriminate between potential subpopulations. However, seasonal variations in the carbon and oxygen isotopic composition of white seabass from southern California and the Gulf of Ulloa were evident during the juvenile stage. Regional differences in the oxygen isotopic composition and back-calculated temperatures obtained from the first seasonal growth ring provide further evidence for two potentially discrete subpopulations divided by Punta Eugenia.

Punta Eugenia is an important biogeographic break in the California Current System (Dawson *et al.*, 2006) and forms the southern boundary for a variety of temperate species, as well as the northern limit of distribution for tropical species of the subtropical equatorial

Pacific (Bernardi *et al.*, 2003; Lluch Belda *et al.*, 2003; Blanchette *et al.*, 2008). Regionally distinct circulation patterns around Punta Eugenia may limit the level of connectivity among fish populations with planktonic larvae, particularly during summer and fall. Specifically, the formation of cyclonic gyres south of Punta Eugenia and an anticyclonic gyre in Vizcaino Bay, coupled with higher sea surface temperatures in the southern province may influence localized larval recruitment (Durazo, 2015). In this study the overlap between the spawning season of white seabass and the warmer summer-fall water conditions in the southern province was reflected in otoliths with a higher growth rate and lighter δ^{18}O values during the first year of life.

Taken together, regional differences in growth rates and the isotopic composition during the first year of growth suggest that white seabass spawned in southern California must consistently experience different environmental conditions than individuals reared within the Gulf of Ulloa. The presence of two potentially discrete subpopulations of white seabass along the Pacific coast is an important finding that has significant management implications. For one, management strategies must be tailored to the sustainable use of each stock at the regional level, with specific considerations regarding harvest, effort and recruitment (Jennings *et al.*, 2001). Fisheries management plan is development from information about what constitutes the harvest population and how it is genetically delineated (Allendorf *et al.*, 2008). While there is information regarding the fishery of white seabass off southern California since the late 19th century (Vojkovich, 1992; Allen *et al.*, 2007), the harvest statistics on the commercial and recreational landings are unavailable for off Baja California (*http://www.conapesca.gob.mx/wb/cona/consulta_ especifica_por_produccion*).

Although genetic investigations based on the analysis of nuclear microsatellite DNA suggest that the white seabass collected from Point Conception, CA to Magdalena Bay, off the southern Baja California peninsula, comprise a single panmictic breeding population (Franklin, 1997). Spatial homogeneity in genetic structure can be achieved with a relatively low rate of fish movement between regions (Allendorf *et al.*, 2008). Therefore, population structure of relevance to fisheries management may therefore exist in the absence of genetic population structure. Likewise, tagging studies have indicated that adult fish may travel hundreds of kilometers seasonally (Aalbers and Sepulveda, 2015). The extensive movements observed in adult white seabass supports mixing throughout the northern extent of the range, specifically between the northern Baja California peninsula and southern California, however, fish tagged in southern California have not been recaptured off the southern Baja California coast (Sepulveda and Aalbers pers. com.). Nevertheless, additional tagging studies off southern Baja California are necessary to evaluate the connectivity of adult populations below Punta Eugenia.

Findings from this study provide evidence to support the presence of regionally distinct larval rearing grounds between southern California and the Gulf of Ulloa. However, if further research indicates a high level of connectivity between the populations of adult white seabass throughout California and Baja California, then a binational management strategy based on the presence of a single stock should be developed. Regardless, information on white seabass population size, harvestable population, seasonal spawning regions, and natural mortality is limited, particularly for the regions south of Punta Eugenia.

Given the regional importance of white seabass to commercial and recreational fisheries of North America, and the established susceptibility to overexploitation demonstrated through California fisheries history, studies on stock structure are critical for effective long-term management.

Chapter 5. General conclusions

The similar growth rates and asymptotic lengths between white seabass captured in southern California, northern and southern Baja California peninsula suggest the presence of a single population of white seabass along the Pacific coast of North America. Nevertheless, the individual growth analysis suggests that the white seabass from Southern Baja California grew under different environmental conditions during their first year of life than fish from the northern regions.

The isotopic composition (δ^{13}C and δ^{18}O) of carbonate from the otolith nuclei of adults white seabass caught in the southern California, Vizcaino Bay and Gulf of Ulloa varied substantially and did not differ sufficiently to discriminate between potential subpopulations of larvae reared in each region.

There were differences between the oxygen isotopic composition and the back-calculated temperature of the first seasonal growth ring of fish captured in the southern California and Gulf of Ulloa, suggesting the presence of two potentially discrete subpopulations divided by Punta Eugenia in the central Baja California peninsula.

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