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EFECTOS DE LA DENSIDAD DE SIEMBRA Y EL DESDOBLE SOBRE EL CRECIMIENTO Y LA SUPERVIVENCIA EN UN CULTIVO SUSPENDIDO EXPERIMENTAL DEL MEJILLÓN *Mytilus platensis* D'ORBIGNY, 1842, EN EL GOLFO SAN JORGE, ARGENTINA

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RESUMEN. En los últimos años, ha habido un renovado interés en el desarrollo del cultivo de mejillones en la Argentina. Sin embargo, esta actividad todavía tiene lugar a pequeña escala o de forma experimental en la región patagónica. Conocer los efectos de las densidades iniciales y el desdoble sobre el crecimiento y la supervivencia en un cultivo experimental es información de base necesaria para el desarrollo de experiencias que permitan estudiar parámetros productivos en cultivos a mayor escala. Por estos motivos, este trabajo tuvo como objetivo analizar el efecto de las densidades iniciales y el desdoble sobre el crecimiento y la supervivencia del mejillón *Mytilus platensis* en un cultivo suspendido experimental en la región costera central del Golfo San Jorge, Argentina. Para ello, se estudiaron dos técnicas de cultivo, con y sin desdoble, durante un período de 9 meses, a dos densidades iniciales (400 y 700 ind. m^{-1}). La semilla fue obtenida de un criadero artificial. Se monitorearon talla, peso y supervivencia de los mejillones. El mayor crecimiento en talla y peso, y la supervivencia más elevada se observaron en la estrategia sin desdoble con la densidad más baja. En esta estrategia, los animales alcanzaron una talla promedio mayor a 65 mm, llegando a la talla comercial en menos de un año. Estos resultados permiten concluir que, a pequeña escala, la estrategia sin desdoble es la recomendada para cultivar mejillones en la región a una densidad de 400 ind. m^{-1} durante un mínimo de 9 meses.

Palabras clave: Cultivo de mejillón, desdoble, crecimiento, supervivencia.

EFFECTS OF STOCKING DENSITY AND THINNING-OUT ON GROWTH AND SURVIVAL IN AN EXPERIMENTAL SUSPENDED CULTURE OF THE MUSSEL *Mytilus platensis* D'ORBIGNY, 1842, IN SAN JORGE GULF, ARGENTINA

ABSTRACT. There has been a renewed interest in the development of mussel farming in Argentina in the recent years. However, this activity still takes place on a small scale or experimentally in the Patagonian region. Knowing the effects of initial densities and thinning-out on growth and survival at an experimental scale is a necessary basic infor-

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†El Dr. Héctor E. Zaixso falleció el 28 de abril de 2015.

mation for the development of experiences that allow the study of productive parameters in larger-scale culture. For these reasons, this work aimed to analyze the effect of initial densities and thinning-out on the growth and survival of the mussel *Mytilus platensis* in an experimental suspended culture in the central coastal region of San Jorge Gulf, Argentina. Two cultivation techniques were studied, with and without thinning-out, for 9 months at two initial densities (400 and 700 ind. m^{-1}). Seed was supplied by a hatchery. Size, weight and survival of the mussels were monitored. The best performance was achieved without thinning-out at the lower density. Additionally, animals reached an average of more than 65 mm with this strategy, obtaining commercial sizes in less than one year. These results allow us to conclude that the thinning-out strategy is recommended for cultivating mussels on a small scale in this region at a density of 400 ind. m^{-1} for a minimum of 9 months.

Key words: Mussel culture, thinning-out, growth, survival.

INTRODUCCIÓN

Durante las últimas décadas, el cultivo suspendido de mejillón ha sido una actividad comercial de gran expansión en países con litorales marítimos apropiados (Ross et al. 2013). En la Argentina, esta actividad aún se realiza de manera esporádica, a pequeña escala o de forma experimental (RMCP 2013; Isola 2017). En 2014, las importaciones realizadas por la Argentina de productos derivados del cultivo de mejillón superaron las 1.000 t, con un valor de más de US$ 2.500.000, siendo Chile el país que acapara casi la totalidad (99,7%) de dichas importaciones (PROCHILE 2014). Por otro lado, el cultivo suspendido de diversos moluscos bivalvos en la Argentina (entre los que se encuentra el mejillón *Mytilus platensis* d'Orbigny, 1842 y la cholga *Aulacomya atra* (Molina, 1782)), alcanzó un producción de 16 t en 2015 (Panné Huidobro 2015). Esta enorme brecha entre los niveles de demanda interna y la producción nacional revela un importante nicho para el desarrollo de actividades productivas relacionadas al cultivo del mejillón.

Estudios en todo el mundo han demostrado la importancia de la densidad de siembra inicial de animales (individuos por metro, ind. m^{-1}) en el desarrollo de un cultivo suspendido de mejillón (Alunno-Bruscia et al. 2000; Cubillo et al. 2012a; Pérez-Camacho et al. 2013; Bordon et al. 2014). Altas densidades iniciales generan competencia por espacio y/o alimentos (Fréchette y Lefaivre 1990), así como mortalidad asociada a la competencia intraespecífica a medida que los animales se desarrollan (Fréchette et al. 1996; Fréchette y Bacher 1998; Alunno-Bruscia et al. 2000; Guiñez 2005; Fréchette et al. 2011; Fuentes-Santos et al. 2014). Se han registrado también efectos densodependientes sobre el desarrollo individual y el aumento en las pérdidas por desprendimiento (Lauzon-Guay et al. 2005a; Cubillo et al. 2012a, 2012b). Por estas razones, conocer cuáles estrategias de manejo y densidades iniciales son las adecuadas para reducir la competencia intraespecífica, optimizando el crecimiento y la supervivencia en un cultivo experimental, es información de base necesaria para el adecuado desarrollo de futuras experiencias a escala comercial que permitan analizar niveles productivos en la región costera central del Golfo San Jorge.

Por lo general, dos estrategias de manejo son utilizadas en el cultivo suspendido de mejillón para mitigar los efectos contraproducentes de la densidad. Una de esas estrategias, conocida como cultivo con desdoble (*thinning-out*, Pérez-Camacho et al. 2013), consiste básicamente en engordar animales jóvenes a altas densidades en las estructuras de cultivo durante un determinado periodo de tiempo (fase de cría o pre-engorde). Pasado este tiempo, los animales son retirados de las estructuras de cultivos y re-colocados en las mismas a densidades menores hasta el tiempo de cosecha (fase de engorde). Este proceso se lleva a cabo para controlar la densidad de individuos en las unidades de cultivo y así favorecer el crecimiento y reducir las pérdidas por desprendimiento.

Esta estrategia posee variaciones de acuerdo al lugar donde se lleve a cabo esta práctica. En España, por ejemplo, en el cultivo del mejillón *M. galloprovincialis* Lamarck, 1819, el proceso de desdoble consta de tres etapas:

1) Obtención de la semilla: consiste en obtener (por captación en cuerdas o redes colectoras y/o recolección del ambiente natural) juveniles con tallas que oscilan entre 15 y 30 mm;
2) Fase de pre-engorde: estos animales se colocan en las cuerdas de cultivo a altas densidades por metro de cuerda durante un período que oscila entre los 3 y 6 meses;
3) Fase de engorde: luego de este período, esas cuerdas se retiran del agua, los mejillones son separados de las cuerdas y re-encordados a densidades menores (desdoble), haciéndolos crecer en estas cuerdas hasta el momento de cosecha (Pérez-Camacho et al. 2013).

En el cultivo del chorito (*M. chilensis*, Hupé, 1854) en Chile, se utiliza un proceso similar al español, en el cual las dos primeras etapas están comprendidas en una, ya que la semilla se obtiene por captación natural en cuerdas colectoras, y luego que los individuos alcanzan un tamaño entre 10 y 30 mm en esas cuerdas, se pone en práctica la fase de engorde (Uriarte 2008).

Otra técnica o estrategia de cultivo consiste en colocar individuos en densidades específicas en las cuerdas y dejarlos hasta el momento de cosecha. Este proceso se conoce como cultivo sin desdoble (Pérez-Camacho et al. 2013). Este tipo de producción minimiza las horas hombre de trabajo y generalmente se usa en países tropicales (Gosling 1992). Estudios comparando la efectividad entre cultivos con y sin desdoble sugieren que este último reduce el tiempo de cultivo y el trabajo asociado con este proceso, con el consiguiente aumento de la productividad (Pérez-Camacho et al. 2013).

En la Argentina, el cultivo de mejillón se ha realizado a pequeña escala en emprendimientos que no han contemplado, de forma sistemática, el efecto de la densidad de siembra sobre la productividad general del cultivo (RMCP 2013). En la región costera norte y central de la Patagonia argentina, la técnica de cultivo suspendido que ha brindado los mejores resultados es el cultivo en *longline* subsuperficiales (Bertolotti et al. 1987; Zaixso y Bala 1993; Pascual y Zampatti 1998; Elvira et al. 2000; Zaixso y Lizarralde 2001; Isola y Zaixso 2012; RMCP 2013). Zaixso y Lizarralde (2001) realizaron estudios experimentales sobre el crecimiento, supervivencia y biomasa cosechable a tres densidades de engorde diferentes en un cultivo con desdoble en el Golfo Nuevo (42° 46′ S, 65° 02′ W). Este trabajo mostró que en un cultivo con desdoble el aumento de la densidad inicial afecta negativamente el crecimiento y la supervivencia.

En la región central del Golfo San Jorge, se estudió el efecto de la densidad inicial sobre el crecimiento y la supervivencia en un cultivo sin desdoble con una variante del método de encordado francés (González et al. 1974), a tres densidades iniciales diferentes (Isola y Zaixso 2012). Los resultados mostraron que el aumento de la densidad inicial afecta negativamente el crecimiento y la supervivencia. Sin embargo, en la región no existe información que unifique, en un único estudio, los efectos conjuntos del desdoble y la densidad de siembra sobre el crecimiento y la supervivencia del mejillón y compare estos resultados frente a un cultivo sin la práctica del desdoble a las mismas densidades iniciales.

Desarrollar un cultivo con y sin la práctica del desdoble, a diferentes densidades iniciales de engorde y estudiar sus efectos sobre el crecimiento y la supervivencia del mejillón, es parte de la información de base necesaria para definir estrategias de manejo en futuros emprendimientos a mayor escala que optimicen el uso del recurso (semilla) y los niveles de producción. Los resultados de un estudio de estas características aportan información para el desarrollo de políticas públicas relacionadas tanto con la sustentabilidad como con la expansión futura de esta actividad en la región, en concordancia con las directivas actuales sobre producción acuícola en el país (InfoLEG 2017).

Por estas razones, el presente estudio tuvo como objetivo comparar el crecimiento y la supervivencia del mejillón *M. platensis*, en cultivo experimental con y sin la práctica del desdoble, a diferentes densidades iniciales en la región costera central del Golfo San Jorge.

MATERIALES Y MÉTODOS

El estudio se realizó en el área costera central del Golfo San Jorge, Chubut, Argentina. Este golfo se caracteriza por ser semiabierto con un área que abarca aproximadamente 39.340 km^2. Los valores de salinidad registrados se ubican dentro del rango comprendido entre los 33 a 33,6 (Akselman 1996; Fernández et al. 2005, 2008). La productividad primaria del área registra dos picos, uno a comienzos de la primavera y otro a comienzos del otoño (Carreto et al. 2007). La experiencia se realizó en Playa Belvedere (45° 59′ 12″ S, 67° 33′ 17″ W, Figura 1), a una profundidad promedio de 15 m en relación a la altura media de las mareas. Para la realización de los ensayos se instaló un *longline* experimental sub-superficial de 100 m de longitud efectiva, fondeado en sus extremos con estructuras de hormigón de base circular de 1,5 t cada una. Mensualmente y durante el período de estudio (mayo de 2016 a febrero de 2017), se registró la concentración de clorofila *a* (Chl *a*), materia orgánica particulada (MOP), temperatura del agua y salinidad. La estimación de Chl *a* se realizó a través de imágenes del satélite Aqua Modis 4 km, y la temperatura del agua de mar y salinidad se registraron con una sonda multiparamétrica YSI 556 MPS. Para determinar el contenido de MOP se tomaron 3 muestras mensuales de 1 l de agua de mar que fueron filtradas utilizando filtros de microfibra de vidrio Munktell MG-160 de 47 mm. El contenido de MOP se determinó luego de calcinar en una mufla los filtros a una temperatura de 550 °C siguiendo el protocolo descripto por Strickland y Parsons (1965).

Experiencia de cultivo

Los mejillones utilizados en el experimento fueron juveniles de *M. platensis* provenientes de un criadero ubicado en la localidad de Bahía Camarones, Provincia del Chubut, Argentina. La semilla presentó una talla promedio de 27.37 mm ($s^2 = 25{,}14$, n = 1.100) y un peso seco promedio de 0,069 g ($s^2 = 0{,}00215$, sub-muestra al azar de 100 individuos). En mayo de 2016 se confeccionaron los encordados utilizando un sistema mixto francés-español, el cual consiste en encordar por el método francés (Gonzales et al. 1974) colocando palillos de madera para distribuir la carga de la cuerda y que funcionan como soportes, como en el método español (Gonzales et al. 1974).

Para estudiar los efectos de la técnica de manejo y las densidades iniciales sobre el crecimiento y supervivencia en un cultivo experimental de mejillón, se analizaron dos técnicas de cultivo: con y sin desdoble a dos densidades iniciales de engorde. Para la experiencia sin desdoble (ESD), se confeccionaron ocho cuerdas de 1 m de longitud con una densidad inicial de 400 ind. m^{-1} cada una (ESD-400) y ocho cuerdas de 1 m con una densidad inicial de 700 ind. m^{-1} (ESD-700). Para la experiencia con desdoble (ECD), se prepararon nueve cuerdas de 1 m de longitud con una densidad inicial de 1.600 ind. m^{-1} (ECD-1.600, cuerdas de cría). La elección de estas densidades iniciales de engorde se basó en los resultados de un trabajo previo en la región (Zaixso y Lizarralde 2001), el cuál mostró que el engorde a altas densidades iniciales (en un cultivo exclusivamente bajo las técnica con desdoble) causa elevados desprendimientos de individuos, amenazando la rentabilidad del cultivo.

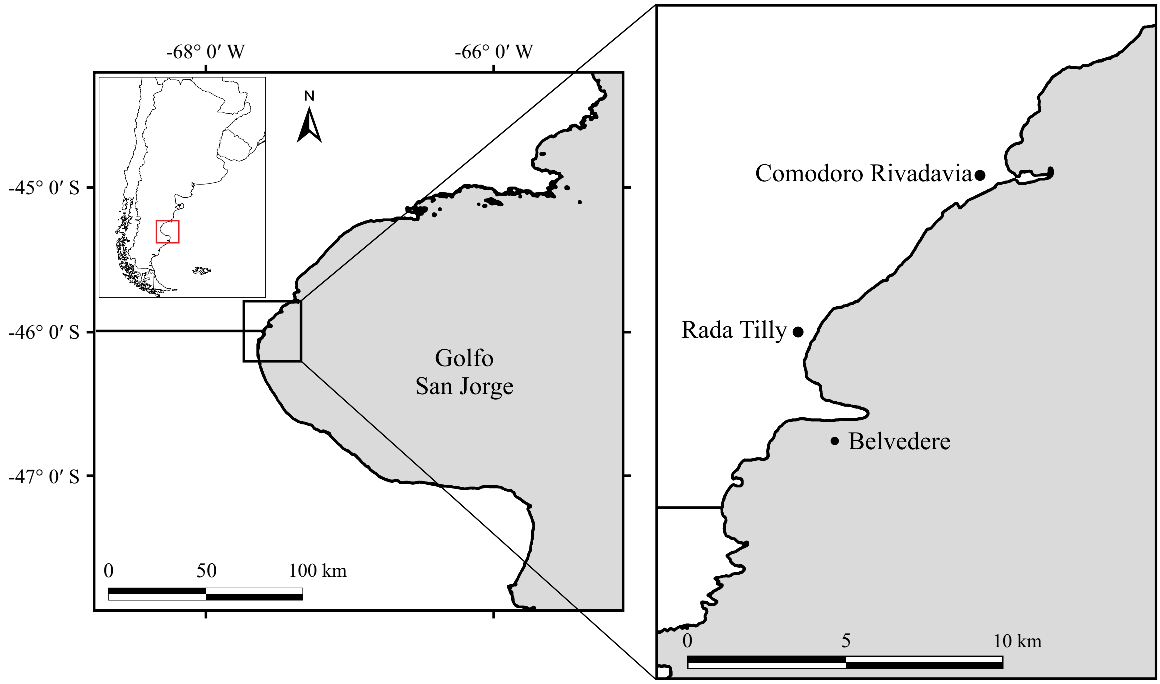

Figura 1. Ubicación de la zona de estudio. Playa Belvedere.
Figure 1. Location of the study area. Belvedere beach.

Para evitar posibles interacciones entre las cuerdas, estas fueron colocadas en el *longline* con una separación de 3 m entre ellas y de forma alternada siguiendo el siguiente esquema: ESD-400, ESD-700, ECD-1.600. El experimento comenzó en mayo de 2016 y finalizó en febrero de 2017 (nueve meses). Se muestrearon cuerdas de cultivo cada tres meses tomando al azar dos cuerdas correspondientes a cada densidad inicial (en ambas estrategias) para medir parámetros de crecimiento y supervivencia.

En la ECD-1.600, tres meses después de iniciado el experimento (agosto), se realizó el desdoble y se extrajeron las nueve cuerdas correspondientes a esta serie experimental. De estas cuerdas, dos se usaron para medir parámetros de crecimiento y supervivencia, mientras que con las restantes (siete) se armaron doce cuerdas de engorde: seis con una densidad inicial de 400 ind. m^{-1} (ECD-400) y otras seis con una densidad inicial de 700 ind. m^{-1} (ECD-700). Los individuos remanentes, una vez finalizado el armado de las cuerdas de engorde y la toma de muestras, fueron reencordados y colocados nuevamente en la línea de cultivo para su utilización con otros fines no vinculados al presente estudio. Luego del desdoble, las cuerdas se distribuyeron en el *longline* siguiendo el siguiente esquema: ESD-400, ECD-400, ESD-700, ECD-700. En cada fecha de muestreo y en cada cuerda retirada, se realizó un conteo de todos los individuos vivos y se tomaron muestras aleatorias de 50 mejillones. A cada individuo se le midió la talla (distancia umbo-borde posterior), se le extrajo el tejido blando y se secó en estufa a 80 °C hasta alcanzar peso constante, para luego pesarlo en balanza analítica.

Análisis de supervivencia

La supervivencia por cuerda se definió como el número de individuos vivos que permanecieron en la cuerda al momento del muestreo. La diferencia entre el número inicial y la supervivencia (sumado a los pocos individuos muertos hallados en cada cuerda) se consideró como individuos desprendidos.

En cada muestreo la supervivencia se estimó como el promedio de las dos cuerdas correspondientes a cada serie experimental (ESD-400, ESD-700 y ECD-1.600 a los 3 meses; y ESD-400, ESD-700, ECD-400 y ECD-700 en los restantes muestreos). Con estos datos se calculó la supervivencia porcentual con respecto a las densidades iniciales correspondientes. A los tres meses y dentro de cada estrategia (en cada fecha de muestreo), se analizó la relación entre densidad inicial y porcentaje de supervivencia a través de una prueba de independencia $\chi2$ ($\alpha = 0,05$, Sokal y Rohlf 1995).

Para analizar la independencia entre las densidades iniciales y el porcentaje de supervivencia al momento de cosecha (nueve meses) entre todas las series experimentales (ESD y ECD), se estimó la probabilidad de supervivencia total correspondiente a cada serie experimental. Para esto, es necesario cuantificar la supervivencia total en la ECD cuando se consideran en conjunto la fase de pre-engorde y la fase de engorde. Por esta razón, se propuso un método teórico para calcular la probabilidad de supervivencia total en ambas experiencias. Desde este punto de vista, la probabilidad de supervivencia total se puede expresar como el producto de dos probabilidades: la probabilidad de sobrevivir a la fase de pre-engorde a una determinada densidad inicial y la probabilidad de sobrevivir a la fase de engorde a una determinada densidad inicial, dado que sobrevivió a la fase de pre-engorde. Por lo tanto, la probabilidad de sobrevivir a todo el proceso se define como:

$$P(ST) = P(F|B).P(B) \qquad (1)$$

donde $P(ST)$ es la probabilidad de supervivencia total (la probabilidad de supervivencia para todo el proceso); $P(B)$ es la probabilidad de sobrevivir a la fase de pre-engorde a una densidad inicial B; y $P(F|B)$ es la probabilidad de sobrevivir a la fase de engorde a una densidad inicial de engorde F condicionada a la fase de pre-engorde a una densidad inicial B.

En el caso de la ESD, $P(B) = 1$ ya que no se realizó desdoble y $P(F|B)$ es, en este caso, sólo la probabilidad de sobrevivir a la fase de engorde a una densidad inicial de engorde $F(P(F))$. Las probabilidades $P(F|B)$, $P(B)$ y $P(F)$ se estimaron a partir de los valores porcentuales de supervivencia observados. Con esta información se estimó el porcentaje de supervivencia total. La dependencia entre cada tipo de tratamiento y el porcentaje de supervivencia total obtenido se analizó a través de una prueba de independencia $\chi2$ ($\alpha = 0,05$).

Análisis de crecimiento

En cada fecha de muestreo, el tamaño promedio (talla y peso) asociado a cada densidad inicial se estimó como el promedio de las muestras correspondientes.

En el caso de la talla, y para las tres densidades determinadas al comienzo del experimento (ECD-1.600, ESD-400 y ESD-700), se analizaron si existían diferencias significativas en el crecimiento después de tres meses a través de un ANOVA de una vía con un test de Tukey *a posteriori* ($\alpha = 0,05$). Se testearon previamente los supuestos de normalidad y homocedasticidad a partir de una prueba de Shapiro-Wilks ($\alpha = 0,05$) y Bartlett ($\alpha = 0,05$), respectivamente. En las fechas de muestreo restantes se analizaron diferencias significativas en la talla dentro de cada estrategia (ESD y ECD) a través de una prueba t de Welsch (Sokal y Rohlf 1995), ya que todas las distribuciones de tallas resultaron normales Shapiro-Wilks ($\alpha = 0.05$) pero las varianzas presentaron heterogeneidad (Bartlett, $\alpha = 0,05$).

Para comparar la talla a los nueve meses entre las cuatro series experimentales, dado que las varianzas resultaron heterogéneas (prueba de Bartlett, $\alpha = 0,05$), se utilizó una prueba de Kruskal-Wallis para analizar si existían diferencias significativas, y una prueba *a posteriori* de Dunn con el ajuste por el método FWER (*Family-Wide Error Rate*) de Holm (α = 0,05) para analizar qué series experimentales diferían entre sí.

La existencia de diferencias significativas para el crecimiento en peso seco a los tres meses, en las tres densidades determinadas al comienzo del experimento, se analizó mediante una prueba de Kruskal-Wallis debido a que los datos resultaron no normales (Shapiro-Wilks, α = 0,05) y heterocedásticos (Levene, α = 0,05). Para determinar qué condición inicial presentaba el mejor rendimiento, se realizó una prueba *a posteriori* de Dunn con el ajuste por el método FWER (Family-Wide Error Rate) de Holm (α = 0,05).

En las fechas de muestreo restantes, dentro de cada estrategia, las diferencias significativas en los pesos secos se estudiaron mediante una prueba de Mann-Whitney para muestras no pareadas (Mann y Whitney 1947, α = 0,05), ya que no se cumplieron las hipótesis de normalidad (Shapiro-Wilks, α = 0,05) ni homogeneidad de varianzas (Levene, α = 0,05). Para comparar los pesos finales de las cuatro series experimentales entre sí, dado que las muestras presentaron distribuciones no normales (Shapiro-Wilks, α = 0,05) y varianzas heterogéneas (Levene, α = 0,05), se utilizó una prueba de Kruskal-Wallis para detectar diferencias significativas entre las distribuciones y un test *a posteriori* de Dunn, con el ajuste por el método FWER de Holm (α = 0,05), para analizar qué serie experimental presentaba el mejor resultado.

RESULTADOS

Variables ambientales

Las concentraciones de MOP registraron su menor valor (4,3 g m^{-3}) en julio de 2016 y los mayores valores se observaron hacia finales de la primavera, con un máximo en noviembre de 2016 (9,3 g m^{-3}). Para la Chl *a*, la menor concentración (1,55 mg m^{-3}) se observó en agosto de 2016. Durante los meses de primavera verano se observó un aumento en las concentraciones de Chl *a* con un máximo en noviembre de 2016 (9,23 mg m^{-3}).

La salinidad registró un valor máximo de 34,75 ppm en octubre de 2016 y un mínimo de 33,92 ppm en noviembre del mismo año. La temperatura registró su valor mínimo en agosto de 2016 con 7,48 °C y su máximo en febrero de 2017 con 16,77 °C (Tabla 1). La falta de datos en alguno de

Tabla 1. Variables ambientales recolectadas a lo largo de la experiencia.
Table 1. Environmental variables measured throughout the experience.

Mes	MOP (g m^{-3})	Chl *a* (mg m^{-3})	Salinidad (ppm)	Temperatura (°C)
Mayo	5,2	8,74	34,26	10,89
Junio	7,9	-	34,22	9,42
Julio	4,3	3,19	34,16	7,8
Agosto	5,15	1,55	-	7,48
Septiembre	7,46	1,93	34,15	9,43
Octubre	5,1	8,67	34,75	9,97
Noviembre	9,3	9,23	33,92	13,9
Diciembre	8,3	5,15	34,14	12,88
Enero	5,5	7,27	-	13,08
Febrero	4,4	4,68	34,07	16,77

los meses para alguna de las variables se debió a un error de calibración de la sonda o la falta de datos satelitales.

Experiencia de cultivo

Análisis de supervivencia

Del análisis de los datos de supervivencia mostró que el porcentaje de supervivencia después de tres meses fue independiente de las densidades iniciales (prueba de independencia $\chi 2$, $p > 0,05$, GL = 2) (Tabla 2).

En los restantes muestreos, dentro de la ESD se observó independencia entre las densidades iniciales y el porcentaje de supervivencia durante los dos primeros muestreos (3 y 6 meses, prueba de independencia $\chi 2$, $p > 0,05$, GL = 1). La supervivencia final mostró dependencia con respecto a las densidades iniciales (prueba de independencia $\chi 2$, $p < 0,0001$, GL = 1), presentando el mayor valor en la ESD-400 (77%). En los muestreos correspondientes a la ECD, se observó dependencia entre la densidad inicial y el porcentaje de supervivencia a lo largo de toda la experiencia (prueba de independencia $\chi 2$, $p < 0,05$, GL = 1), presentando la ECD-700 los mayores valores porcentuales de supervivencia. Estos porcentajes corresponden solo a la fase de engorde.

Tabla 2. Promedio y porcentaje de supervivencia en cada uno de los experimentos. Los porcentajes de supervivencia total considerando las fases de pre-engorde y engorde se muestran en negrita. Para cada fecha de muestreo, independencia entre densidad inicial y supervivencia dentro de cada estrategia se denota con la misma letra. Independencia entre estrategias y supervivencia se denota con * (prueba de independencia $\chi 2$, $\alpha = 0,05$). (#): porcentaje de supervivencia de la fase de engorde solamente.

*Table 2. Average and percentage of survival in each of the experiments. Percentages of total survival considering the pre-fattening and fattening phases are shown in bold. For each sampling date, independence between initial density and survival within each strategy is denoted with the same letter. Independence between strategies and survival is denoted with * (test of independence $\chi 2$, $\alpha = 0.05$). (#): percentage of survival of the fattening phase only.*

	Experiencia sin desdoble		Experiencia con desdoble	
3 meses	400 ind. m^{-1}	700 ind. m^{-1}	1.600 ind. m^{-1}	
Individuos vivos por cuerda	333	583,5	1.225	
Supervivencia porcentual	83,25%^{a,} *	83,36%^{a,} *	76,56%*	
6 meses	400 ind. m^{-1}	700 ind. m^{-1}	400 ind. m^{-1}	700 ind. m^{-1}
Individuos vivos por cuerda	338	520	289	653
Supervivencia porcentual	84,5%^{b}	74,29%^{b}	72,25% (#)	93,29% (#)
9 meses	400 ind. m^{-1}	700 ind. m^{-1}	400 ind. m^{-1}	700 ind. m^{-1}
Individuos vivos por cuerda	308,5	224	224	606
Supervivencia porcentual	77,13%	32%	56% (#)	86,57% (#)
Supervivencia porcentual total (fase de pre-engorde y fase de engorde)	**77,13%***	**32%**	**43%**	**66,2%***

Los datos de supervivencia total resultantes de la aplicación de la ecuación (1) muestran que en la ESD los porcentajes se mantuvieron en todo el experimento, ya que en esta estrategia no se realizó desdoble (Tabla 2). Por el contrario, en la ECD los porcentajes de supervivencia fueron inferiores a los obtenidos cuando solo se consideró la etapa de engorde. En este análisis, los mayores porcentajes de supervivencia se observaron en la ESD-400 (77%) y ECD-700 (66%), siendo estos resultados independientes de la estrategia seleccionada (prueba de independencia $\chi 2$, $p > 0,05$, GL = 1).

Análisis de crecimiento

El análisis a los tres meses (primer muestreo) mostró que casi todas las series experimentales (tanto en talla como en peso) difieren significativamente entre sí con una relación inversa entre las medias y/o distribuciones y las densidades iniciales (Tabla 3). Las excepciones se presentaron en la tallas correspondientes a ESD-400 y ESD-700 (Tukey *post-hoc*, $p > 0,05$), y en los pesos secos correspondientes a ESD-700 y ECD-1.600 (Kruskal-Wallis-Dunn *a posteriori*, $p > 0,05$, GL = 2).

Dentro de la ESD no se observaron diferencias significativas en la talla a los tres (Welch, $p > 0,05$, GL = 193,58) ni a los seis meses (Welch, $p > 0,05$, GL = 197,34) (Figura 2). En el último muestreo, la talla promedio en la ESD-400 presentó un valor de 66,58 mm, siendo este registro significativamente mayor al observado en la ESD-700 (Welch, p = 0,001, GL = 66,8). Además de presentar un tamaño promedio significativamente mayor, la ESD-400 registró también la menor dispersión de tallas al momento de la cosecha entre las cuatro series experimentales (s = 5,31). Para el peso seco dentro de esta estrategia, se observaron diferencias significativas a los tres (Mann-Whitney, p = 0,002) y a los nueve meses (Mann-Whitney, p = 0,0006) en favor de la ESD-400, la cual alcanzó al final de la experiencia un registro de 1,63 g (Figura 2).

En la ECD se observaron diferencias significativas en las tallas solo en la última fecha de muestreo (Welch, p = 0,0017, GL = 135,37) (Figura 3). El mayor crecimiento final se obtuvo en la ECD-400, con 62,53 mm. Para el caso del peso no se presentaron diferencias significativas en ningún momento después del desdoble (Mann-Whitney, $p > 0,05$) (Figura 3).

En la comparación de ambas estrategias al momento de cosecha, el mayor crecimiento en talla se observó en las cuerdas de la ESD, específicamente en la densidad más baja (400 ind. m^{-1}),

Tabla 3. Talla y pesos promedio con su error estándar. Para cada fecha de muestreo, diferencias no significativas dentro de cada estrategia se denota con la misma letra. Diferencias no significativas en la comparación entre estrategias se denotan con *.
*Table 3. Average size and weight with their standard error. For each sampling date, non-significant differences within each strategy are denoted with the same letter. Non-significant differences in the comparison between strategies are denoted with *.*

		Experiencia sin desdoble		Experiencia con desdoble	
		400 ind. m^{-1}	700 ind. m^{-1}	400 ind. m^{-1}	700 ind. m^{-1}
3 meses	Talla (mm)	41,06 (4,32)^{a}	39,98 (3,71)^{a}	37,78 (4,68)	
	Peso (g)	0,2332 (0,059)	0,208 (0,049)*	0,197 (0,09)*	
6 meses	Talla (mm)	50,82 (6,68)^{b}	50,36 (6,94)^{b}	44,16 (5,53)^{d}	43,93 (6,5)^{d}
	Peso (g)	0,8727 (0,25)^{c}	0,8124 (0,26)^{c}	0,6338 (0,19)^{e}	0,5817 (0,23)^{e}
9 meses	Talla (mm)	66,83 (5,31)	62,39 (8,03)*	62,53 (5.97)*	58,62 (8.88)
	Peso (g)	1,63 (0,47)	1,34 (0,465)*	1,17 (0.303)^{f,} *	1,15 (0,5)^{f,} *

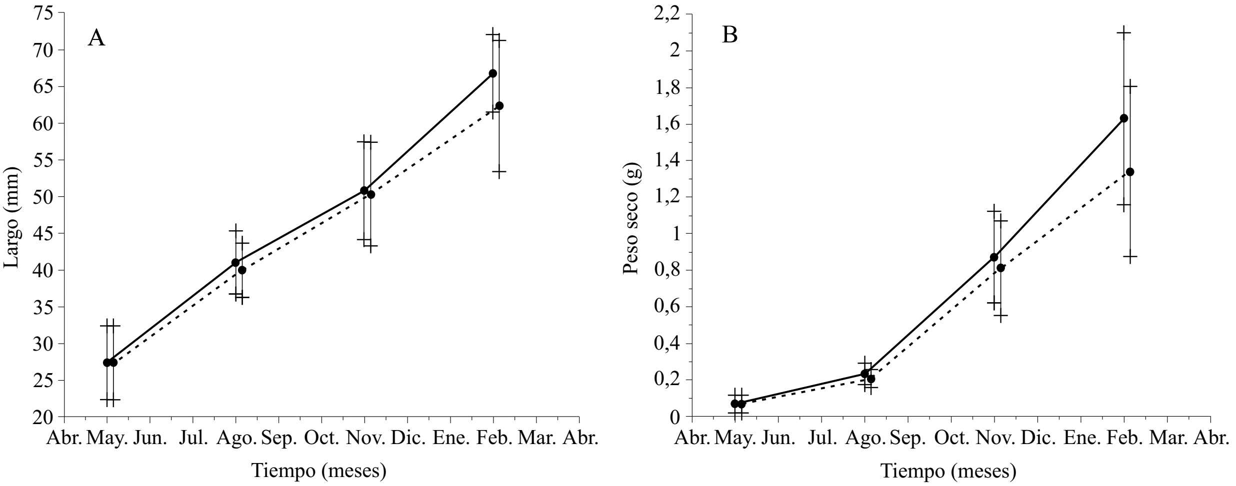

Figura 2. Evolución de crecimiento en ESD en talla (A) y peso seco (B) promedios. Línea continua: ESD-400. Línea punteada: ESD-700 (barras verticales: error estándar).

Figure 2. Evolution of growth in ESD in average size (A) and dry weight (B). Solid line: ESD-400. Dotted line: ESD-700 (vertical bars: standard error).

siendo este resultado significativamente mayor que las otras medias (Kruskal-Wallis, Dunn *a posteriori*, p < 0,05, GL = 3). El peso seco mostró la misma tendencia, con ESD-400 presentando el mayor peso final y diferencias significativas con las restantes observaciones (Kruskal-Wallis-Dunn *a posteriori*, p < 0,05, GL = 3).

DISCUSIÓN Y CONCLUSIONES

Los efectos de la densidad sobre los parámetro productivos generales han sido ampliamente estudiados en lugares donde el cultivo de mejillón se desarrolla de manera intensiva (Fuentes et al. 1992; Grant 1996; Fréchette y Bacher 1998; Alunno-Bruscia et al. 2000; Zaixso y Lizarralde 2001; Lauzon-Guay et al. 2005a, 2005b; Fréchette et al. 2010, 2011, 2013; Lachance-Bernard et al. 2010; Cubillo et al. 2012a; Bordon et al. 2014, entre otros).

En la Argentina, el desarrollo del cultivo intensivo del mejillón es aún una actividad pendiente. Los emprendimientos en la región costera del Golfo San Jorge son esporádicos, a baja escala y a densidades iniciales no reguladas sistemáticamente. En este contexto, el objetivo de este trabajo consistió en estudiar el engorde y la supervivencia en cultivos experimentales con y sin la práctica de desdoble, a dos densidades iniciales de engorde.

A lo largo de la experiencia se registraron dos picos de Chl *a*, a mediados otoño (mayo) y en primavera (octubre y noviembre). El valor máximo registrado de MOP se observó en el mes de noviembre. Las concentraciones de Chl *a* sufrieron marcadas disminuciones en los meses de invierno. Los valores máximos, tanto de Chl *a* como de MOP, se registraron en el mes de noviembre y estuvieron en concordancia con un marcado aumento de temperatura durante ese mes. Estos resultados fueron consistentes con otros estudios realizados en el área (Akselman 1996; Fernández et al. 2005, 2008; Carreto et al. 2007).

En términos generales, durante los primeros tres meses de cultivo (temporada de invierno en la región) todos los animales multiplicaron su peso promedio por tres, y su talla promedio por 1,5. Este desarrollo individual puede deberse al

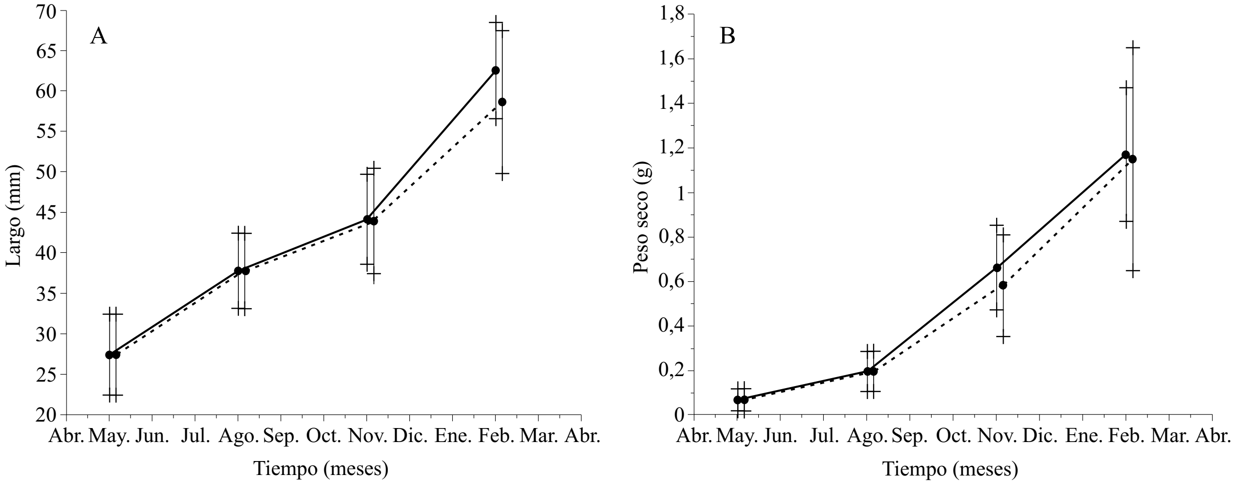

Figura 3. Evolución de crecimiento en ECD en talla (A) y peso seco (B) promedios. Línea continua: ECD-400. Línea punteada: ECD-700 (barras verticales: error estándar).
Figure 3. Evolution of ECD growth in average size (A) and dry weight (B). Solid line: ECD-400. Dotted line: ECD-700 (vertical bars: standard error).

estadío de vida de los animales dado que, al momento de siembra, los individuos eran juveniles (no más de 4 meses), una etapa en la que el crecimiento es muy marcado en cortos períodos de tiempo (Bayne 1976; Gosling 1992).

A los 6 meses (segundo muestreo), se registró un aumento en la temperatura y la cantidad de alimento disponible en la columna de agua (Chl *a* y MOP), asociado con la temporada de primavera y el comienzo del verano. Esta mejora en las condiciones está en concordancia con el desarrollo gonadal y la primera madurez sexual de los individuos informados en el área de estudio en esta época del año (Isola 2017), lo que explica el aumento de peso promedio observado de todos los animales. En el último trimestre del experimento, las condiciones ambientales favorables observadas en los meses de primavera-verano explicarían el aumento de talla y peso registrado.

El análisis de las diferentes estrategias de cultivo planteadas en la experiencia mostró que la estrategia sin desdoble a bajas densidades (ESD-400) brindó los mejores resultados en casi todas los parámetros de crecimiento estudiados. La supervivencia final presentó los valores más altos (77%), y tanto la talla (incremento de 39 mm) como el pesos seco (1,6 g en promedio) mostraron valores significativamente mayores a los obtenidos en las series experimentales restantes.

En un experimento de engorde similar (sin desdoble) realizado en España durante en el cultivo del mejillón *M. galloprovincialis* durante 12 meses*,* los animales alcanzaron tallas similares y valores de peso seco inferiores a los valores observados en este trabajo para ESD-400 (Pérez-Camacho et al. 2013). Cabe señalar que en el trabajo citado los mejillones se cultivaron a densidades más altas y por un período mayor que en este trabajo (9 meses).

Los animales, independientemente de la técnica utilizada, alcanzaron tallas promedios superiores a 58 mm al final de la experiencia. Sin embargo, la ESD-400 presentó la mayor talla promedio (66,58 mm) y el menor valor de dispersión (menor error estándar, s = 5,31). Estos valores sugieren un mejor crecimiento y tallas más uniformes al momento de la cosecha en esta serie experimental, a diferencia de lo observado en las restantes.

Diversas experiencias realizadas en la región patagónica muestran que el tiempo de cultivo requerido para alcanzar tallas superiores a 65 mm va de los 7 (Elvira et al. 2000) a los 9 meses (Bertolotti et al. 1987). El tiempo de cultivo observado en este trabajo (9 meses) es comparable a estos registros, y menor a lo generalmente empleado en otras partes del mundo (Uriarte 2008; Cubillo et al. 2012a; Díaz et al. 2019). Estos resultados muestran el potencial para el desarrollo del cultivo de mejillón en la región de estudio.

La densidad inicial óptima determinada en este trabajo es menor que la utilizada en países como Chile (Díaz et al. 2011) en el cultivo de mejillones del Género *Mytilus*, aunque similar a la utilizada en Brasil en el cultivo de mejillones del Género *Perna* (Bordon et al. 2014), y en el cultivo del mejillón *M. platensis*, en el Golfo San Matías, Chubut, Argentina (Pascual y Zampatti 1998; Elvira et al. 2000). Como consecuencia de la siembra a bajas densidades se reduce la competencia intraespecífica por alimento y espacio (Fréchette y Bacher 1998; Cubillo et al. 2012a), posibilitando un mayor desarrollo individual.

Los resultados de este trabajo muestran que la siembra de individuos de un tamaño de alrededor de 25 mm a una densidad inicial de 400 ind. m^{-1} a mediados de otoño (mayo en la región de estudio) permite obtener tamaño comercial al cabo de 9 meses. La densidad inicial, el crecimiento en talla y los tiempos requeridos para alcanzar estas tallas están dentro de los rangos observados en otras experiencias en la región patagónica (Bertolotti et al. 1987; Elvira et al. 2000). Sumado a esto, resultados de otras experiencias en la región mostraron que el cultivo por un período mayor a 12 meses genera pérdidas masivas debido al aumento de peso individual (Zaixso y Lizarralde 2001), estableciendo un período de cosecha que va de 9 a 12 meses desde la siembra de los animales.

Dado que en el área de estudio no existen emprendimientos continuos ni de gran escala, los resultados obtenidos en esta investigación constituyen una línea de base en relación a la evaluación de técnicas de manejo que permitan optimizar el crecimiento y la supervivencia. Se necesitarán futuros estudios, a una escala comercial, que contemplen parámetros productivos (rendimientos por metro de cuerda, índices de condición, diversos orígenes de la semilla, etc.) y aspectos ecosistémicos para determinar cómo el aumento en la escala de producción puede afectar la capacidad de carga del sistema (Ross et al. 2013). Sobre la base de los resultados del presente estudio, la estrategia de engorde sin desdoble a una densidad inicial de 400 ind. m^{-1} sería la recomendada para el cultivo de mejillón en la región, alcanzando una talla mayor a 66 mm al cabo de nueve meses de engorde y tallas más homogéneas al momento de la cosecha (menor error estándar observado). Por otra parte, el cultivo sin desdoble reduce las horas/hombre de trabajo (dado que no se practica desdoble). La información obtenida establece la estrategia de manejo adecuada y las densidades iniciales óptimas para maximizar el crecimiento y la supervivencia, generando conocimiento de base fundamental para futuros emprendimientos a mayor escala, contemplando el desarrollo sustentable de la actividad.

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MARCACIÓN Y RECAPTURA DEL GATUZO (*Mustelus schmitti*) EN EL ECOSISTEMA COSTERO BONAERENSE (ARGENTINA)

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RESUMEN. El presente trabajo está referido a los primeros resultados obtenidos sobre marcado y recaptura en el gatuzo, *Mustelus schmitti*, como medio para reconocer sus desplazamientos y migraciones en el Ecosistema Costero Bonaerense (ECB). Este tiburón es relevante no solo por su gran abundancia a lo largo del ECB sino también por su importancia comercial para la flota pesquera de arrastre argentina. Entre noviembre de 2010 y mayo 2011 se marcaron 2.483 ejemplares cerca de Monte Hermoso, dentro del sector marino conocido como "El Rincón", utilizando como plataforma una embarcación de la flota artesanal. Se logró recuperar 43 individuos entre 2010 y 2013. A partir del análisis de los individuos recapturados se señalaron los patrones de movimientos, migración, distribución espacial y temporal en el ECB, y además se discutieron y relacionaron dichos patrones con el ciclo de vida. Los resultados pusieron en evidencia la utilización por parte del gatuzo de áreas extensas, mayoritariamente costeras, sin alta afinidad con áreas particulares. Este es el modelo tradicional propuesto para tiburones pequeños como el gatuzo. Sin embargo, la modalidad reproductiva indicaría un ajuste al modelo señalado para grandes tiburones. Por lo tanto, el gatuzo en su comportamiento parece contener aspectos correspondientes a ambas modalidades con fidelidad por los sitios de reproducción pero sin evidencias de filopatría.

Palabras clave: Marcas convencionales, Mar Argentino, patrones de movimiento, gatuzo, *Mustelus schmitti*.

TAG-RECAPTURE OF THE NARROWNOSE SMOOTH-HOUND (*Mustelus schmitti*) IN BUENOS AIRES COASTAL ECOSYSTEM (ARGENTINA)

ABSTRACT. The present work refers to the first results obtained on tagging and recapture in the Narrownose smooth-hound, *Mustelus schmitti*, along the Coastal Ecosystem off Buenos Aires Province (BCE) with the aim of describing their migratory movements. This shark is relevant not only because of its high abundance throughout the BCE but also for its commercial significance for the Argentine trawling fishing fleet. Between November 2010 and May 2011 2,483 specimens were tagged in a marine sector known as "El Rincón", near Monte Hermoso (Buenos Aires Province), using an artisanal fishery vessel belonging to the local fleet as a platform. Fourty-three specimens were recaptured between 2010 and 2013. From the recapture data collected in this study, patterns of movement, migration, spatial and temporal distribution were established and related to the life cycle of the species. Our results evidenced that both juveniles and adults make extensive use of coastal areas, exhibiting low levels of phylopatry. This is the traditional model proposed for small sharks, such as the Narrownose smooth-hound. However, their reproductive aspects would indicate an adjustment to the model indicated for large sharks. Therefore, Narrownose smooth-hound behaviour would seem to include features corresponding to both modalities, i.e. with fidelity for the breeding sites albeit without evidence of phylopathy.

Key words: Conventional tags, Argentine Sea, movement patterns, Narrownose smooth-hound, *Mustelus schmitti*.

INTRODUCCIÓN

La utilización del marcado ha sido reconocida como un valioso procedimiento para estudiar distintos aspectos poblacionales (Hilborn y Walters 1992). Esto incluye desde movimientos y migraciones hasta la estimación de parámetros biológico-pesqueros como el tamaño poblacional, crecimiento somático, sobrevivencia y tasa de explotación (Brownie et al. 1985; Pollock et al. 1991; Hoenig et al. 1998a, 1998b). Existen distintos tipos de marcas, siendo las convencionales las más usadas dados su bajo costo y fácil aplicación. Las marcas convencionales se definen como aquellas que pueden identificarse visualmente en oposición a las que requieren algún otro tipo de instrumental para su utilización (marcas archivos, acústicas y satelitales). La utilización de dichas marcas es una técnica extendida internacionalmente para aportar información relativa a desplazamientos y migraciones (Kohler y Turner 2001).

Los escasos antecedentes disponibles sobre resultados de la aplicación de esta técnica en especies marinas de la Argentina están referidos casi exclusivamente a peces óseos. Como antecedentes en peces cartilaginosos pueden señalarse la marcación de gatuzo *Mustelus schmitti* Springer, 1939 y el cazón (*Galeorhinus galeus*), acotada a la zona de Bahía Anegada-San Blas (Cuevas et al. 2013), y de los actuales planes de marcación de grandes tiburones, principalmente para el moteado (*Notorynchus cepedianus*) y el cazón (Irigoyen et al. 2015). En este trabajo se eligió como especie objetivo al gatuzo por ser el tiburón más abundante y el de mayor interés comercial por parte de la flota pesquera argentina.

M. schmitti es un tiburón demersal-bentónico que alcanza una longitud máxima de 94 cm (Cousseau 1986; Menni et al. 1986; Cousseau y Perrotta 2013). Es una especie endémica del Atlántico Sudoccidental que se distribuye entre 22° S (Brasil) y 47° 45′ S (Argentina), desde zonas costeras hasta los 120 m de profundidad (Menni et al. 1986) (Figura 1). Al sur de los 34° S (límite entre Uruguay y Brasil) las principales concentraciones se encuentran en aguas de las plataformas argentina y uruguaya correspondientes a la Zona Común de Pesca Argentino-Uruguaya (ZCPAU), en aguas de jurisdicción provincial y en la plataforma bonaerense hasta los 42° S aproximadamente, por fuera de la ZCPAU (Figura 1). Esta especie es capturada principalmente por parte de la flota argentina (alrededor de 4.000 t anuales durante los últimos años) en la pesquería multiespecífica del área costera de la Provincia de Buenos Aires.

Aunque no se ha realizado aún una evaluación de *stock* formal de la especie para la totalidad de su área de distribución en la Argentina, a partir de 2011 y dentro del ámbito del área del Tratado del Río de la Plata y su Frente Marítimo, se han elaborado evaluaciones mediante modelos de producción excedente. Como resultado, las biomasas estimadas indicaron un decrecimiento sostenido (Cortés et al. 2016) y la biomasa total a comienzos de 2016 fue entre un 43% y un 64% menor con respecto al nivel correspondiente al año inicial del período de evaluación (1983). El gatuzo ha sido incorporado a la lista roja de la Unión Internacional para la Conservación de la Naturaleza (UICN 2015) como especie “en peligro”, con indicadores de disminución de la abundancia en su área de distribución, con un importante impacto por efecto de la pesca en aguas de Brasil y con la mención de la necesidad de entender sus patrones migratorios para sugerir medidas pertinentes de ordenación pesquera (Massa et al. 2006).

En trabajos previos, tanto a partir de datos biológicos colectados en campañas de investigación como los originados a partir de muestreos de los desembarques de las flotas comerciales, se han discutido e hipotetizado los potenciales desplazamientos del gatuzo vinculados con cambios estacionales de la estructura poblacional y de los parámetros reproductivos en la Argentina (Menni et al. 1986; Cousseau et al. 1998; Massa et al. 2004; Cortés et al. 2011), Uruguay (Oddone et al. 2007; Pereyra et al. 2008) y Brasil (Vooren 1997). En el marco del Programa "Pesquerías de Condrictios" del Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), se diseñó un plan para la utilización de la técnica de marcado y recaptura en el gatuzo con la finalidad de poder reconocer patrones de movimiento de la especie en el Ecosistema Costero Argentino-Uruguayo (Pérez y Massa 2011). El presente trabajo es una descripción de los resultados de dicho plan que también son los primeros disponibles para esta especie mediante la aplicación de la técnica de marcas convencionales. A partir de 2016, y con objetivos similares, se estableció en la ZCPAU un plan de marcación de gatuzo conjunto entre Argentina y Uruguay actualmente en desarrollo (Silveira et al. 2018).

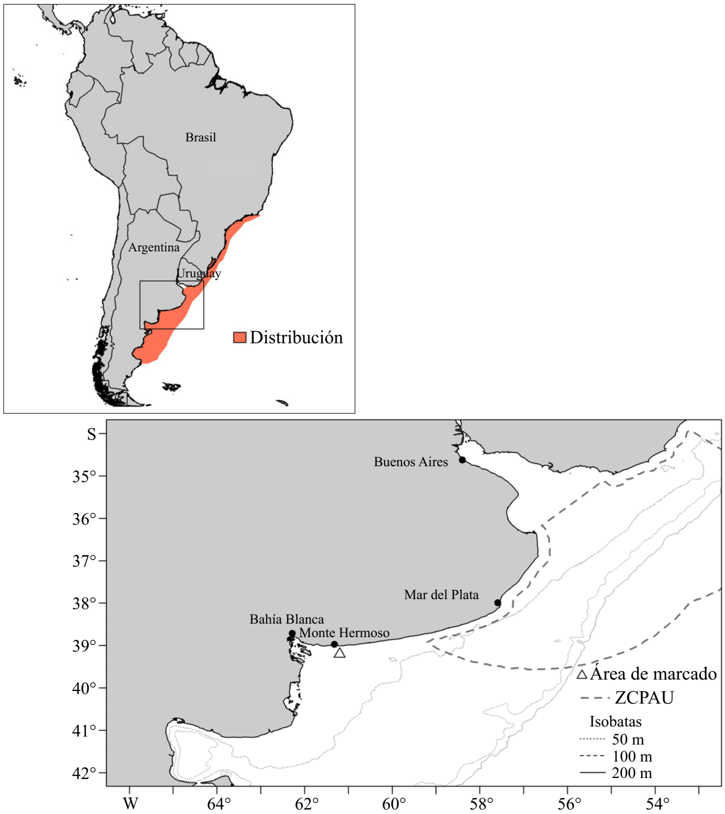

Figura 1. Distribución del gatuzo en el Atlántico Sudoccidental con detalle del área de trabajo en el litoral de la Provincia de Buenos Aires, Argentina. Zona de marcado de ejemplares de gatuzo (triángulo) frente a Monte Hermoso, Provincia de Buenos Aires, Argentina.

Figure 1. Narrownose smooth-hound distribution in the Southwestern Atlantic indicating the working area. Tagging area (triangle) in front of Monte Hermoso, Buenos Aires Province, Argentina.

MATERIALES Y MÉTODOS

Área de estudio

Características oceanográficas a lo largo de la costa de la Provincia de Buenos Aires

En esta zona la temperatura es función de la profundidad y de la latitud, con variaciones importantes en el plano vertical, mientras que la salinidad puede ser considerada como indicador más conservativo para caracterizar las distintas masas de agua presentes estacionalmente. Debido a esto, las masas de agua se clasificaron según su salinidad mediante el criterio de Lucas et al. (2005):

- Mínima salinidad debido a la descarga del Río de la Plata (0-33,0).
- Aguas características de baja salinidad de "El Rincón" (30,0-33,3).
- Máxima salinidad, aguas dentro y boca del Golfo San Matías (33,9-34,1) y área muy costera cercana al este de "El Rincón" (33,7-34,1).
- Aguas de plataforma continental (33,5-33,7).

Sistemas frontales

Acha et al. (2004) describieron los frentes presentes en el Mar Argentino y señalaron las características particulares de las áreas frontales del Río de la Plata y de "El Rincón". El primero está caracterizado por una fuerte estratificación vertical con agua de baja salinidad originada por la descarga del río en las capas más superficiales y el agua salada en las capas más profundas en forma de cuña. Se ubica al sur de Punta Rasa (Provincia de Buenos Aires) entre los 35° S y 37° S. El segundo corresponde al sur de la Provincia de Buenos Aires, en la costa de "El Rincón" (39° S a 41° S, profundidades menores a 40 m) con orientación norte-sur, y se caracteriza por tener aguas homogéneas verticalmente debido al forzante de las mareas, entre aguas diluidas correspondientes a los aportes de los ríos próximos (Negro y Colorado) por "dentro" (*inshore*) y aguas de alta salinidad originadas en el Golfo San Matías por "fuera" (*offshore*).

Ecosistema Costero Bonaerense

Está definido por el sector bonaerense desde la línea de costa hasta la isobata de 50 m de profundidad al este, y desde 34° S en el norte hasta los 42° S en el sur. Forma parte del mismo el área denominada "El Rincón" cuya delimitación aproximada es entre 38° 40′ S y 41° S. En este ecosistema la fauna presenta características propias que en el caso de los peces está dominada por los sciénidos y otras especies (algunas de peces cartilaginosos como el gatuzo) que desde un punto de vista comercial u operativo se conoce como "variado costero", sobre el cual desarrolla sus actividades la flota pesquera costera fresquera marplatense (Lasta et al. 2001).

Marcación de ejemplares y variables consideradas

Entre noviembre de 2010 y diciembre de 2011 se marcaron 2.483 ejemplares de gatuzo mayores de 50 cm de longitud total, mediante marcas convencionales tipo DART (*Hallprint*, *PDS small plastic tipped tags*) con "cabeza" de plástico con un largo del tubo de 10 cm. La metodología y proceso de marcación en Monte Hermoso (Provincia de Buenos Aires, Argentina), en conjunto con el plan de divulgación para la recuperación de marcas, fueron presentados en Pérez et al. (2014). En ese trabajo también se describen las cuestiones operativas inherentes al proceso de marcado, la descripción del origen de los reportes de ejemplares marcados, el criterio de asignación de posiciones (criterio de mínima distancia) y fechas de recapturas mediante la utilización de los Partes de Pesca en los que se detectaron marcas en las plantas de procesamiento de pescado.

La marcación se realizó en cuatro campañas o comisiones realizadas en noviembre de 2010

(1.199 individuos marcados) y en marzo, mayo y diciembre de 2011 (599, 550 y 135 individuos marcados respectivamente). De la totalidad de los ejemplares marcados se dispuso del número de identificación de la marca (Nro_marca), la fecha en el que fue marcado como el día, mes y año (Comisión: mes y año), la longitud total (talla_cap_cm, variable continua), la posición de marcado (Latitud y Longitud) y el sexo (Tabla 1).

Hasta diciembre de 2012 se habían recuperado 42 marcas. Luego en 2013 fue declarada una marca adicional, por lo que el número total de ejemplares recapturados fue de 43. No hubo nuevos reportes con posterioridad. De este total, 3 ejemplares no fueron considerados para este análisis debido a la carencia de las posiciones en las declaraciones de recapturas respectivas. Por lo tanto, la base de datos a analizar fue construida con 40 ejemplares (Tabla 1). De cada ejemplar recapturado se obtuvo: la posición asignada a cada recaptura (Latitud y Longitud), el origen de la declaración de la recaptura (Origen_recaptura y origen_declar), la fecha asignada y el mes de recaptura (mes_recaptura) (Tabla 1). A partir de estos datos se estimaron las siguientes variables: el tiempo de recaptura expresado en días (Tiempo_recaptura_días, variable continua), el rumbo verdadero (rumbo, variable continua) expresado en grados (de 0, rumbo Norte, a 360) y la distancia (distancia, variable continua expresada en millas náuticas) entre las posiciones de marcado y de recaptura estimados mediante las funciones *bearingRhumb* y *distrumb* del entorno estadístico R (v 3.0.2) (R Core Team 2013) (Tabla 1). Además, la profundidad asignada a cada posición de recaptura (Profundidad, variable continua) en metros obtenida de una base de datos internacional (Becker et al. 2009; Scripps 2014). Por otra parte, la velocidad de natación fue estimada como la distancia entre la posición de marcación y la de recaptura, dividida por el tiempo en libertad.

Mediante el test de Kolmogorov-Smirnov (KS) se compararon las tallas al momento del marcado, entre los individuos que fueron y no fueron recapturados. El test de *Chi* cuadrado se utilizó para evaluar las diferencias en la proporción de sexos del total de los individuos recapturados. Con el test espacial de Rao (1967) se evaluó la uniformidad en la distribución de las direcciones de desplazamiento o si existió alguna direccionalidad sesgada, al utilizar Estadística Circular Estándar (Zar 1999), mediante el mismo entorno estadístico R.

Se consideró la temperatura superficial correspondiente al día y posición de marcación y de recaptura (ssts_marcado y ssts_recap, variables continuas) con las que también se estimó la diferencia entre ambas (gradiente de temperatura, gradtemp, variable continua), disponibles en la base de datos de la agencia gubernamental NOAA de EE. UU. (NOAA 2014) (Tabla 1). Para la caracterización de las masas de agua presentes en la zona se estimó la salinidad de superficie (sal_recap, variable continua) como un promedio histórico mensual en una grilla de 0,5° de Latitud y Longitud que incluyó las posiciones y el mes de cada recaptura correspondientes a observaciones realizadas en campañas de investigación del INIDEP (INIDEP 2015). Dada la proximidad a la costa y a la falta de observaciones en algunos meses del año, no pudo asignarse un valor de salinidad a tres marcas recuperadas, por lo tanto se la consideró solo en la discusión.

Las relaciones entre las variables estimadas a partir del marcado y recaptura (Tabla 1) se presentan en la Figura 2. Para detectar posibles relaciones (agrupamiento) entre los individuos recuperados se realizaron análisis multivariados: Agrupamiento Jerárquico Aglomerativo (Análisis de *cluster*, *agglomerative hierarchical clustering*) y Análisis de Componentes Principales (ACP). En ambos fueron consideradas como variables continuas el gradiente de temperatura (gradtemp), el tiempo de recaptura, el rumbo, la profundidad y la distancia. El Agrupamiento Jerárquico Aglomerativo fue realizado mediante la distancia euclídea con las variables estandarizadas y el promedio como enlace mediante la función *agnes* del

Tabla 1. Variables analizadas a partir del marcado y recaptura. Comisión: mes correspondiente a la marcación, ssts_marcado: temperatura superficial (°C) en la posición de marcado, ssts_recap: temperatura superficial (°C) de la posición asignada a cada recaptura, Tiempo_recaptura_días: tiempo de permanencia (días) en el mar de cada ejemplar marcado, rumbo: rumbo (°) entre posición de marcado y la asignada a cada recaptura, distancia: distancia (mn) punto a punto entre ambas posiciones sin considerar trayectorias, Profundidad: profundidad (m) correspondiente a la recaptura a partir de base de datos internacional, talla_cap_cm: talla correspondiente a cada ejemplar al momento de la marcación, origen_declar: variable categórica adjudicada a cada forma de declaración de cada marca, mes_recaptura: mes correspondiente con la fecha asignada a cada recaptura, sal_recap: salinidad superficial asignada a la posición de recaptura.

Table 1. Variables analyzed from tagging and recapture. Comisión: tagging month, ssts_marcado: surface temperature (°C) in the tagging position, ssts_recap: surface temperature (°C) at recapture position, Tiempo_recaptura_días: time (days) in liberty, rumbo: course (°) between the tagging and each assigned recapture positions, distancia: distance (nautical miles) point-to-point between the two positions without considering trajectories, Profundidad: depth (m) corresponding to the recapture from international database, talla_cap_cm: size corresponding to each specimen at tagging time, sexo: sex, origen_declar: categorical variable to each form of tags declaration, mes_recaptura: month corresponding to the date assigned to each recapture, sal_recap: surface salinity assigned to the recapture position.

Nro_marca	Comisión	ssts_marcado	ssts_recap	Tiempo_recaptura_días	Origen_recaptura	rumbo	distancia	Profundidad	talla_cap_cm	sexo	origen_declar	mes_recaptura	sal_recap
104	mar-11	20,31	11,64	207	Acopiador MH	93,55	30,51	-11	62	2	4	10	33,98
147	mar-11	20,31	18,47	13	Pescador artesanal MH	237,47	6,82	-6	57	1	4	4	34,26
160	mar-11	20,31	18,90	7	Planta Pesquera 1	62,80	257,38	-21	50	2	3	3	32,79
222	mar-11	20,31	13,06	212	Acopiador MH	239,69	43,23	-2	55	2	4	10	32,88
223	mar-11	20,31	12,66	202	Planta Pesquera 2	63,68	274,96	-28	56	1	3	10	29,38
282	mar-11	20,31	17,08	27	Pescador deportivo	265,98	18,63	-7	61	2	1	4	34,74
294	mar-11	20,31	20,01	2	Pescador artesanal MH	268,46	17,55	-7	63	2	4	3	33,73
298	mar-11	20,31	18,47	13	Pescador artesanal MH	246,85	6,43	-6	51	1	4	4	34,26
310	mar-11	20,31	19,16	239	Acopiador MH	244,62	21,62	-10	56	1	4	11	32,99
346	mar-11	20,30	19,67	5	Pescador artesanal MH	249,96	10,43	-6	67	2	4	3	33,66
351	mar-11	20,30	19,04	20	Planta Pesquera 1	121,26	11,48	-10	56	2	3	4	34,19
388	mar-11	20,30	15,37	37	Pescador artesanal MH	260,71	14,87	-8	53	1	4	4	34,26
396	mar-11	20,30	17,00	34	Planta Pesquera 3	73,54	166,56	-20	63	1	3	4	33,70
402	mar-11	20,30	15,37	37	Pescador artesanal MH	260,09	14,78	-8	60	1	4	4	34,26
408	mar-11	20,30	19,94	602	Filetero	277,81	54,19	-6	55	1	2	11	NA
425	mar-11	20,30	12,66	201	Planta Pesquera 2	63,26	270,93	-28	57	1	3	10	29,38
493	mar-11	20,30	19,17	9	Planta Pesquera 1	82,05	46,78	-18	59	1	3	4	34,70
538	mar-11	19,60	19,17	5	Planta Pesquera 1	82,68	51,22	-18	51	1	3	4	34,70
604	mar-11	19,60	15,37	33	Pescador artesanal MH	255,38	9,93	-8	75	2	4	4	34,26
734	may-11	14,28	14,65	173	Pescador artesanal MH	243,47	36,66	-2	49	2	4	11	32,99
769	may-11	14,28	8,64	100	Pescador artesanal MH	263,26	20,99	-8	63	2	4	8	33,21
779	may-11	14,31	10,33	752	Pescador artesanal MH	266,53	28,27	-9	51	1	4	6	35,75
834	may-11	14,28	14,65	173	Pescador artesanal MH	242,24	37,22	-2	54	1	4	11	32,99
932	may-11	14,28	21,53	313	Pescador artesanal MH	312,47	4,83	-8	51	1	4	3	33,66
953	may-11	14,28	15,17	14	Planta Pesquera 2	64,14	283,32	-39	52	1	3	5	33,68
978	may-11	14,28	14,65	173	Pescador artesanal MH	240,57	38,32	-2	57	2	4	11	32,99
986	may-11	14,28	14,65	173	Pescador artesanal MH	240,57	38,32	-2	57	2	4	11	32,99
1073	may-11	14,49	11,13	90	Planta Pesquera 2	64,21	283,54	-39	48	1	3	8	33,18
1210	may-11	14,49	14,33	12	Planta Pesquera 2	165,70	121,06	-69	51	2	3	5	NA
1279	nov-10	15,91	19,15	20	Planta Pesquera 1	59,47	289,67	-23	61	1	3	11	30,24
1415	nov-10	15,91	17,18	172	Pescador artesanal MH	80,82	22,37	-10	53	1	4	4	34,19
1517	nov-10	15,93	19,07	32	Pescador artesanal MH	38,34	1,56	-10	55	2	4	12	33,80
1608	nov-10	15,93	16,92	156	Planta Pesquera 1	66,01	189,52	-8	53	2	3	4	NA
1754	nov-10	15,93	17,77	12	Pescador artesanal MH	275,85	6,60	-6	56	2	4	11	33,72
1990	nov-10	15,93	15,17	189	Planta Pesquera 2	63,85	278,28	-39	65	1	3	5	33,68
2020	nov-10	16,20	15,75	7	Pescador deportivo	77,52	37,83	-2	78	1	1	11	33,45
2026	nov-10	16,20	14,65	347	Pescador artesanal MH	241,37	43,00	-2	68	1	4	11	32,99
2074	nov-10	16,20	12,66	326	Planta Pesquera 2	63,36	275,20	-28	59	2	3	10	29,38
2188	nov-10	16,20	18,40	16	Pescador artesanal MH	263,33	7,51	-5	60	2	4	12	33,80
2426	nov-10	16,20	16,49	10	Planta Pesquera 1	64,36	219,24	-19	61	1	3	11	32,57

Figura 2. Relaciones entre variables estimadas a partir del marcado y recaptura. Comisión: mes correspondiente a la marcación, ssts_marcado: temperatura superficial (°C) en la posición de marcado, ssts_recap: temperatura superficial (°C) de la posición asignada a cada recaptura, Tiempo_recaptura_días: tiempo de permanencia (días) en el mar de cada ejemplar marcado, rumbo: rumbo (°) entre posición de marcado y la asignada a cada recaptura, distancia: distancia (mn) punto a punto entre ambas posiciones sin considerar trayectorias, Profundidad: profundidad (m) correspondiente a la recaptura a partir de base de datos internacional, talla_cap_cm: talla (cm) correspondiente a cada ejemplar al momento de la marcación, sexo, origen_declar: variable categórica adjudicada a cada forma de declaración de cada marca, mes_recaptura: mes correspondiente con la fecha asignada a cada recaptura, sal_recap: salinidad superficial asignada a la posición de recaptura.

Figure 2. Relationships between variables estimated from the mark-recapture. Comisión: tagging month, ssts_marcado: surface temperature (°C) in the tagging position, ssts_recap: surface temperature (°C) recapture position, Tiempo_recaptura_días: time (days) in liberty, rumbo: course (°) between the tagging position and the one each recapture assigned, distancia: distance (nautical miles) point-to-point between the two positions without considering trajectories, Profundidad: depth (m) corresponding to the recapture from international database, talla_cap_cm: size (cm) corresponding to each specimen at tagging time, sex, origen_declar: categorical variable to each form of tags declaration, mes_recaptura: month corresponding with the date assigned to each recapture, sal_recap: surface salinity assigned to the recapture position.

paquete de programas estadísticos R (R Core Team 2013). El ACP fue realizado mediante la función *prcomp* del mismo programa con las variables logaritmizadas (logaritmo natural, aunque en todos los casos expresadas como *log*) y estandarizadas. Aunque correlacionadas, se conservaron la profundidad, el rumbo y la distancia, relevantes para la descripción de los desplazamientos. La talla correspondió a la estimada al momento del marcado, ya que en la mayoría de los casos no se la declaró con la recaptura. Por lo tanto, no se la consideró para estos análisis, pero sí se la incluyó luego en la discusión. De todas maneras, la talla no se correlacionó con ninguna de las variables restantes (Figura 3).

Se construyó un Modelo Líneal Generalizado (MLG) con distribución lognormal del término de error, con la distancia como variable respuesta y como explicativas, el resto de las consideradas en los análisis anteriores. Fueron logaritmizadas las variables continuas Tiempo_recaptura_días y talla_cap_cm. Profundidad y rumbo no fueron incorporadas debido a las correlaciones detectadas entre estas y la variable respuesta. Además de los factores sexo y mes_recaptura, se incorporó también el mes_marcado equivalente a la variable Comisión (Tabla 1). Este modelo también fue construido mediante el paquete de programas estadísticos R (R Core Team 2013). El MLG diseñado fue:

$$\begin{aligned}\log(\mathit{dis}\text{tancia}_i) = \mu &+ \mathit{sexo}_i + \mathit{mes\_marcado}_i \\ &+ \mathit{mes\_recaptura}_i + \mathit{gradtemp}_i \\ &+ \log(\mathit{Tiempo\_recaptura\_días}_i) \\ &+ \log(\mathit{talla\_cap\_cm})_i + \varepsilon_i\end{aligned}$$

donde:

$\log(\mathit{dis}\text{tancia}_i)$ = logaritmo natural de la distancia (mn) entre la posición de marcado y la asignada de recaptura para cada individuo *i*;
μ = constante del modelo;
ε_i = término de error del modelo.

Tiempos de permanencia

En aquellos casos cuya recaptura se produjo en rumbos menores a 122°, y para evitar sesgos en las trayectorias punto a punto que podrían atravesar partes terrestres, se las forzó a pasar por dos posiciones arbitrarias. La primera fue 39° S-59° W considerada como la primera posición dentro de la Zona Común de Pesca Argentino-Uruguaya (ZCPAU). La restante fue un punto al sur de la ciudad de Mar del Plata (38° 30′ S-57° 24′ W) para permitir "girar" las trayectorias debido a la forma de la costa de la Provincia de Buenos Aires. En función de este criterio se estimaron nuevamente las distancias correspondientes a los 18 ejemplares recapturados en este rango de rumbos, dentro y fuera de la ZCPAU. Luego las distancias se consideraron proporcionales al tiempo de recaptura.

RESULTADOS

Desplazamientos, distribución espacial y temporal a partir de la recaptura de ejemplares marcados

Debido a las dificultades propias del método de marcado con marcas convencionales, es decir, la posibilidad de pérdida inmediata de marcas, la falta de reportes de marcas recuperadas y los efectos de las mortalidades naturales y por pesca, los modelos fueron ajustados con los individuos recapturados (McGarvey y Feenstra 2002). El test de KS manifestó una diferencia ($p = 2{,}44\ 10^{-7}$) entre la distribución de tallas al momento de la marcación de los individuos recapturados (40 individuos) respecto de aquellos no recapturados (2.483 individuos). Esto fue debido posiblemente al bajo número de recapturas. Por lo tanto, como aporte, los análisis se realizaron bajo el supuesto de representatividad de los individuos recapturados.

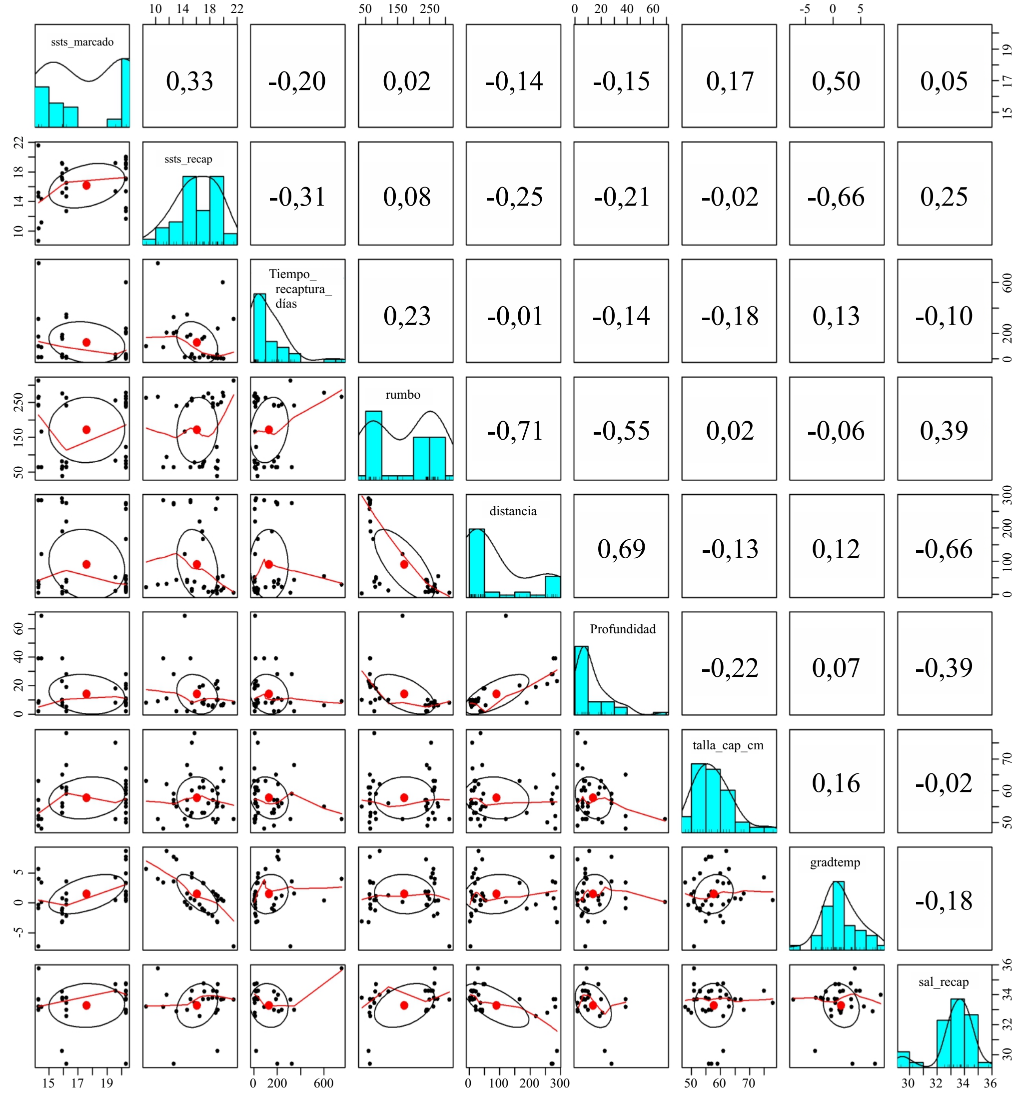

Figura 3. Distribución y correlaciones entre las variables continuas disponibles en la base de datos. Ssts_marcado: temperatura (°C) superficial posición de marcado, ssts_recap: temperatura (°C) superficial de la posición asignada a cada recaptura, Tiempo_recaptura_días: tiempo de permanencia en el mar de cada ejemplar marcado, rumbo: rumbo (°) verdadero entre posición de marcado y la asignada para cada recaptura, distancia: distancia (mn) punto a punto entre ambas posiciones sin considerar trayectorias, Profundidad: profundidad (m) correspondiente a la recaptura obtenida a partir de base de datos internacional, talla_cap_cm: talla correspondiente a cada ejemplar al momento de la marcación, gradtemp: diferencias entre la temperatura (°C) asignada a la posición de marcado y la correspondiente a la recaptura, sal_recap: salinidad superficial asignada a la posición de recaptura.

Figure 3. *Distribution and correlations between continuous variables available in the database. Ssts_marcado: surface temperature (°C) in the tagging position, ssts_recap: surface temperature (°C) recapture position, Tiempo_recaptura_días: time (days) in liberty, rumbo: course (°) between the tagging position and the one each recapture assigned, distancia: distance (nautical miles) point-to-point between the two positions without considering trajectories, Profundidad: depth (m) corresponding to the recapture from international database, talla_cap_cm: size corresponding to each specimen at tagging time, gradtemp: differences between the temperature (°C) assigned to the position of tagging and the corresponding to the recapture, sal_recap: surface salinity assigned to the recapture position.*

Hubo recapturas en 8 meses del año (marzo, abril, mayo, junio, agosto, octubre, noviembre y diciembre) aunque la mayor proporción correspondió a los meses de primavera (18, entre octubre y diciembre) y otoño (19, entre marzo y mayo) (ver Figura 2). En invierno (agosto) se recapturaron 2 individuos. No hay una clara relación entre el momento de marcación, el mes de recaptura y el rumbo respecto del tiempo en libertad transcurrido. Tampoco entre estas últimas variables con la talla y el sexo de los ejemplares.

Las posiciones de recaptura de los 40 individuos marcados en Monte Hermoso en noviembre de 2010, marzo y mayo de 2011, objeto de este análisis, abarcaron el área costera, al este de Cabo San Antonio, hasta la boca del Golfo San Matías, aproximadamente entre 36° 30′ S y 41° 10′ S (Figura 4). Las profundidades correspondientes a las posiciones de las recapturas fueron estimadas entre 2 (cercanas a la línea de costa) y 69 m, esta última correspondiente al individuo recapturado frente a la boca del Golfo San Matías. Puede observarse también que, con excepción del último individuo mencionado, el resto (39 individuos) fue recapturado en profundidades menores a 50 m.

De los 40 individuos recapturados, 11 (27,5%) lo fueron al norte o en zonas cercanas a la ciudad de Mar del Plata (Zona Norte) (Figura 4). El resto lo fue en áreas cercanas a Monte Hermoso (Zona Sur), un caso dentro de la Ría de Bahía Blanca y un caso frente a la boca del Golfo San Matías (Figura 4). El número y el porcentaje del total de las recapturas también se estimó considerando como unidad espacial el rectángulo estadístico de un grado de Latitud por uno de Longitud (RE) (Tabla 2). El RE con mayor número de recapturas (21; 52,5 % del total) fue el 3961 dentro de la Zona Sur (“El Rincón”). El siguiente en cuanto a las recapturas fue el 3960 (3; 7,5%). En el norte, fueron el 3655 (4; 10%) y el 3755 (3; 7,5%) (Figura 5).

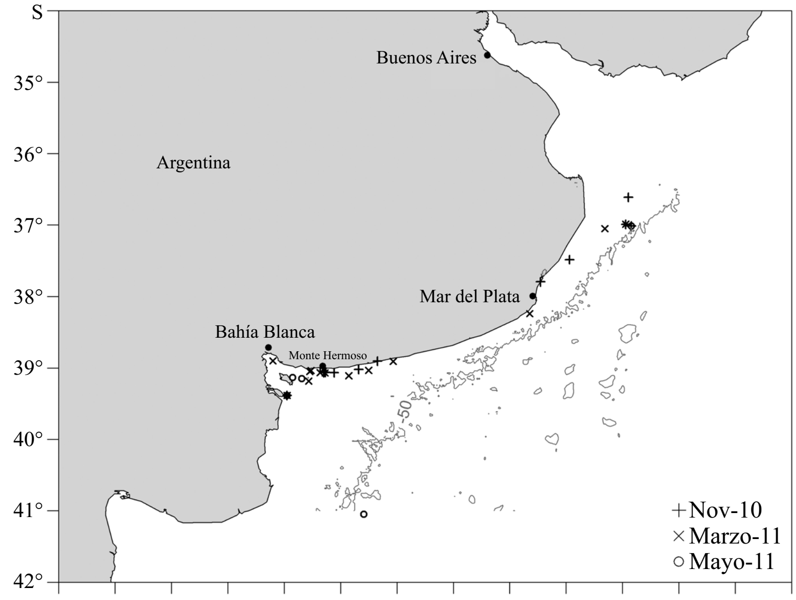

Figura 4. Posiciones asignadas a cada recaptura según el mes de marcación, noviembre de 2010 (Nov-10), marzo de 2011 (Marzo-11) y mayo de 2011 (Mayo-11). La línea continua gris representa la isobata de 50 m de profundidad.

Figure 4. *Positions assigned to each recapture according to the tagging month, November 2010 (Nov-10), March 2011 (Marzo-11) and May 2011 (Mayo-11). The solid gray line represents the 50 m isobath.*

Tabla 2. Número y porcentaje de individuos recapturados totales por rectángulo estadístico de un grado de Latitud por uno de Longitud (RE).

Table 2. Number and percentage of total recaptured individuals by statistical rectangle of one degree of Latitude by one of Longitude (RE).

RE recaptura	Número de recapturas	% recapturas
3655	4	10,0
3755	3	7,5
3756	2	5,0
3757	1	2,5
3857	1	2,5
3860	3	7,5
3862	1	2,5
3960	3	7,5
3961	21	52,5
4160	1	2,5
Total	40	100,0

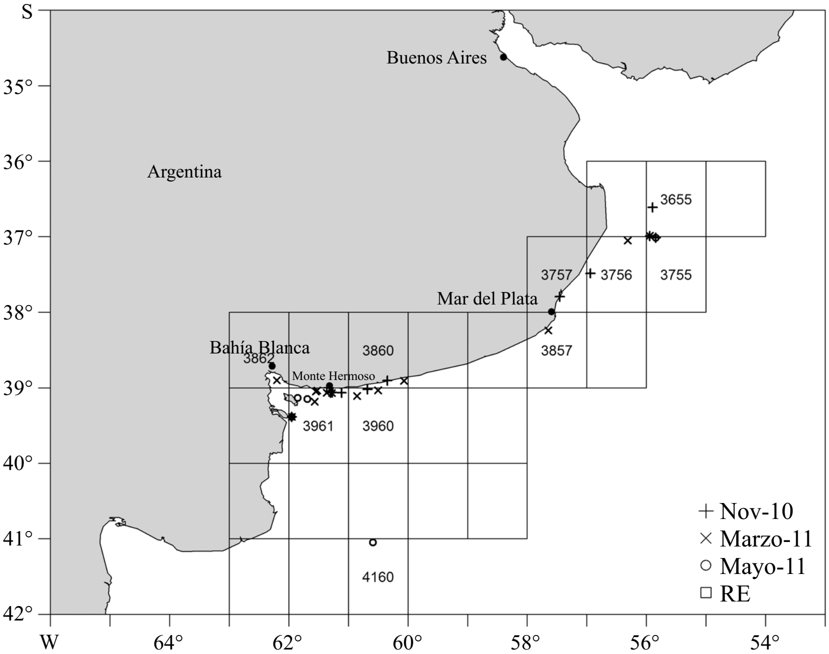

Figura 5. Posiciones de recapturas por rectángulo estadístico (RE) según el mes de marcación. Los RE sin recapturas figuran en blanco.

Figure 5. Positions of recaptures by statistical rectangle (RE) according to the tagging month. The RE without recaptures are contained in white.

Existen principalmente dos tendencias mayoritarias en los rumbos; menores a 100° (con mayoría de valores entre 50° y 100°), y aquellos entre 225° y 300° (Figura 6). En función de este criterio se calcularon los promedios de 68,5° (rumbo ENE) y 254° (rumbo OSO). De los 40 individuos recapturados, 17 (43%) correspondieron a rumbos promedio ENE. 20 individuos (50%) fueron recapturados con rumbo OSO y los tres ejemplares restantes lo fueron en otros rumbos.

El rango de distancias de recaptura, estimadas punto a punto entre la posición de marcado y la de recaptura, fue entre 1,56 y 289,67 mn, equivalentes a 2,89 y 536,46 km, respectivamente. Las mayores distancias correspondieron a rumbos ENE, aunque estuvieron subestimadas debido a la imposibilidad de determinar la trayectoria de cada ejemplar entre el lugar de marcación y las posiciones de recapturas correspondientes a la Zona Norte, ya que necesariamente los individuos debieron ir hacia el este y "rodear" la costa de la provincia de Buenos Aires. Con una trayectoria supuesta, considerando una poligonal entre la posición de marcado, el extremo este de la provincia como punto geográfico y las posiciones de recaptura, la mayor distancia estimada fue 580 km.

Los tiempos de recaptura variaron entre 2 y 752 días. Hasta los 400 días se recapturaron ejemplares en ambos rumbos promedio. Los dos ejemplares con mayores tiempos de recaptura (602 y 752 días) fueron machos, cuyas distancias de recapturas fueron menores a 55 mn, con posiciones que correspondieron a rumbos OSO (Figura 7).

Para conocer el potencial efecto del momento de la marcación (noviembre 2010 y marzo y mayo 2011) respecto de las posiciones y tiempos de recaptura, se graficaron los tiempos de recaptura expresados en días correspondientes a los individuos marcados en noviembre de 2010 (Figura 8 A). Se recapturaron individuos en un

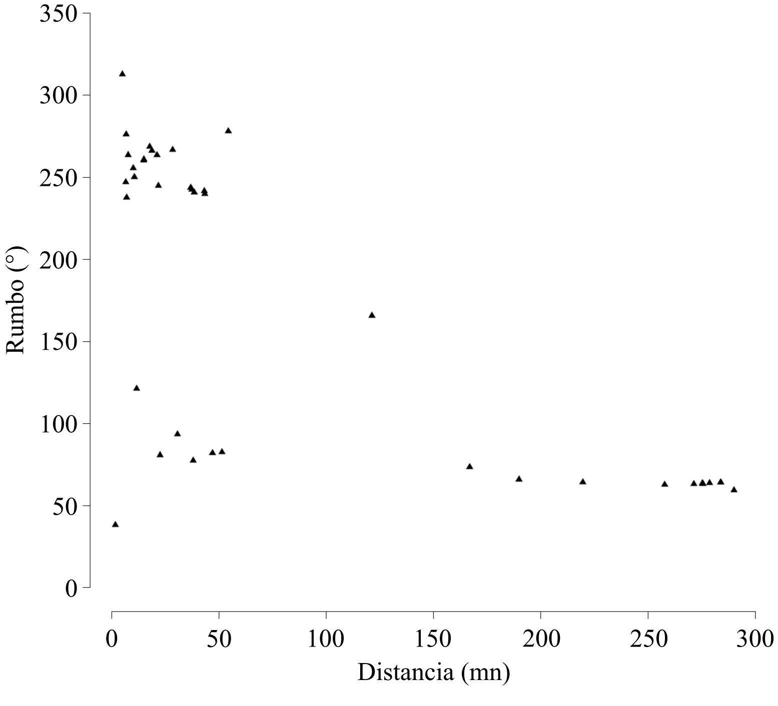

Figura 6. Relación entre el rumbo y la distancia. Ambas estimaciones consideradas entre la posición de marcado y recaptura.
Figure 6. Relationship between the course and the distance. Both estimates considered between the tagging and recapture position.

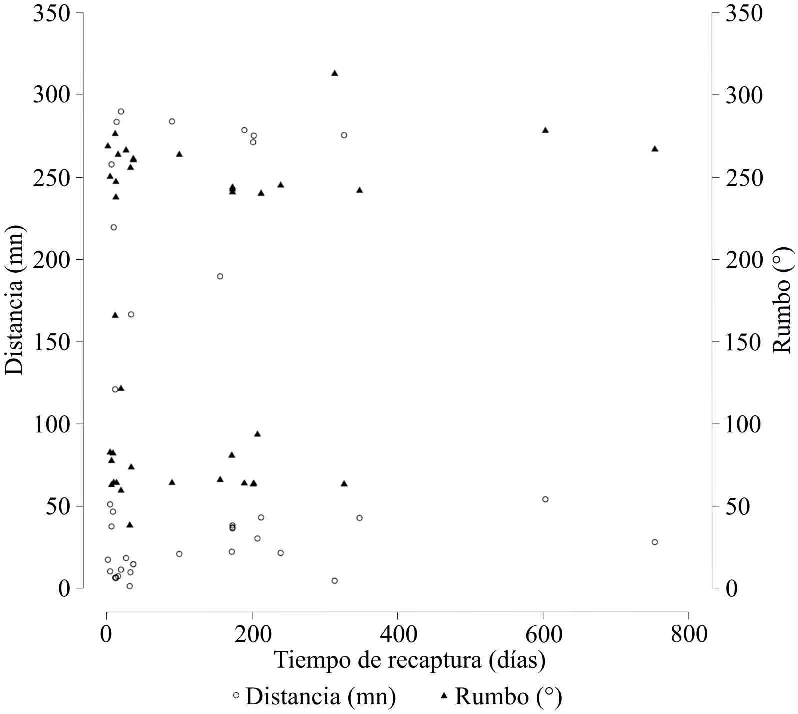

Figura 7. Distancia y rumbo (eje secundario), entre la posición de marcado y recaptura, versus tiempo de recaptura.
Figure 7. Distance (mn) and course (secondary axis), between the tagging and recapture position, versus recapture time.

rango de 7 a 347 días de permanencia en libertad. Existieron casos con pocos días (entre 7 y 32) y con muchos (más de 100) recapturados tanto al norte de Mar del Plata como en la zona cercana a Monte Hermoso. Para los marcados en marzo de 2011, se observa un patrón similar (Figura 8 B). Los tiempos de recaptura fueron entre 2 y 602 días similares en ambas zonas. Los marcados en mayo 2011 presentan la misma tendencia que en los casos anteriores, se observan dos ejemplares con características particulares, uno con el mayor tiempo de recaptura (752 días) y el único ejemplar recapturado frente al norte del Golfo San Matías con 12 días de permanencia en libertad (Figura 8 C).

Respecto de la velocidad de natación, para disminuir la variabilidad debido a la imposibilidad de medir la trayectoria en aquellos casos de recapturas al norte o frente a la costa de Mar del Plata, la estimación de velocidades se realizó sin ellos (subconjunto remanente de 29 individuos). En este subconjunto, el rango de velocidades estuvo comprendido entre 0,03 y 19 km día^{-1}, con un promedio de 3,1 km día^{-1}. Sin embargo, en dos casos con los menores tiempos de recaptura (2 y 7 días) que fueron considerados de alta confiabilidad en la declaración de la fecha y posición (pescador artesanal de Monte Hermoso y de un pescador deportivo), la estimación fue de 16 y 10 km día^{-1} respectivamente. Las mayores velocidades estimadas (19 km día^{-1}), correspondieron a un macho y una hembra con la misma talla (51 cm). Las menores (0,03 y 0,07 km día^{-1}) también correspondieron a dos machos de la misma talla. De los 29 individuos solo 6 desarrollaron velocidades superiores a los 3,5 km día^{-1}. Con el resto fueron menores a 1,3 km día^{-1}.

Los individuos marcados en noviembre fueron recapturados en casi las mismas condiciones de temperatura superficial en la que fueron marca-

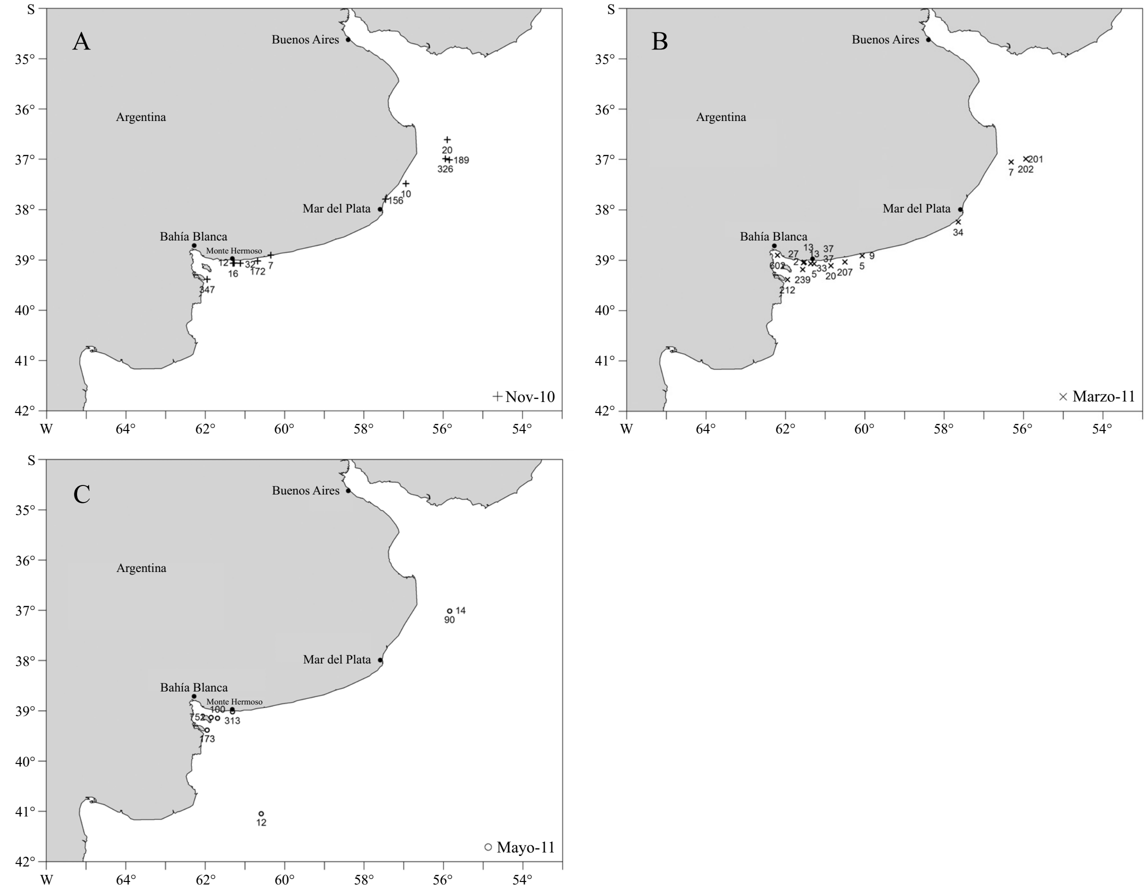

Figura 8. Posiciones de recaptura y días de permanencia en el mar de los individuos marcados en noviembre de 2010 (A), en marzo (B) y en mayo de 2011 (C).

Figure 8. Recapture positions and days in liberty at sea of individuals tagged in November 2010 (A), March (B) and May 2011 (C).

dos. Los marcados en mayo y marzo fueron recapturados en zonas con menores temperaturas superficiales respecto de las imperantes al momento de la marcación (Figura 9), con la excepción de un individuo marcado en mayo que fue recapturado frente a Monte Hermoso muy cerca de la costa, con temperaturas muy superiores a la correspondiente al momento de la marcación (Nro_marca 932, Tabla 1).

Las recapturas en aguas de baja salinidad de superficie, tanto en “El Rincón” como en el área de descarga del Río de la Plata, indican que los individuos fueron recapturados en áreas “frontales” (Figura 10). El resto mayoritariamente fue recapturado en altas salinidades correspondientes a aguas costeras de “El Rincón” y con influencia de aguas del Golfo San Matías. En la Tabla 1 puede observarse que al ejemplar recapturado en la boca del Golfo San Matías, no pudo asignársele una salinidad de superficie. Sin embargo, en función de lo descripto por Lucas et al. (2005) y Matano et al. (2014), en dicha zona también se encontrarían dos masas de agua, una de alta salinidad superficial correspondiente al Golfo San Matías por el oeste y por el este Aguas de Plataforma Continental.

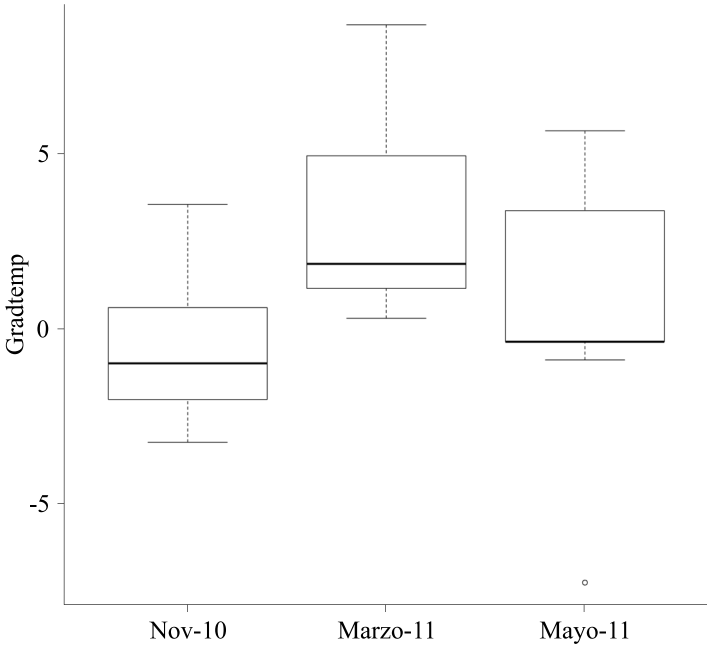

Figura 9. *Boxplot* con las diferencias entre la temperatura de captura y recaptura (gradtemp) según el mes de marcación.
Figure 9. Boxplot differences between capture and recapture temperature (gradtemp) according to the tagging month.

Análisis Multivariado

El dendrograma o *cluster* con las agrupaciones de los registros de la Tabla 1 al considerar las variables continuas gradiente de temperatura (gradtemp), el tiempo de recaptura, el rumbo, la profundidad y la distancia, indica que aunque pueden establecerse distintos grupos según las diferencias entre ellos (4 a 6), se consideraron 6 para su caracterización (Figura 11). Para el ACP se realizó una primera corrida en la que se estimó la varianza acumulada explicada por cada componente detectada. Las primeras tres componentes explicaron el 86% de la varianza. En una segunda corrida se descartaron las componentes 4 y 5. En ese caso, las primeras dos explicaron el 82%. Las variables rumbo y Profundidad resultaron inversamente correlacionadas, esperable según los resultados de la Figura 2. La Profundidad estuvo altamente correlacionada con la distancia, mientras que fue muy baja la correlación entre estas dos últimas variables con el tiempo de recaptura y el gradiente térmico. A mayores rumbos (OSO, 254° promedio), correspondieron menores distancias y profundidades y viceversa. Además, estas tres variables no estarían linealmente vinculadas con el gradiente de temperatura y el tiempo de recaptura. Por lo tanto, las distancias no estarían en relación con “cambios” importantes en las temperaturas de marcado y recaptura, mientras que sí lo estarían con el rumbo y la profundidad.

Para caracterizar los distintos Grupos (1 a 6), se incorporó dicha agrupación como variable categórica al ACP (Figura 12). Los Grupos producto del dendrograma se caracterizaron por:

- G1: altos tiempos de recaptura y gradientes térmicos (registros 1 y 4).
- G2: cercanía al lugar de marcación (bajas distancias recorridas) y bajas profundidades, con rumbo mayoritario OSO (registros 2, 6, 7, 8, 9, 10, 12, 14, 19, 20, 21, 22, 23, 26, 27, 34, 37 y 39).

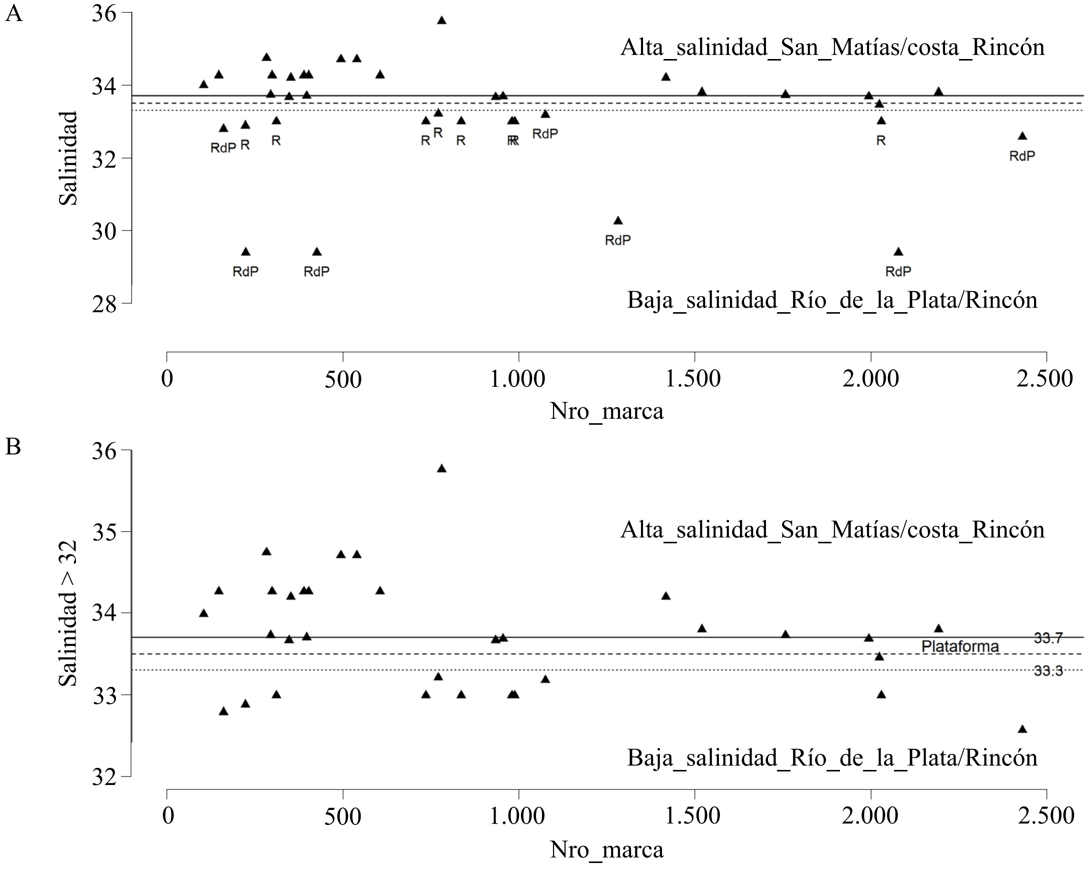

Figura 10. A) Salinidades de superficie promedio mensuales asignadas a cada posición de recaptura según registros históricos de campañas del INIDEP, en una grilla de 0,25° de Latitud por 0,25° de Longitud. R: "El Rincón", RdP: Río de la Plata. Línea punteada nivel 33,3 correspondiente a límite de aguas de baja salinidad según Lucas et al. (2005), entre la línea de guiones de 33,5 y la línea llena de 33,7, salinidades superficiales correspondientes con aguas de plataforma, salinidades > 33,7 aguas de alta salinidad correspondientes con San Matías y área costera de "El Rincón" según los mismos autores. B) Ídem A pero con salinidades superficiales mayores a 32 para visualizar en detalle en este rango.

Figure 10. A) Average monthly surface salinities assigned to each recapture position according to INIDEP's historical records in a grid of 0.25° Latitude by 0.25° Longitude. R: "El Rincón", RdP: Río de la Plata. Dotted line level 33.3 corresponding to low salinity water limit according to Lucas et al. (2005), between the dashed line 33.5 and the line full of 33.7, superficial salinities corresponding to the waters of platform, salinities > 33.7 waters of high salinity corresponding to San Matías and coastal area of "El Rincón" according to the same authors . B) Idem A but with surface salinities greater than 32 to visualize in detail in this range.

- G3: rumbos distintos a los mayoritarios correspondientes con el G2 y G4. Profundidades intermedias, bajo gradiente térmico y distancias de recaptura (registros 11, 17, 18, 31, 32 y 36). Se agruparon en el *cluster* con el G2 por la cercanía al lugar de marcación y el bajo tiempo de recaptura, pero con rumbo próximos al Norte y al Este.
- G4: rumbo ENE, altas distancias de recaptura y profundidades (registros 3, 5, 13, 16, 25, 28, 30, 33, 35 y 40).
- G5: altos tiempos de recaptura, rumbos mayores al promedio OSO y baja profundidad (registros 15, 22 y 24).
- G6: única observación frente al Golfo San Matías. La mayor profundidad registrada (69 m, registro 29).

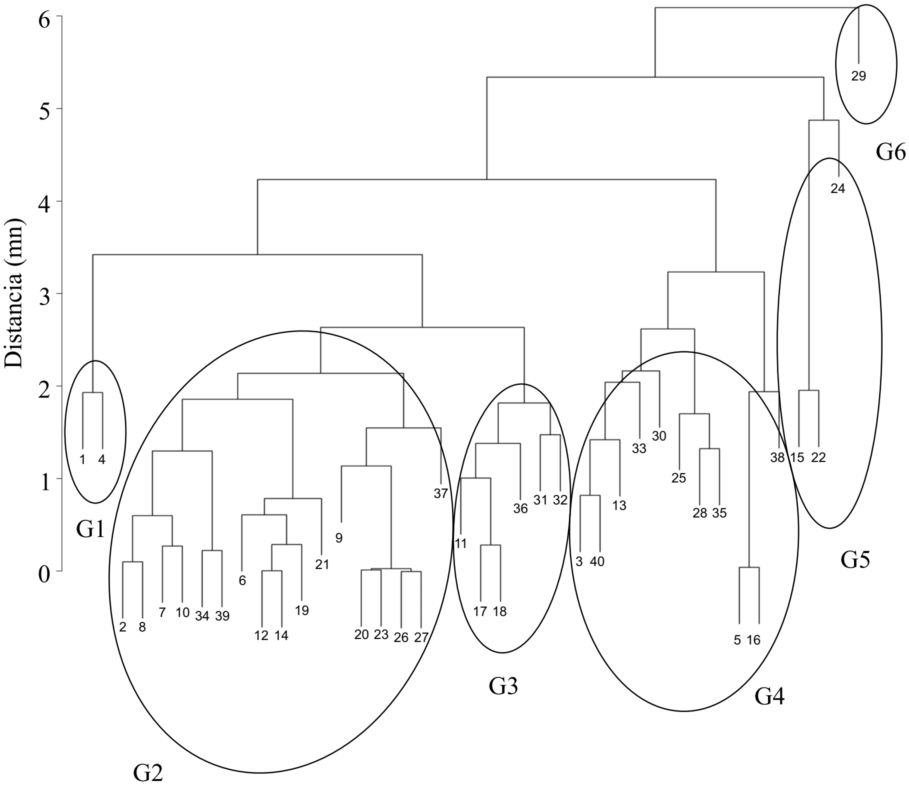

Figura 11. Dendrograma resultado del agrupamiento jerárquico aglomerativo mediante la distancia euclídea y su promedio como enlace, con las variables estandarizadas. El número corresponde a cada registro de la base de datos (Tabla 1). Se señalan los grupos (G1 a G6) caracterizados producto del Análisis de Componentes Principales.

Figure 11. Dendrogram from the agglomerative hierarchical clustering by euclidean distance and its average as a link with standardized variables. The number corresponds to each record in the database (Table 1). The groups (G1 to G6) characterized by the Principal Component Analysis are indicated.

De manera similar se realizó el mismo tipo de análisis considerando como variable categórica el mes de marcación (Figura 13). No habría tendencia clara de alguna agrupación en relación con el momento del marcado, hecho esperable según la Figura 2. Lo mismo resultó al evaluar el sexo, por lo tanto no habría tendencia clara de agrupación en relación con el sexo (Figura 14). Además, según el test de Chi cuadrado, la proporción de sexos de los individuos recapturados no resultó significativamente distinta a 1:1 (p = 0,53).

Los resultados del MLG, construído para evaluar estadísticamente que variables disponibles (continuas y discretas) podrían aportar a explicar la variación de la distancia de recaptura, indicaron que el ajuste no fue bueno, aunque se cumplieron los supuestos de normalidad de residuales y homocedasticidad (Figura 15). Este modelo resultó apenas significativo para explicar la variabilidad de la distancia:

Error estándar Residual: 1,166 con 26 GL
Multiple R^2: 0,5355, Ajustado R^2: 0,3033
F-estadístico: 2,306 con 13 y 26 GL, p = 0,03381

En la tabla de ANOVA correspondiente, se observa la falta de significación de las variables explicativas consideradas, salvo para la variable mes_marcado que resultó apenas por debajo del 5% de probabilidad (Tabla 3).

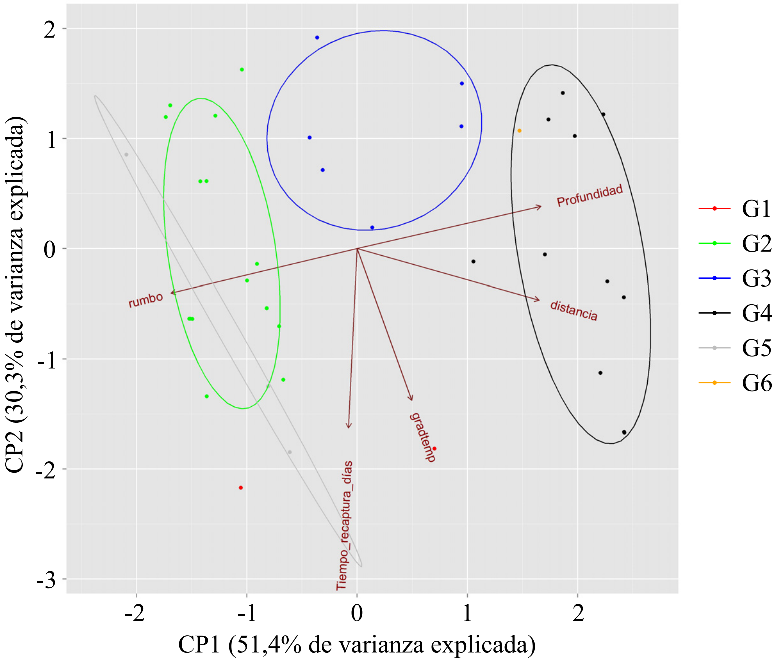

Figura 12. Cada color corresponde con las agrupaciones producto del ACP, señaladas en las leyendas (ver texto) y los diferentes contornos.

Figure 12. Each color corresponds with the groupings product of the ACP, identified in the legends (see text) and the different contours.

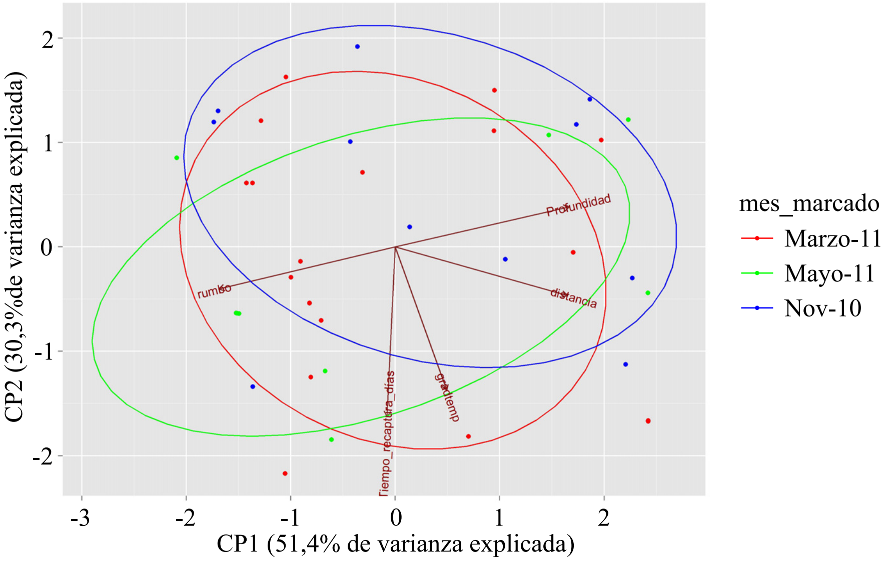

Figura 13. Cada color de los puntos se corresponde con el mes de marcación (mes_marcado) y los diferentes contornos para cada uno de ellos producto del ACP.

Figure 13. Each dots color corresponds to the tagging month (mes_marcado) and the different contours for each of them product of the ACP.

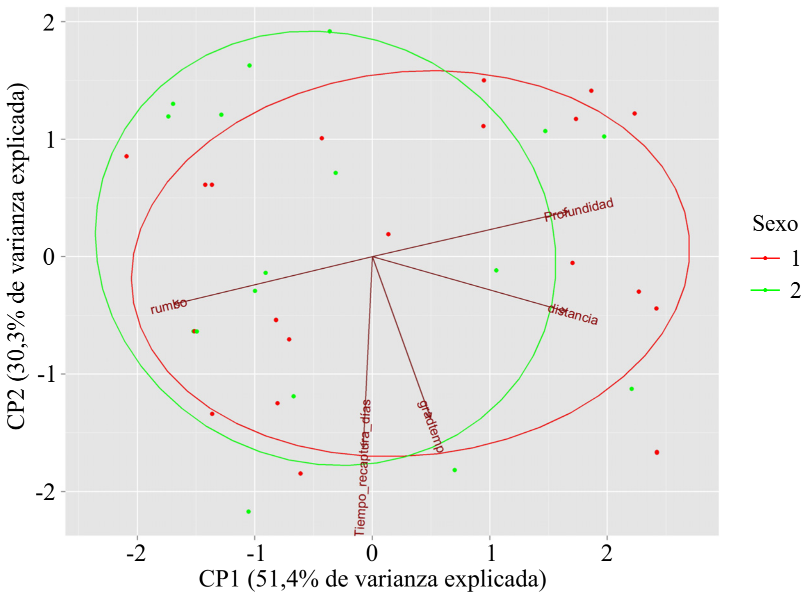

Figura 14. Cada color de los puntos se corresponde con las agrupaciones para cada sexo (número 1 machos en rojo y 2 hembras en verde) y los diferentes contornos para cada uno de ellos producto del ACP.

Figure 14. Each color of the dot corresponds to the groupings for each sex (number 1 males in red and 2 females in green) and the different contours for each of them product of the ACP.

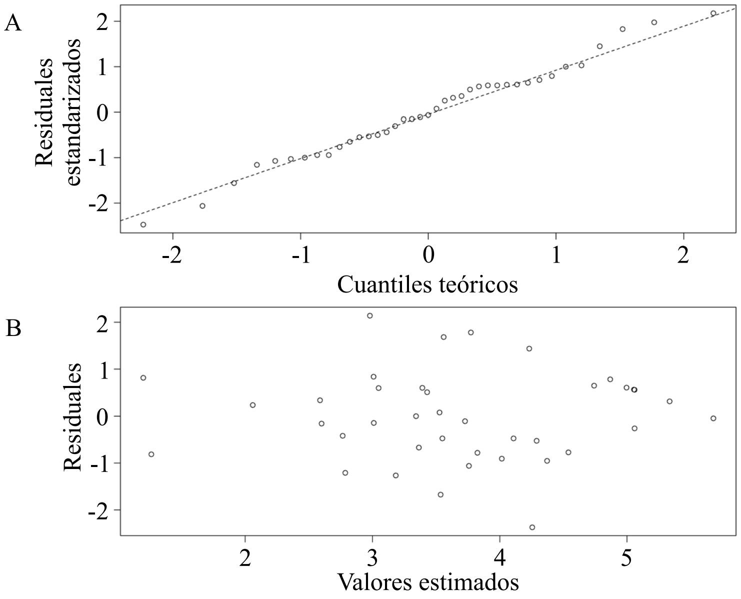

Figura 15. Gráficos de diagnóstico del ajuste del MLG lognormal con variable respuesta el logdistancia (mn) entre las posiciones asignadas de marcado y recaptura. A) Gráfico QQ de residuales estandarizados. B) Residuales crudos versus valores estimados.

Figura 15. Diagnostic graphs of the Lognormal MLG with response variable logdistancia (mn) between the assigned tagging-recapture positions. A) Residuals standardized QQ plot. B) Raw residual versus estimated values.

Tabla 3. Tabla de ANOVA correspondiente al GLM lognormal con el logdistancia como variable respuesta.
Tabla 3. ANOVA corresponding to the lognormal GLM with logdistance as a response variable.

	GL	Suma de cuadrados	F	Pr (> F)
log(talla_cap_cm)	1	0,5820	0,4284	0,5185
sexo	1	4,1168	3,0303	0,0935
gradtemp	1	4,6777	3,4432	0,0749
log(Tiempo_recaptura_días)	1	0,2699	0,1987	0,6595
mes_marcado	2	9,1785	3,3781	0,0496*
mes_recaptura	7	21,9015	2,3031	0,0574
Residual	26	35,3219		

Desplazamientos

En la Figura 16 se presentan señaladas con flechas, a modo de esquema según el mes de marcación, las potenciales trayectorias de los individuos entre las posiciones de marcado y de recaptura correspondientes, en las que se detallan el tiempo de permanencia en libertad de cada individuo. En la Figura 16 B, que corresponde a las marcaciones realizadas en el mes de marzo de 2011, no se presentan las flechas con rumbos OSO debido al alto número de recapturas cercanas a Monte Hermoso.

Los resultados mencionados hasta aquí, indicaron una tendencia a que un grupo de individuos se desplace a zonas lejanas, con rumbo ENE, mientras que otro parece hacerlo a aguas cercanas con rumbo OSO, aunque existen otras situaciones como la recuperada en la cercanía del Golfo San Matías, que indicarían también desplazamientos en otras direcciones. Los resultados del test espacial de Rao (1967) al considerar todos los datos en conjunto, no permiten rechazar la hipótesis nula de uniformidad en las direcciones de desplazamiento desde el lugar de marcación. El mismo test se aplicó separando los datos por cada uno de los meses de marcación, con los mismos resultados. Pudo observarse que hubo individuos recapturados tanto en la Zona Norte como cerca de Monte Hermoso con tiempos similares de permanencias en libertad, correspondientes a los tres meses de marcación. Esto podría indicar que, principalmente para los individuos que presentaron los menores tiempos de recaptura, algunos migraron al Norte y otros permanecieron en el área de Monte Hermoso. También hubo recapturas en ambas zonas para tiempos en libertad mayores a 6 meses (Figura 16). A medida que incrementa el tiempo en libertad, aumenta la incertidumbre sobre las trayectorias, ya que los individuos pudieron realizar desplazamientos en otras direcciones o haber realizado numerosos en sentido ENE y retornar.

Tiempos de permanencia en áreas de interés particulares. Zona Común de Pesca Argentino-Uruguaya

La proporción y el tiempo en libertad de los ejemplares cuya recaptura se produjo en rumbos menores a 122°, dentro y fuera de la ZCPAU, indica que once individuos permanecieron alrededor de un 60% de su período en libertad en la ZCPAU o en aguas próximas de jurisdicción provincial, mientras que los 7 restantes permanecieron el 100% fuera de la ZCPAU (Figura 17). Si se considera el mismo criterio, para los ejemplares restantes recapturados en posiciones correspondientes a rumbos mayores a 122° (22 individuos, Tabla 1), el 100% de su tiempo en libertad transcurrió fuera de la ZCPAU. Por lo tanto, más de un 70% de los individuos recapturados pasaron el 100% de su tiempo en libertad fuera de la ZCPAU, mientras que los restantes permanecieron alrededor de un 60% dentro.

DISCUSIÓN

Relaciones entre los desplazamientos horizontales del gatuzo (*Mustelus schmitti*) en el ecosistema costero bonaerense y su ciclo de vida

Posiciones de recaptura y relación con factores ambientales

Según los resultados del ACP y del GLM, ninguna de las variables consideradas fue altamente significativa para explicar la variación de la distancia recorrida. Existió un conjunto de individuos que se desplazó y fue recapturado en zonas distantes, al sur de la Bahía de Samborombón entre 37° S y 38° S al este de la costa de la Provincia de Buenos Aires, y en proximidades del área de descarga del Río de la Plata (Zona Norte). Otro grupo mayoritario parece haber permanecido o vuelto a la zona de "El Rincón" (Zona Sur).

La relación de las concentraciones de condrictios con áreas frontales ya fue mencionada por Lucífora et al. (2012), particularmente vinculadas con ambos frentes ya descriptos. Estos autores señalaron que algunas rayas costeras y el pez ángel, son más abundantes y tienen zonas de cría a lo largo de las áreas frontales "estuarinas". Según los resultados de la marcación, los RE en los que se declaró la mayor proporción de recapturas, tanto en la Zona Norte (RE 3655 y 3755) como en "El Rincón" (RE 3961 y 3960), fueron coincidentes con las áreas de mayor actividad de la flota comercial (Massa et al. 2004, Hozbor y Massa, 2015) en proximidades de las zonas frontales. Los casos restantes, con la salvedad del caso del procedente de la boca del Golfo San Matías, pueden considerarse como posiciones de "transición" entre ambas. En la franja costera entre Necochea y Mar Chiquita, tanto en otoño como en primavera, se encontraron individuos adultos de tallas intermedias, a diferencia de las distribuciones de tallas tanto de la Zona Norte como de "El Rincón", donde se detectaron tanto juveniles como adultos (Cousseau 1986; Massa et al. 2004).

Recientemente ha sido señalada nuevamente la importancia ecológica de los frentes del Atlántico Sudoccidental (Acha et al. 2015), en particular en el caso de la megafauna como tortugas, aves y mamíferos marinos (González Carman et al. 2016). La ubicación de las áreas frontales tanto costeras como oceánicas del litoral de la Provincia de Buenos Aires, señaladas por González Carman et al. (2016), y el total de las posiciones de las recapturas de gatuzo, evidencian la asociación espacial de las recapturas con los frentes tanto del Río de la Plata como de "El Rincón" (Figura 18). Ya fue señalada la limitante del uso de marcas convencionales respecto del sesgo vinculado a la distribución espacial del esfuerzo pesquero. Sin embargo, fue coincidente la distribución espacial del esfuerzo y en consecuencia de las capturas de gatuzo, con aquellos RE cercanos a las áreas frontales.

Desplazamiento de juveniles

Cousseau (1986) y Cousseau et al. (1998) señalaron la presencia de dos áreas de cría, una al sur de Bahía Samborombón frente a Cabo San Antonio (36° 20′ S) y otra en "El Rincón" desde Claromecó hasta Faro Segunda Barranca, ambas coincidentes con las áreas frontales señaladas. Massa et al. (2004) también asociaron ambos sistemas frontales de salinidad de fondo con las áreas de cría de gatuzo. Cortés et al. (2011), mediante datos de campañas de investigación, indicaron que los juveniles de gatuzo (< 50 cm de talla) permanecerían en la costa durante el año, en profundidades menores a 25 m. También mencionaron dos áreas de cría, una cercana a Punta Medanos en la región costera y otra en la parte

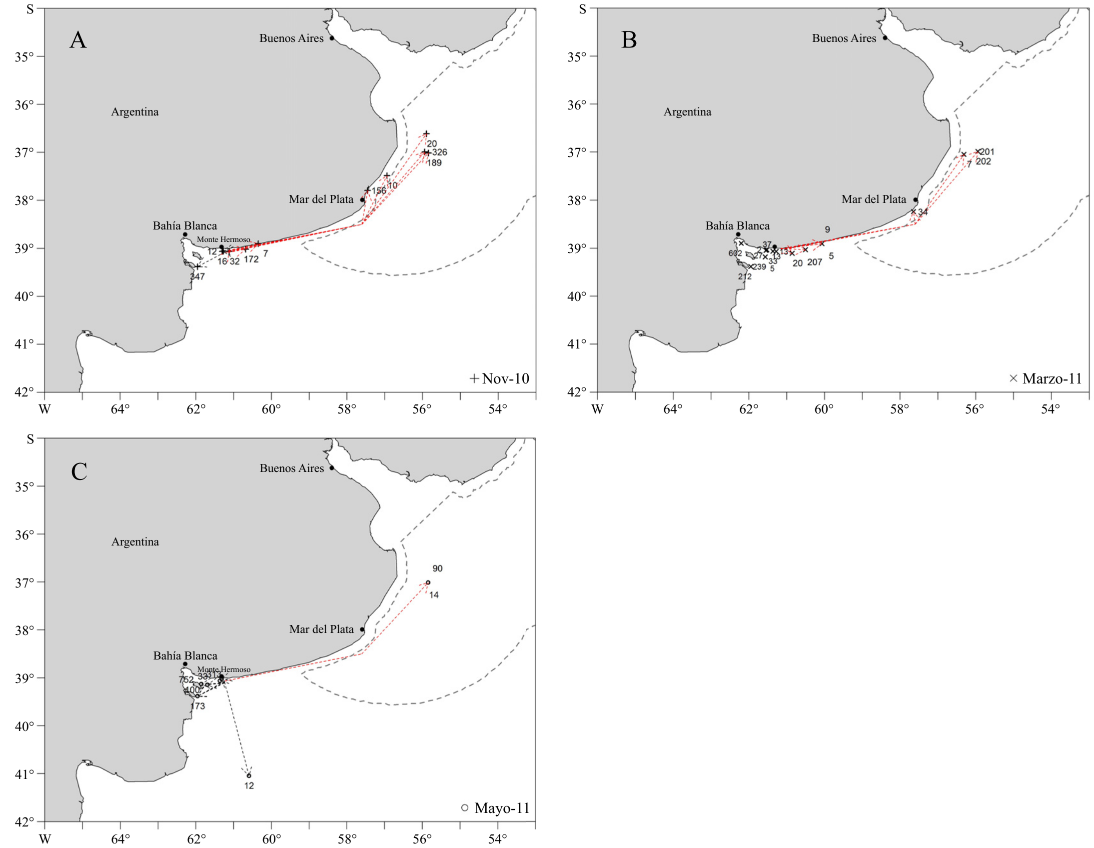

Figura 16. Esquema de las trayectorias de los individuos marcados en noviembre de 2010 (A), marzo (B) y mayo de 2011 (C). En la posición de recaptura se presenta el tiempo de permanencia en el mar. En líneas punteadas y flechas las trayectorias considerando los rumbos mayoritarios ENE y OSO.

Figure 16. Trajectories scheme of each individuals tagging in November 2010 (A), March (B) and May 2011 (C). In the recapture position is presented the time at liberty. Dotted lines and arrows indicate trajectories considering the main courses ENE and WSW.

interna de “El Rincón”. También se señaló que tanto el área de influencia del frente salino del Río de la Plata como aquel de “El Rincón” (Figura 18), desde el punto de vista de utilización del hábitat, cumplen un papel importante como áreas de cría, ya que los juveniles dispondrían de alimento abundante y altas temperaturas relativas que contribuiría a su crecimiento rápido (Oddone et al. 2007; Cortés et al. 2011). Estas áreas frontales favorecerían la retención de larvas de especies bentónicas y por lo tanto el establecimiento de invertebrados bentónicos como fuente de alimento (Acha et al. 2015).

Algunos individuos de alrededor de 50 cm de talla al momento de la marcación fueron recapturados a grandes distancias relativas. Según los antecedentes, la talla de primera madurez para las hembras fue estimada entre 56 y 72 cm, y para los machos entre 55 y 60 cm (Colautti et al. 2010). Los ejemplares correspondientes a las marcas 953 y 1073, machos marcados en mayo de 2011, de 52 y 48 cm de talla respectivamente, fueron recuperados al norte de Mar del Plata a los 14 y 90 días. Ambos individuos, según la escala de madurez macroscópica (estadio 2, Colonello et al. 2007), se clasificaron como juveniles al momento de la mar-

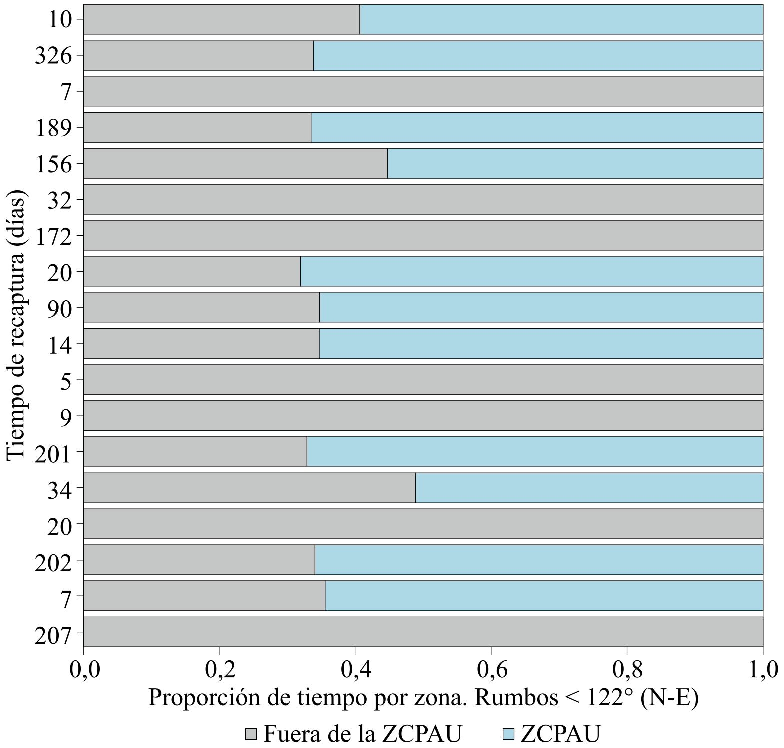

Figura 17. Proporción de tiempo en libertad dentro y fuera de la Zona Común de Pesca Argentino-Uruguaya (ZCPAU). Cada barra de distinto color representa el número de días transcurrido en cada zona correspondiente a los 18 individuos recapturados con rumbos menores a 122° a partir de las posiciones de marcado.

Figure 17. Proportion of time at liberty inside and outside the Argentine-Uruguayan Common Fishing Zone (ZCPAU). Each bar of different color represents the number of days spent in each zone by the 18 individuals recaptured with courses less than 122° from the tagging positions.

cación. Esto indicaría desplazamientos de individuos en sentido sur-norte entre ambas zonas frontales que podrían ser considerados juveniles. Los antecedentes sobre crecimiento (Hozbor et al. 2010) sugieren para las edades correspondientes a juveniles (edades 1 y 2) un incremento promedio de alrededor de 5 cm año^{-1} en ambos sexos. Por lo tanto, aunque no se dispuso de las tallas al momento de la recaptura de los individuos mencionados, es improbable que hayan alcanzado la madurez sexual en esos plazos.

Hipótesis sobre los desplazamientos de adultos

Al analizar los resultados de dos campañas de investigación, una realizada en primavera y otra en otoño, Cousseau (1986) señaló que habría un movimiento con fines reproductivos en primavera desde aguas más profundas hacia aguas más costeras, evidenciado tanto por las abundancias como por la estructura de tallas. Los adultos se concentran en la costa en la primavera tardía para la parición y aparearse tanto al norte como en "El Rincón", luego migran hacia mayores profundidades (Cousseau 1986; Massa et al. 2004). Cortés et al. (2011) mencionaron que las abundancias de los adultos estarían asociadas desde el punto de vista ambiental, con la profundidad y la temperatura. En otoño-invierno la abundancia de adultos estaría vinculada con aguas más profundas (> 25 m), mientras que en primavera, en la temporada reproductiva, los adultos migrarían hacia la costa segre-

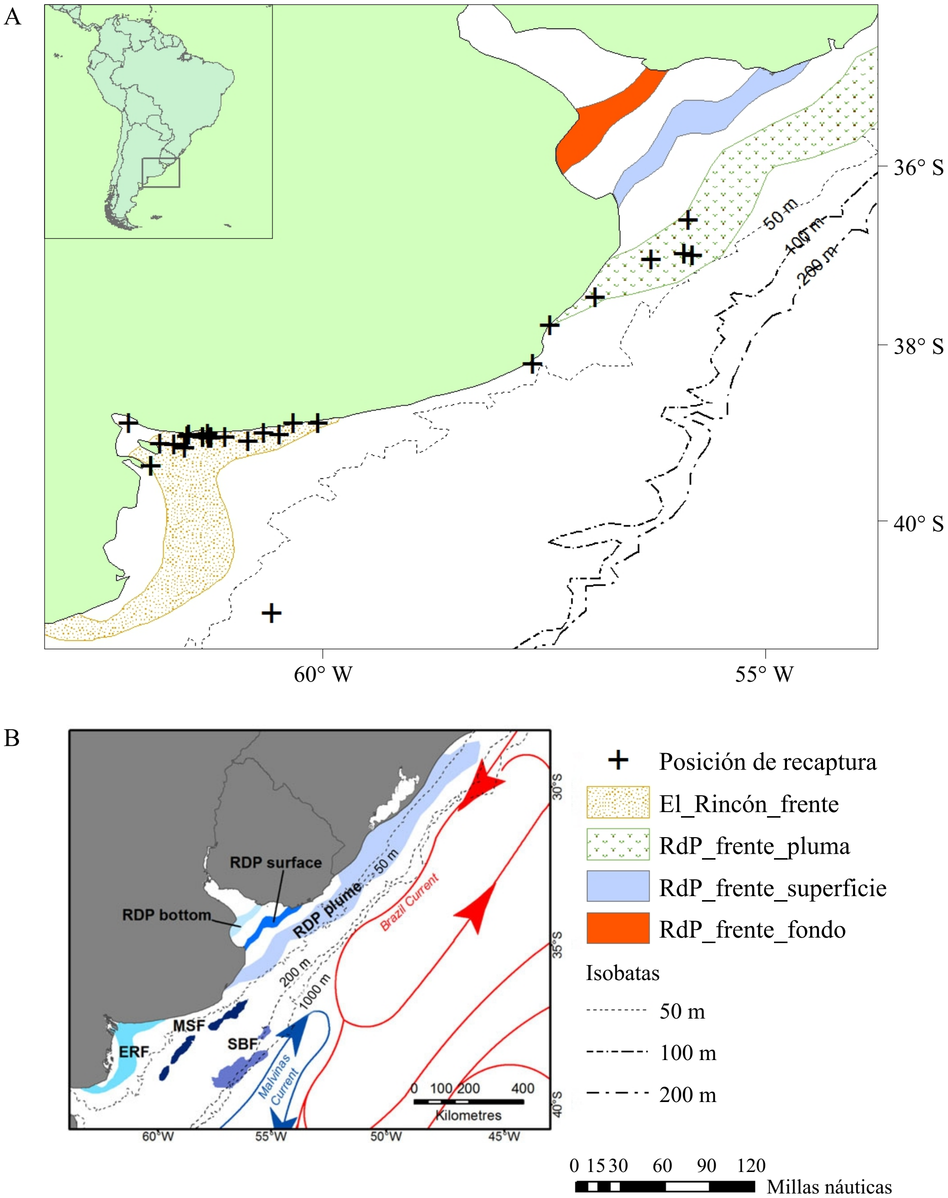

Figura 18. A) Posiciones de recapturas de gatuzo con la proyección de las áreas frontales en la costa de la Provincia de Buenos Aires extraídas de González Carman et al. (2016) y cedida por los autores. Frentes salinos del Río de la Plata y "El Rincón". B) Posición de los frentes en el litoral de la Provincia de Buenos Aires y aguas de la plataforma continental tomada de González Carman et al. (2016): RDP bottom frente de fondo del Río de la Plata, RDP surface frente de superficie del Río de la Plata, RDP plume frente de la pluma del Río de la Plata, ERF frente de "El Rincón", SBF frente del talud de la plataforma continental, MSF frente de la plataforma continental media.

Figure 18. A) Recapture positions with the projection of the Buenos Aires Province frontal areas extracted from González Carman et al. (2016) and ceded by the authors. Río de la Plata and "El Rincón" saline fronts. B) Position of the fronts on the coast of Buenos Aires Province and waters of the continental shelf taken from González Carman et al. (2016). RDP bottom: Río de la Plata bottom front, RDP surface: Río de la Plata surface front, RDP plume: Río de la Plata plume front, ERF: "El Rincon" front, SBF: continental shelf break front, MSF: mid-continental shelf front.

gados sexualmente. Colautti et al. (2010) indicaron máximas abundancias relativas de hembras con embriones y machos fluyentes dentro de Bahía Anegada en primavera, al sur de "El Rincón", por lo que habría movimiento hacia adentro de la Bahía en primavera temprana y saldrían en primavera tardía y verano, estando ausentes en otoño e invierno. Esta Bahía representaría un área de nacimiento y cría de juveniles.

Oddone et al. (2007), mediante datos de campañas de investigación realizadas en la ZCPAU, concluyeron que los adultos de ambos sexos preferirían aguas más costeras y cálidas durante la primavera y el verano, con fines reproductivos. Pereyra et al. (2008) con datos de observadores a bordo de la flota comercial uruguaya, señalaron que en la plataforma del sector uruguayo de la ZCPAU, las diferencias entre las distribuciones de tallas por sexo a menores y mayores profundidades de 50 m, estarían en relación con los movimientos reproductivos. La mayor proporción de hembras maduras en aguas de menor profundidad en primavera y verano indicaría la temporada de reproducción para esta zona. Luego de ser fecundadas, las hembras se desplazarían nuevamente hacia aguas más profundas.

La marcación de ejemplares en noviembre correspondió a la temporada reproductiva de la especie (Menni et al. 1986; Sidders et al. 2005; Cortés et al. 2011, entre otros). En particular, existieron dos casos, los ejemplares identificados con las marcas 2026 y 2074. La hembra con la marca 2074 fue recapturada 11 meses después en la Zona Norte y el ejemplar restante (macho, marca 2026) casi un año después en las islas frente a Monte Hermoso. Los tiempos de las recapturas eran próximos a la siguiente temporada reproductiva, pero estos individuos se encontraron en zonas distantes entre sí. En el caso correspondiente a la hembra con la marca 2074, pudo recuperarse el ejemplar entero y se verificó que, con 64 cm de talla al momento de la recaptura, asignada al 11 de octubre de 2011, estaba grávida con embriones de 22 cm de longitud de longitud total modal. Aunque la talla observada de los embriones pueda ser considerada dentro de su variabilidad al momento de la parición (Sidders et al. 2005; Cortés 2007), no se puede afirmar que estuviera próxima a parir en la Zona Norte. Menni et al. (1986) señalaron que la talla (longitud total) de los embriones al momento de la parición sería de 27/28 cm, mientras que para Oddone et al. (2005) sería de 26 cm. Esto podría indicar que esta hembra aún no se encontraba en esta situación. El ejemplar macho restante (Marca 2026) no pudo ser recuperado, pero correspondía a un individuo maduro sexualmente, de 68 cm de talla en el momento de la marcación, con fecha de recaptura asignada al 1 de noviembre de 2011. Además, existieron recapturas en la Zona Norte a los 10 y 20 días luego de la marcación en Monte Hermoso en noviembre de 2010, por lo que fue posible para otros ejemplares marcados en el mismo mes, realizar ese trayecto en tiempos que permitirían su retorno al lugar de marcación. Sin embargo, la presencia de recapturas en la Zona Norte, la falta de correlación detectada entre las variables distancia, mes de marcación y tiempo de recaptura, además del desplazamiento sur-norte de los juveniles ya planteado, podría indicar un importante grado de mezcla de juveniles y reproductores con baja filopatría, definida como el retorno preferencial de reproductores a sus sitios de nacimiento y por lo tanto un uso multigeneracional que llevaría al desarrollo de cierta estructura poblacional desde el punto de vista genético (Chapman et al. 2015). Habría evidencias en el caso del gatuzo de que alguna proporción importante de ejemplares podrían moverse a lo largo del litoral y, en condiciones propicias, se apareen y realicen la parición en distintos lugares a lo largo de su vida.

Los antecedentes sobre el gatuzo mencionados hasta aquí, con evidencias producto de distintas fuentes de información, indican un desplazamiento de ambos sexos hacia aguas costeras con agregación con fines reproductivos en primavera, tanto en la Zona Norte como en la Sur, en proximidades de ambas zonas frontales. Los resultados de la marcación no sugieren una agregación por sexo ni por mes de recaptura. Tampoco hubo recapturas en profundidades mayores a 50 m (salvo el caso frente al Golfo San Matías), lo que indicara una tendencia a que algunas tallas o sexos se desplazaran a mayores profundidades en alguna época del año. Esto pudo no ser percibido debido al número de recapturas y/o de la distribución del esfuerzo de la flota que operó a profundidades mayores de 50 m. Sin embargo, aparecieron evidencias de desplazamientos que tendrían rumbo ENE a partir del lugar de marcación, de una proporción importante de individuos de ambos sexos en un amplio rango de tallas (juveniles y adultos). Estos desplazamientos se realizarían en escalas temporales diversas, aún en plazos muy cortos debido a las velocidades de natación detectadas (hasta 19 km día^{-1}). Hubo recapturas en la Zona Norte a los 7, 10 y 14 días a partir del momento de marcación, en los tres meses (noviembre, marzo y mayo) en que se marcaron individuos en Monte Hermoso. Además, hubo recapturas de individuos de ambos sexos (macho juvenil de 48 cm y hembra adulta de 63 cm) en invierno (agosto), en proximidades del lugar de marcación luego de 90 y 100 días de permanencia en libertad, lo que indicaría que tanto juveniles como adultos permanecerían o potencialmente "volverían" a la Zona Sur. Estos resultados sugieren una dispersión a partir de la zona de marcación, principalmente en sentido ENE, pero también en otras direcciones por ejemplo el caso frente al Golfo San Matías.

Desde el lugar de marcación, no se detectaron indicios de desplazamientos de juveniles en primavera ni de los machos adultos mayoritariamente en alguna temporada en sentido ENE. Tampoco de los adultos de ambos sexos principalmente en invierno con este mismo rumbo de desplazamiento (Oddone et al. 2005, 2007). No se declararon recapturas al norte de 36° S, por lo tanto no puede inferirse sobre posibles desplazamientos hacia menores latitudes.

Es probable que haya permanencias en la zona de marcación durante todo el año, aunque no es posible caracterizarlos como residentes debido al desconocimiento de sus trayectorias. Esto no excluiría las concentraciones reproductivas detectadas con numerosos antecedentes y los desplazamientos en sentido oeste-este, o de mayores a menores profundidades tanto en la Zona Norte como en la Sur. Pero, según los resultados de la marcación, existiría un importante grado de "mezcla" en sentido sur-norte de adultos reproductores de ambos sexos y juveniles, hecho congruente con los antecedentes de genética de poblaciones (Pereyra et al. 2010; Andreoli y Trucco 2015, 2018) y con el test de uniformidad en las direcciones de dispersión, desde el lugar de marcación para los distintos meses en que se realizó la marcación. Por lo tanto, habría fidelidad por sitios de reproducción pero sin reconocimiento por parte de los reproductores de su propio sitio de nacimiento (filopatría).

Existen antecedentes sobre el uso de bahías y estuarios costeros para alimentación, apareamiento y parición, como en el caso de *M. californicus* y *M. henlei* en la costa de California (Espinoza et al. 2011). En el caso de *M. californicus,* mediante marcas acústicas a lo largo de dos años, se observó el uso de una bahía costera por parte de individuos de esta especie. De 22 ejemplares marcados solo dos tuvieron una permanencia superior a dos meses y ninguno regresó con posterioridad luego de su salida durante el invierno. Su abundancia dentro de la bahía estaría relacionada con mayores temperaturas en la temporada cálida y cambios en la disponibilidad de presas. Este antecedente sería un indicador similar al gatuzo en cuanto a la baja "fidelidad" por algunos ambientes particulares. Contrariamente en *M. mustelus* en Sudáfrica, también mediante el uso de marcas acústicas y durante dos años, habría evidencias de fidelidad y residencia en una bahía costera al evaluar el uso de un área marina protegida delimitada dentro de ella. Sin embargo, el análisis se realizó solo sobre los individuos presentes durante por lo menos un ciclo anual en la bahía, 15 sobre 24 marcados (da Silva et al. 2013).

Mediante el uso de marcas convencionales, recientemente se propuso a *M. asterias* en el Atlántico Nororiental como especie filopátrica, debido a variaciones estacionales de las recapturas por zonas, pero sin considerar las variaciones correspondientes al esfuerzo pesquero en dichas zonas (Brevé et al. 2016). La carencia de información sobre la distribución espacio temporal del esfuerzo influye en las consideraciones respecto de las definiciones de residencia, fidelidad por un sitio y filopatría, al utilizar marcas convencionales. La componente genética debe ser considerada para la calificación de una especie como filopátrica (Chapman et al. 2015).

Según Schlaff et al. (2014), en rayas y tiburones los vínculos entre los movimientos y el medio ambiente están correlacionados, y no proveen evidencia concluyente de que un único factor abiótico o biótico, sea la causa de los movimientos. Además, estos factores no ocurren separadamente, por lo tanto se dificulta determinar cual es de mayor importancia o cuando existen interacciones entre ellos. Los movimientos estarían conducidos por una combinación de factores, bióticos y abióticos, con una selección de hábitat resultante de un balance entre la necesidad de optimizar funciones metabólicas y fisiológicas, y a la vez acceder a recursos valiosos, por ejemplo alimento o refugio. Espinoza et al. (2011) señalan para *M. californicus* que los patrones espaciales de abundancia estarían influenciados por la temperatura y la disponibilidad de presas. En el caso de *M. henlei* en California, se movería hacia aguas someras en condiciones de mareas entrantes a una bahía costera, presumiblemente con fines alimenticios (Campos et al. 2009). Elisio et al. (2015) propusieron a la temperatura como disparador abiótico de la agregación reproductiva de *M. schmitti* en la zona de "El Rincón". Jaureguizar et al. (2016), analizando campañas de investigación en "El Rincón" en la temporada reproductiva, indicaron vínculos entre la abundancia y factores abióticos como profundidad, cercanía a la costa, salinidad y la descarga de los ríos próximos. Según los resultados de este trabajo, mediante el método de marcado y recaptura, la componente biótica parece relevante. Como ya fue discutido, hubo casos de ejemplares adultos marcados en noviembre de 2010 (temporada reproductiva) en Monte Hermoso, que fueron recapturados al norte a más de 400 km de distancia luego de 10 y 20 días de libertad. Dicha componente asociada con áreas frontales estaría vinculada con la disponibilidad de recursos alimenticios. La descripción de la dieta de la especie (Bellegia et al. 2012) parece coincidir con las características propias de las áreas frontales señaladas por Acha et al. (2004), ya que ambas zonas "estuarinas" se caracterizan por fondos blandos, habitados principalmente por organismos bentónicos como poliquetos, bivalvos y crustáceos. También serían áreas de depredación para especies de alto nivel trófico, como tiburones costeros y rayas. Lucífora et al. (2012) propusieron que la gran diversidad de especies de condrictios en ambas zonas frontales sería producto de la abundancia de presas (invertebrados bentónicos). Estos indicios, en conjunto con las recapturas de gatuzos adultos y juveniles, indicaría la utilización de ambas zonas frontales a lo largo del año por parte de esta especie.

Francis (1988) estableció objetivos similares a este trabajo mediante el uso de marcas convencionales en *M. lenticulatus* en Nueva Zelanda. En el mismo trabajo incorpora en la discusión resultados en otra especie de Australia, *M. antarticus,* obtenidos con la misma metodología. Las mayores velocidades de natación estimadas en *M. lenticulatus* fueron similares a las mayores estimadas para *M. schmitti*. La mayor distancia en *M. antarticus* fue de 2.200 km, escala comparable con los resultados en *M. lenticulatus.* En el gatuzo, la mayor distancia estimada fue menor a 600 km, sin diferencias en las distancias entre los sexos. Tanto en *M. antarticus* como en M. *lenticulatus*, las hembras fueron recapturadas a mayores distancias que los machos. Las diferencias en la velocidad y en las distancias entre estas especies del mismo género eran esperables ya que *M.*

lenticulatus presenta mayores tallas en ambos sexos que *M. schmitti* (Hozbor et al. 2010). Debido al sesgo en la distribución del esfuerzo, no fue posible establecer el hábitat invernal de *M. lenticulatus*, ya que la mayor parte de las recapturas ocurrieron durante el verano (Francis 1988). Sin embargo, el autor señala que pasaría el invierno en aguas del talud o aún a mayores profundidades mientras habitaría la plataforma de Nueva Zelanda en primavera y verano. No descarta la posibilidad de que en invierno permanezca en la plataforma aunque se disperse en un área mayor. Según este autor, los desplazamientos de ambos sexos estarían vinculados al ciclo reproductivo anual, al igual que en otras especies correspondientes al mismo género, pero no descarta que las hembras también podrían agregarse en la costa para obtener mediante el alimento algunos componentes esenciales no disponibles en su hábitat invernal. En el caso del gatuzo, se marcaron ejemplares en otoño (Mayo) y se los recapturó en invierno a los 90 y 100 días, tanto en la Zona Norte como en la Sur, por fuera de la temporada reproductiva de la especie. Esto indica que los desplazamientos no solo estarían vinculados con la reproducción sino también con otros factores por ahora desconocidos.

Los resultados sobre la marcación de gatuzo pusieron en evidencia la utilización de áreas extensas mayoritariamente costeras (principalmente profundidades menores a 50 m) con una proporción importante de individuos (juveniles > 47 cm de talla y adultos) sin alta afinidad con algunas áreas particulares. Este fue el modelo propuesto por Knip et al. (2010) a escala mundial para tiburones pequeños. Sin embargo, como ya había sido discutido por Oddone et al. (2005) y Cortés et al. (2011), la migración y agregación reproductiva en primavera-verano, la utilización de algunas áreas reducidas como áreas de cría (Colautti et al. 2010) con presencia de individuos adultos para parir y luego aparearse y su posterior desaparición de esas áreas en otoño-invierno (Oddone et al. 2007; Colautti et al. 2010; Cortés et al. 2011; Elisio et al. 2015), indicaría un ajuste al modelo propuesto por Springer (1967), habitualmente señalado en el caso de grandes tiburones. Por lo tanto, el caso del gatuzo parece contener algunos aspectos correspondientes a ambos modelos, un modelo mixto entre los ya señalados, con fidelidad por los sitios de reproducción pero sin evidencias de filopatría.

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MORPHOLOGICAL SHELL VARIATION OF *Zidona dufresnei* (CAENOGASTROPODA: VOLUTIDAE) FROM THE SOUTHWESTERN ATLANTIC OCEAN

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ABSTRACT. The volutid gastropod *Zidona dufresnei* is an important fishery resource from the Southwestern Atlantic Ocean. This species exhibits strong interpopulation differences in life history features, which lead to postulate the existence of two morphotype ('normal' and 'dwarf'). In this study, we combine and compare traditional and geometric morphometrics to capture shell shape variation of *Z. dufresnei* among three populations from Mar del Plata (37° S) to San Matías Gulf (42° S) to test the hypothesis that the phenotypic variation already described in the life cycle and size is also expressed in the shell shape. Significant differences in the shell morphology among these three populations were detected, mainly associated to the maximum size of individuals and shell shape. The Bahía San Antonio morphotype had shells with higher general roundness and weight compared to San Matías Gulf and Mar del Plata morphotypes, which were not differentiated. Our results support the hypothesis of Lahille (1895) who distinguished the morphotype of Bahía San Antonio ('dwarf' morphotype) as *Voluta angulata affinis*. The functional significance of the variability found is discussed in terms of the ecological and genetic effects on shape and size.

Key words: Marine gasteropod, shell variation, geometric morphometry, South Atlantic.

INTRODUCTION

Comparison of the anatomical characteristics of organisms has been a key point in biological research. Studies focused on taxonomic classification of organisms have mainly been on the characterization of body size and shape of individuals (Rohlf 1990; Adams et al. 2004). In the case of gastropods, shell morphology has been one of the most important features to identify species and to understand phenotypic variation within species (e.g. Trussell 2000; Hollander et al. 2006; Conde-Padín et al. 2007, 2009). Several methods have been used to analyze intra- and inter-specific shell variation in morphology, but traditional and geometric morphometrics have been the most frequent since the shell is rigid and characterized by noticeable anatomical points (Carvajal-Rodríguez et al. 2005; Marko 2005; Guerra-Varela et al. 2009; Avaca 2010; Valladares et al. 2010; Teso et al. 2011).

The volutid gastropod *Zidona dufresnei* (Donovan, 1823), known locally as 'caracol fino' (fine snail) or 'caracol atigrado' (tabby snail), is distributed on the western coast of the South Atlantic Ocean from Río de Janeiro, Brazil (22° S-42° W) to Patagonian waters of San Matías Gulf, Argentina (42° S-64° W) (Kaiser 1977; Rosenberg 2009). This species lives on sandy or muddy bottoms between the low intertidal zone and 200 m water depth and exhibits a patchy distribution pattern (Scarabino 1977; Pereyra et al. 2009; Medina et al. 2015, 2016).

Z. dufresnei is one of the most important gastropods which have been subject to fishing pressure in Argentina and Uruguay with annual landings ranging from 500 to 3,000 t (Fabiano et al. 2000; Giménez et al. 2005; Roche et al. 2013). Similar to other volutid gastropods, their life history parameters (large body size and somatic production, slow growth rate, late reproductive maturity and direct development) make this species extremely vulnerable to overexploitation (Giménez and Penchaszadeh 2002; Giménez et al. 2004; Medina et al. 2015, 2016). Further, the occurrence of direct (intracapsular) development and absence of a pelagic larval stage is usually recognized as a factor preventing gene flow and leading to genetic differentiation of allopatric populations (e.g. Scarabino 1977; Darragh et al. 1998; Pereyra et al. 2009). Several studies reported differences in the maximum size and weight of individuals of *Z. dufresnei* along the geographical distribution of the species, possibly due to different environmental conditions (Pereyra et al. 2009; Medina et al. 2015). Particularly, two different populations were described in San Matias Gulf based on the maximum size and weight of mature individuals (Medina et al. 2015, 2016). One of these populations, whose individuals reach 230 mm long and 831 g in weight, inhabits deep waters (between 35 and 130 m) inside the gulf. The other population, with individuals reaching 120 mm long and 113 g in weight is located in shallow waters of the gulf (less than 2 m depth) (Medina et al. 2015) (Figure 1). These differences led to postulate the existence of two morphotypes: a 'normal' (from relatively deep waters) and a 'dwarf' morphotype (from shallow waters) (Lahille 1895). Even Lahille (1895) referred to a small volutid identified as *Voluta angulata affinis*, which would be a specimen from the San Antonio Bay. Later, Clench and Turner (1964) based on morphological characters unified the variety *V. angulata affinis* with *Z. dufresnei* leading to potential taxonomic inconsistencies related to the issue of whether these morphotypes are subspecies or even separate (cryptic) species.

Considering the high degree of morphological variation reported for the species (Roche et al. 2013; Medina et al. 2015, 2016), *Z. dufresnei* offers the opportunity to investigate morphological pattern in heterogeneous environment. Despite that, no studies have been conducted to determine differences in shell shape since differences in shell size have already been investigated. In this context, the aim of this study was to analyze the differences in shape between morphotypes of *Z. dufresnei* using traditional and geometric morphometrics approaches among and within three populations distributed along the Argentine Sea. The results obtained by both methodologies were also compared. We tested the hypothesis that the isolation among populations favors a phenotypic variation expressed at the shell shape level. Overall, these results are expected to contribute to a better understanding of the taxonomic status of *Z. dufresnei*, and thus provide basic knowledge to achieve a sustainable management of this fishing resource by designing strategies that account for the variability between local taxonomic units.

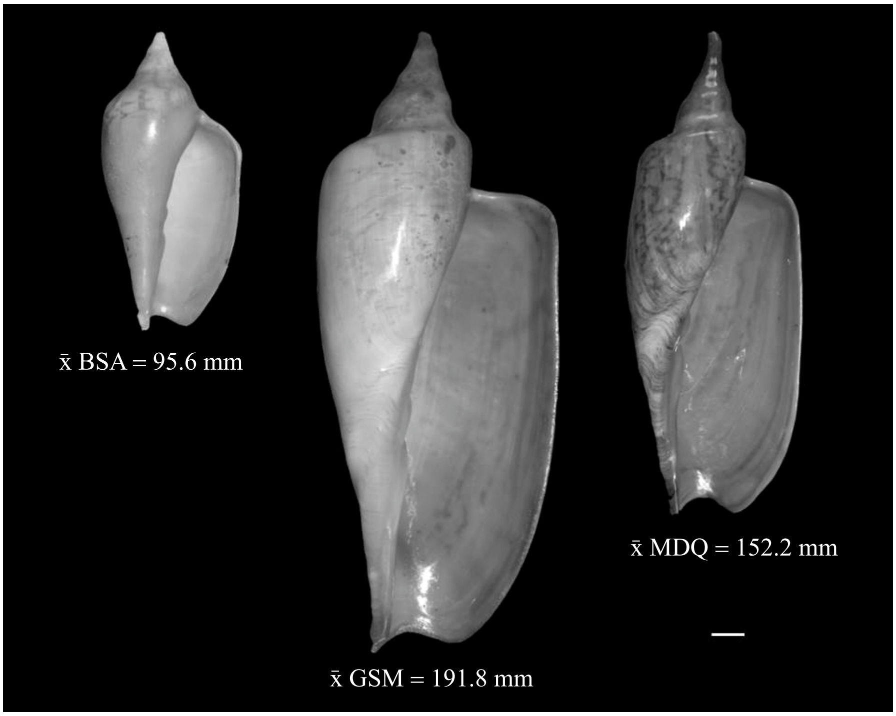

Figure 1. Representative specimens of mean total length of each studied population of *Zidona dufresnei*. BSA: San Antonio Bay, GSM: San Matías Gulf, MDQ: Mar del Plata. Scale bar = 10 mm.

MATERIALS AND METHODS

Study sites and samples collection

Individuals of *Z. dufresnei* were collected in three locations along the Argentine Sea: Mar del Plata (MDQ), San Antonio Bay (BSA) and San Matías Gulf (GSM) (Figure 2), from 2007 to 2011. These locations were selected since they are the only places where stable populations of this species in Argentine waters were properly described. At the same time, BSA population is the only 'dwarf' morphotype population of *Z. dufresnei* known so far. MDQ site was characterized by sandy bottom, mean salinity of 35, sea surface temperature (SST) range of 9-17 °C, and depth between 40 to 60 m (Guerrero et al. 1997). GSM is a semi-enclosed gulf with a surface of 19.700 km^2, characterized by a high rate of water retention due to its topography. Its maximum depth is 200 m in the center of the gulf and decreases up to 45 m in the mouth (Mazio and Vara 1983). The SST and salinity in the gulf vary between 11.3 and 13.5 °C and between 33.5 and 34.1, respectively (Williams et al. 2010). The seabed of the fishing zone consists mainly of a mixture of sand and mud. BSA is a shallow macrotidal system located in the northwestern region of GSM with tidal amplitudes of up to 9 m and strong tidal currents within their main channels. The dominant bottom type is sand, with variable content of interspersed pebble and cobble. Due to its narrow mouth (5 km long), the bay presents a low rate of water exchange with GSM. The water temperature in BSA oscillates between 6 and 28 °C throughout the year and salinity varies between 31.8 and 39.0 (Piola and Scasso 1988; Saad 2018 pers. comm.) but it could decrease to

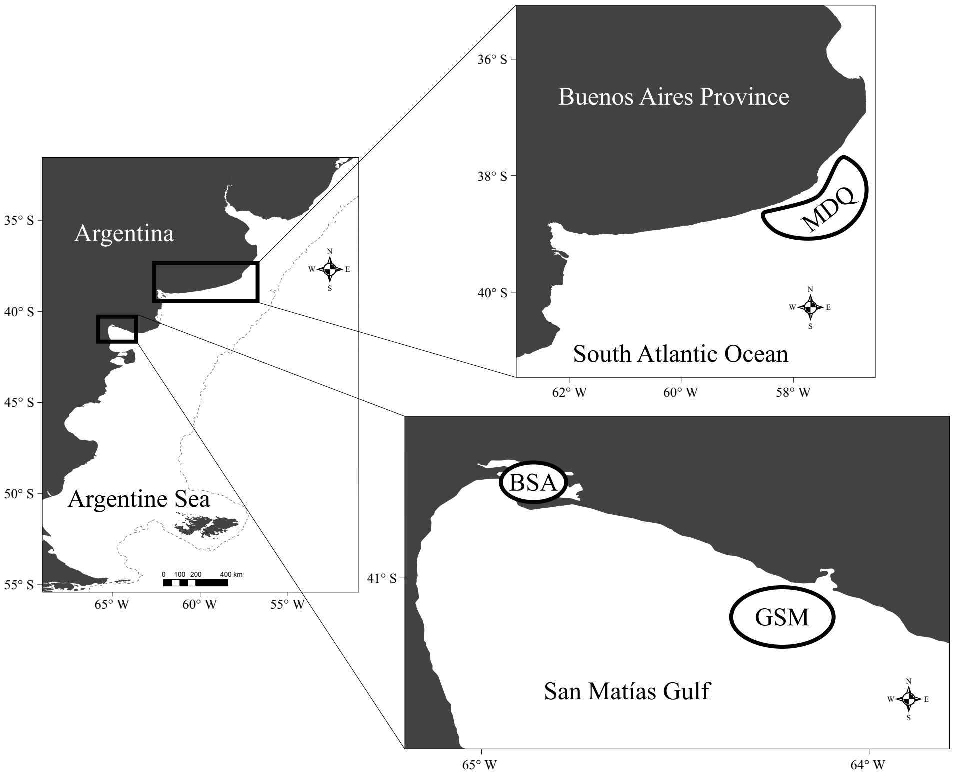

Figure 2. Collection site of *Zidona dufresnei*. MDQ: Mar del Plata, BSA: San Antonio Bay, GSM: San Matías Gulf.

29.0 with extreme rainfall (Salas 2019 pers. comm.). Contrary to MDQ and GSM sites, BSA area is a wave exposed intertidal environment.

In MDQ, individuals were obtained from the bottom trawl fishery that targets this species at 40-60 m depth. In this fishery, vessels are equipped with bottom nets of 42 mm mesh size. In GSM, individuals were collected from the bycatch of the bottom trawling fleet that targets the Argentine hake (*Merluccius hubbsi*). The depth at which the specimens of *Z. dufresnei* were obtained averaged 100 m. Mesh size used in this fishery ranges between 110 and 120 mm. In BSA, individuals were hand-collected by artisanal fishermen from the intertidal region (0-1 m depth), using an iron gaff. All specimens were sexually mature adults. Maximum size for each population was recorded (Lahille 1895; Clench and Turner 1964; Kaiser 1977; Scarabino 1977; Roche et al. 2013; Medina et al. 2015). Adult size was established separately for each population according to size at maturity described in the literature (Roche et al. 2015, Giménez and Penchaszadeh 2003). Although smallest individuals were not sampled in any of the populations we were able to compare among adults and maximum sizes.

Morphometric analysis

Both traditional and geometric morphometric methodologies were used to study shell shape variation as complementary analysis. The traditional morphometric analysis was conducted using 253 individuals (MDQ: 99, GSM: 78 and BSA: 76). These sample sizes were in concordance to the sample sizes estimated by power analysis method using G*power software (freeware, Faul et al. 2009). Power of the study was 95%. Only individuals in good enough condition to take the measurements were used for the traditional morphometric analysis (e.g. apically eroded specimens were discarded from the analysis). Animals were sexed based on the presence of the pedal gland in females and the presence of a penis in males. The following measures (mm) were taken for each individual shell using a digital caliper: total length (TL), total width (TW), aperture length (AL) and aperture width (AW) (Figure 3 A). Additionally, total weight (TW) and shell weight (SW) in grams were recorded. To analyze morphometric variations six indexes were used: general roundness (GR = TW/TL), relative length of the aperture (RLA = AL/TL), relative width of the aperture (RWA = AW/LT), relative shape of the aperture (RSA = AW/AL), relative expansion of the aperture (REA = AW/TW) and relative weight of the shell (RWS = SW/TW). Differences between populations were analyzed by Principal Component Analysis (PCA) and nonparametric tests using all indexes. Also, the following linear regressions were estimated and differences between sites and sexes were analyzed using ANCOVA for the relationships TL versus AL, TL versus AW, and SW versus TW. Before the analyses, data were tested for normality with the Shapiro-Wilk test and for homogeneity of variance with the Levene test.

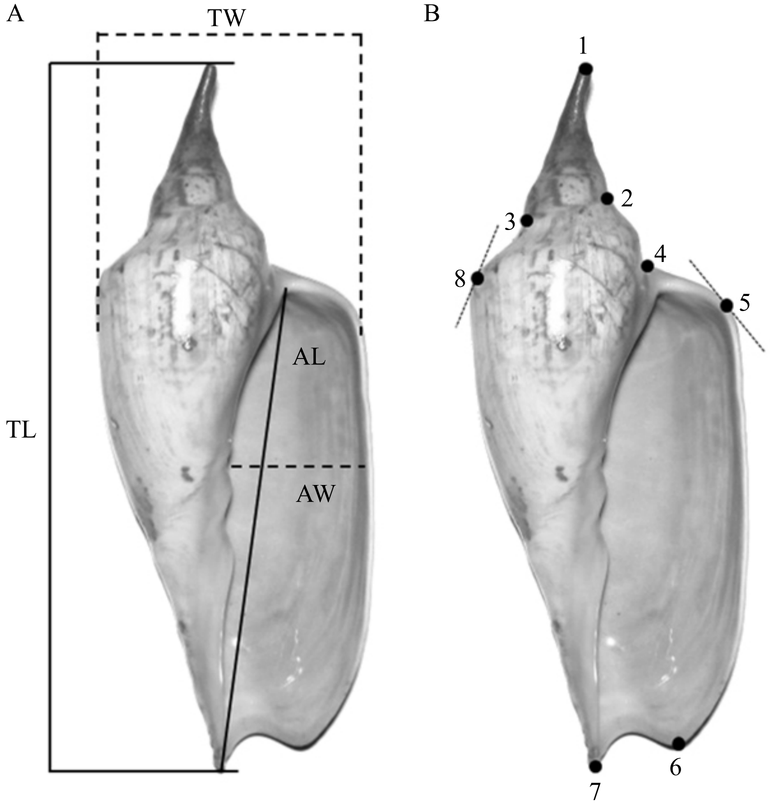

Figure 3. Diagram of the shell of *Zidona dufresnei*. A) Measurements used in the traditional morphometric analysis: total length (TL), total width (TW), aperture length (AL), aperture width (AW). B) The eight landmarks used in the geometric analysis. Landmark (L) 1: apex, L2: right border of the suture of the last anfract, L3: left border of the suture of the last anfract, L4: outer-end of the suture of the last right anfract, L5: posterior border of the outer lip, L6: right border of the siphonal channel, L7: left border of the siphonal channel, L8: end of the suture of the last left anfract.

Geometric morphometrics approach was conducted using a subset of 68 adult snails shells (MDQ: 19, GSM: 19, BSA: 30). We selected individuals with unbroken shells, which were difficult to obtain due to fishing procedures. In this way, the sample size was limited by the availability of samples in good condition. Shell photographs were taken with a digital camera (Nikon Coolpix P5100, 12.1 megapixels) mounted on a table top to ensure parallelism between the focal plane of the camera and frontal plane of individuals. All photographs were taken at the same resolution including a graded scale in each one as a reference. In order to reduce experimenter bias the photographic method was carried out by A.I.M. and repeatability was tested. Repeatability between sessions was high (t-test, $p > 0.90$ for all comparisons). Shells were placed with the aperture facing the plane of the camera and distance between shells and camera was large enough (respect to shell size) to minimize the error caused by the optical distortion of the lens (Zelditch et al. 2004). Eight landmarks to analyze shape variation were selected following the criteria of Conde-Padín et al. (2007) with slight modifications (Figure 3 B). Three landmarks (1, 6 and 7) were of type I (points where at least two distinct structures meet; i.e. the posterior tip of the body) and the remaining five landmarks of type II (points that are supported by geometric criteria; i.e. border of the suture of the last anfract) (Bookstein 1991). These landmarks are typically chosen to study shell variation in snails (Chiu et al. 2002; Cruz et al. 2012; Avaca et al. 2013; Vergara et al. 2016, Vaux et al. 2017; Amini-Yekta et al. 2019). Landmark coordinates were obtained by using TPSDig v.2 software (Rohlf 2001).

Translation, rotation and scale effects were removed by Generalized Procrustes Analysis (GPA) (Zelditch et al. 1998; Adams et al. 2004). In this method, landmark configurations are superimposed by least squares optimization and the process is iterated to compute the mean shape (Atchley and Hall 1991; Zelditch et al. 2004). After GPA, shape differences were analyzed by Procrustes distance differences. Centroid size (CS), which is calculated as the square root of the sum of the squared deviations of landmarks from a centroid (Bookstein 1991; Zelditch et al. 2004) for each specimen was used as a size proxy. The centroid size is a measure of size uncorrelated with all pure shape changes (Bookstein 1991). One-way ANOVA was used to compare the means of the centroid size between the three populations. Tukey test was used for *post-hoc* analyses.

The presence of allometry (changes in shape related to changes in size) was examined by a multivariate regression analysis between shape scores as a dependent variable (Procrustes coordinates) and centroid size (CS) as an independent variable. A canonical variation analysis (CVA) was performed, including the study site as a categorical variable, in order to obtain the Procrustes distances matrix. Subsequently, the main tendencies in shape variation between specimens within samples were summarized through PCA of the variance-covariance matrix of the Procrustes coordinates. All shape analyses were performed by using MorphoJ v1.05d (Klingenberg 2011). More details of the framework of geometric morphometrics using landmarks can be found in Zelditch et al. (2004).

RESULTS

The analysis of the six morphometric indexes based on *Z. dufresnei* shell morphology showed significant differences between populations (Kruskal-Wallis, $p < 0.01$). General roundness (GR) and relative shape of the aperture (RSA) indexes were significantly higher in the individuals from San Antonio Bay (BSA) compared to the other populations (Table 1). Regarding relative length of the aperture (RLA) and relative expansion of the aperture (REA), individuals from Mar del Plata (MDQ) presented higher values than individuals from BSA and San Matias Gulf (GSM) (Table 1). Relative weight index of the shell (RWS) presented higher values in individuals from BSA.

Regressions between AL and TL were significant for the three populations studied (BSA $F_{1, 75} = 114.52$, IC β: 0.58 – 0.84; GSM $F_{1, 77} = 289.80$, IC β: 0.67 – 0.85; MDQ $F_{1, 98} = 361.16$, IC β: 0.68 – 0.84) (Table 2). Comparison of regression model between sexes was not significant for BSA and GSM (ANCOVA, $p > 0.05$), but was significant for MDQ. Regression between AW and TL was significant for the three populations (BSA $F_{1, 74} = 49.52$, IC β: 0.18 – 0.32; GSM $F_{1, 60} = 36.89$, IC β: 0.14 – 0.28; MDQ $F_{1, 81} = 148.60$, IC β: 0.24 – 0.33) (Table 2). There were not significant differences between sexes for the populations. Regressions between log(SW) and log(TW) were significant (BSA $F_{1, 52} = 216.04$, IC β: 0.90 – 1.18; GSM $F_{1, 53} = 18.17$, IC β: 0.24 – 0.67; MDQ $F_{1, 57} = 89.51$, IC β: 0.54 – 0.83) (Table 2). Comparison between sexes revealed no significant differences for the populations BSA and MDQ,

Table 1. Morphometric indexes for *Zidona dufresnei*. GR: general roundness, RLA: relative length of the aperture, RWA: relative width of the aperture, REA: relative expansion of the aperture, RSA: relative shape of the aperture, RWS: relative weight of the shell, BSA: San Antonio Bay, GSM: San Matías Gulf, MDQ: Mar del Plata.

		GR	RLA	RWA	REA	RSA	RWS
BSA	Mean ± SD	0.45 ± 0.05	0.73 ± 0.05	0.23 ± 0.02	0.52 ± 0.06	0.32 ± 0.04	0.61 ± 0.06
	Min-max	0.38-0.73	0.44-0.82	0.20-0.36	0.28-0.77	0.27-0.50	0.51-0.74
GSM	Mean ± SD	0.33 ± 0.03	0.74 ± 0.03	0.22 ± 0.02	0.65 ± 0.05	0.30 ± 0.03	0.16 ± 0.03
	Min-max	0.21-0.40	0.61-0.81	0.18-0.26	0.48-0.80	0.24-0.35	0.10-0.22
MDQ	Mean ± SD	0.34±0.04	0.76 ± 0.05	0.23 ± 0.02	0.66 ± 0.06	0.30 ± 0.03	0.25 ± 0.06
	Min-max	0.24-0.60	0.62-0.88	0.18-0.28	0.54-0.78	0.23-0.37	0.17-0.47

SD: standard deviation, min: minimum, max: maximum.

Table 2. Parameters of the relationships (linear regression analyses) obtained for *Zidona dufresnei*. TL: total length, AL: aperture length, AW: aperture width, SW: shell weight, TW: total weight, BSA: San Antonio Bay, GSM: San Matías Gulf, MDQ: Mar del Plata. R^2 values are expressed in parenthesis. All regressions were significant ($p < 0.01$).

	Females	Males	Total
BSA	AL = 0.7176TL + 2.2186 (0.68)	AL = 0.6918TL + 3.5171 (0.55)	AL = 0.7114TL + 2.2889 (0.60)
	AW = 0.2363TL – 0.9183 (0.39)	AW = 0.2782TL – 3,8232 (0.50)	AW = 0,2489TL – 1,6614 (0.46)
	SW = 0.42TW$^{1.09}$ (0.84)	SW = 0.62TW^{0,996} (0.77)	SW = 0.5085TW^{1,0423} (0.80)
GSM	AL = 0.7701TL – 4.6479 (0.82)	AL = 0.7407TL – 0.1231 (0.72)	AL = 0.7634TL – 3.8373 (0.79)
	AW = 0.2467TL – 4.1621 (0.46)	AW = 0.1739TL + 8.9763 (0.29)	AW = 0.2142TL + 1.6694 (0.38)
	SW = 4.86TW$^{0.47}$ (0.32)	SW = 7.28TW$^{0.44}$ (0.19)	SW = 5.096TW$^{0.4563}$ (0.26)
MDQ	AL = 0.7317TL + 6.1449 (0.81)	AL = 0.8004TL – 7.4892 (0.79)	AL = 0.7707TL – 1.3581 (0.78)
	AA = 0.289LT – 9.407 (0.69)	AA = 0.2759LT – 7.2562 (0.57)	AA = 0.2843LT – 8.6399 (0.65)
	SW = 1.16TW$^{0.76}$ (0.72)	SW = 1.77TW$^{0.62}$ (0.53)	SW = 1.293TW$^{0.6846}$ (0.61)

while for GSM females presented heavier shell than males (ANCOVA, $p < 0.01$). When comparing regression models between BSA and MDQ and between BSA and GSM, significant differences in the slope were observed (β BSA $\neq$ β GSM, $p < 0.05$; β BSA $\neq$ β MDQ, $p < 0.01$), while comparing GSM and MDQ no significant differences were observed.

PCA conducted with morphometrical indexes explained 75.9% of total variation of data when the first two components were used (Figure 4). In this analysis, individuals from GSM and MDQ populations presented some degree of overlapping. *A posteriori* comparisons revealed significant differences between GSM and BSA and between MDQ and BSA, while no differences were detected between GSM and MDQ.

Geometric morphometric analyses showed a significant difference in centroid size (CS) among populations. Comparison of the centroid size (CS) between populations showed that individuals from GSM (CS: 2.99) were significantly larger than individuals of MDQ (CS: 2.82) and BSA (CS: 2.31) (ANOVA: $F_{2, 65} = 843$, $p < 0.01$). Multivariate regression of shape on CS was significant (permutation test with 10,000 random permutation, $p < 0.01$). Thus, subsequent analyses were performed with the residuals of the regression which are free of allometric effects. PCA explained 87.8% of total shape variation when the first four components were considered (PC1 61.1%, PC2 12.4%, PC3 9.8% and PC4 4.4%). Individuals from BSA were represented by positive values of PC1 which means a more rounded-shape shell

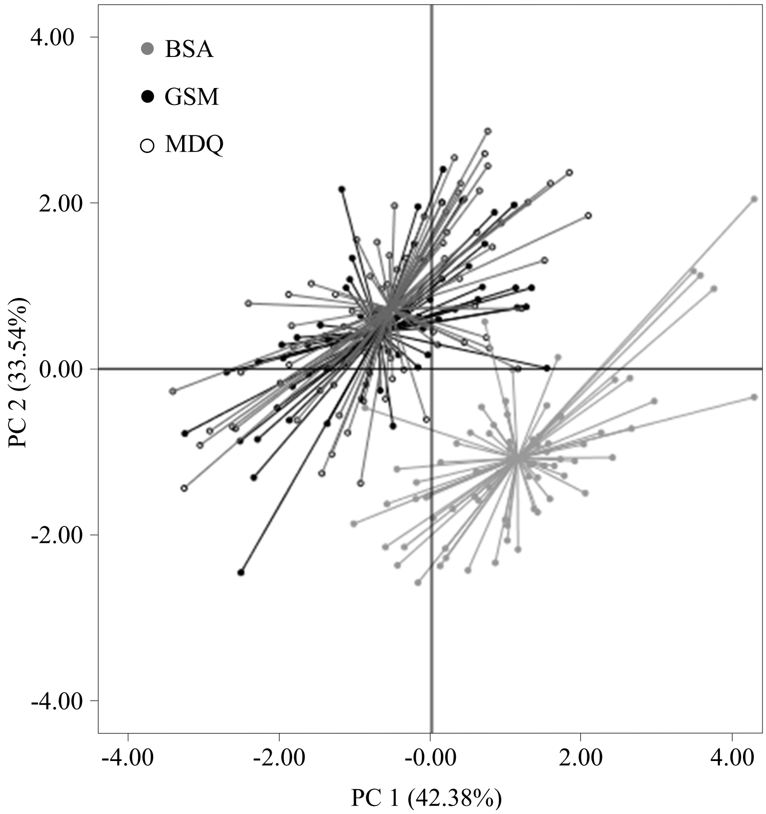

Figure 4. Principal Component Analysis (PCA) for shell shape variation of *Zidona dufresnei* with percentage of explained variance. GSM: San Matías Gulf, BSA: San Antonio Bay, MDQ: Mar del Plata.

than individuals from GSM and MDQ (Figure 5). Analysis of canonical components revealed a smaller distance between individuals from MDQ and GSM, and higher distance between individuals from BSA and MDQ (Procrustes distance: BSA-GSM: 0.0878; BSA-MDQ: 0.0954; GSM-MDQ: 0.0381, $p < 0.01$) (Figure 6).

DISCUSSION

Studying the adaptation of a population to a changing environment, whether modeled by selection, plasticity or the interaction of both, is an ongoing challenge in evolutionary studies (Reed et al. 2011; Grenier et al. 2016). These studies contributed to elucidate different local adaptive strategies to avoid predation or reduce intraspecific competition, among others (Trussell 1996; Marchinko 2003; Andrade and Solferini 2006; Hollander et al. 2006; Avaca et al. 2013).

Morphometric techniques, both traditional and geometric, have been widely used in ecological and evolutionary studies (Carvajal-Rodríguez et al. 2005; Fedosov et al. 2011; Epherra et al. 2015). Shape variation of body structures, such as shells in gastropods, has a genetic basis but is also influenced by environmental and epigenetic processes (Atchley and Hall 1991; Valentin et al. 2002; Rufino et al. 2006; Amini-Yekta et al. 2019). Therefore, to fully understand factors that determine shape it is necessary to consider the ontogenetic development and also adaptations to

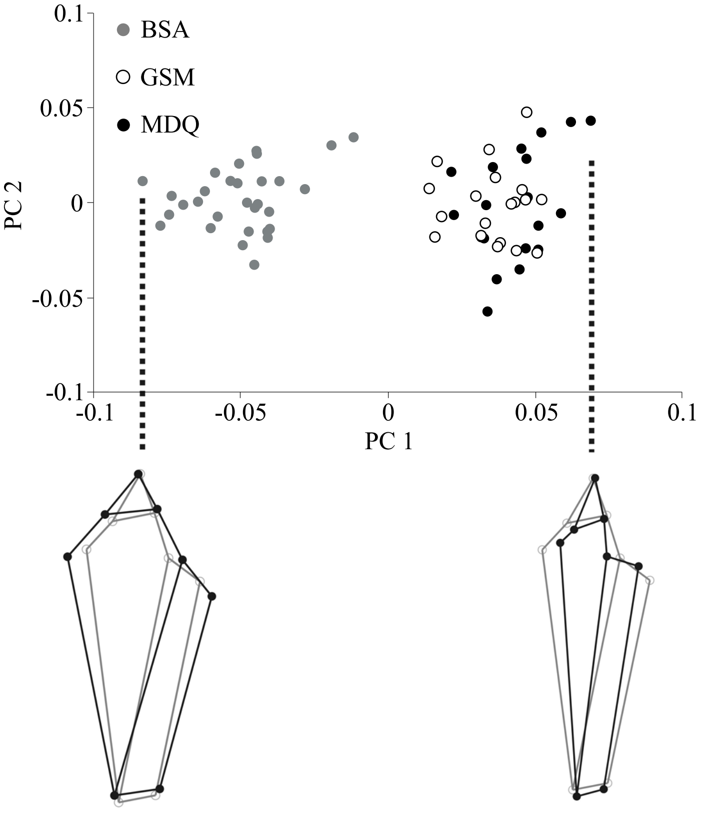

Figure 5. Principal Component Analysis (PCA) of Procrustes coordinates for *Zidona dufresnei* that explains 87.8% of total variation of data. GSM: San Matías Gulf, BSA: San Antonio Bay, MDQ: Mar del Plata.

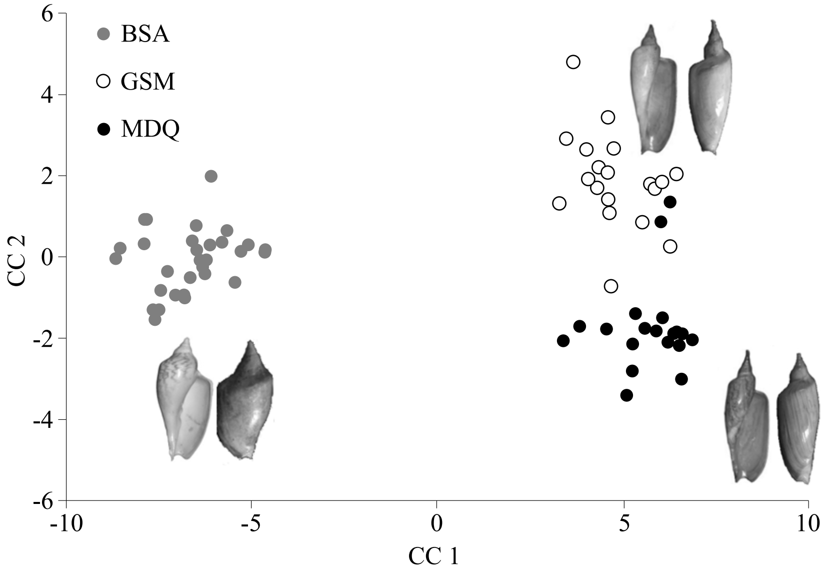

Figure 6. Canonical analysis of Procrustes coordinates of the shell of *Zidona dufresnei*. GSM: San Matías Gulf, BSA: San Antonio Bay, MDQ: Mar del Plata, CC: canonic components.

environment besides genetics (Hanken and Wake 1991; Lombard 1991; Müller 1991). In this paper, we combined traditional and geometric morphometric tools to analyze at the first time the shell morphology variation of *Z. dufresnei* in different locations along the geographical distribution of the species. According to these results, the three populations presented significant differences in size, but also in shell shape, showing allometric effects between populations. The analysis of morphological indexes showed that the shell of the individuals from BSA presented a higher value of general roundness compared to individuals from GSM and MDQ. In the case of relative length and width of the aperture, individuals from MDQ presented the highest values. The relative weight of the shell was higher in individuals from BSA. In general terms, individuals from BSA presented a shell characterized by a higher general roundness and relative weight, and lower relative aperture compared to individuals from GSM and MDQ. This was reflected in the multivariate analysis where individuals from BSA were notably different from individuals of MDQ and GSM.

Mean values of shell length and width were significantly different between individuals of the three populations studied. Comparisons between regression models showed that main differences between BSA and GSM were related to the size of individuals since the relationships between length and width with total length were represented by the same model. When MDQ and GSM populations were compared, individuals from GSM presented larger shells than individuals from MDQ. The differences found in morphological variables in the present study may be related to differences in individual growth of each population (Giménez et al. 2004), and to particular environmental conditions at each location. The observed differences in maximum size between MDQ and GSM individuals could be also related to a long-term anthropogenic selection pressure by fishing which decreases the relative frequency of individuals with large body sizes. MDQ population has been directly exploited by the Argentinean and Uruguayan fleets for the last 40 years and seems to be in the over-exploitation phase (Giménez et al. 2005) while GSM population is not under direct fishing pressure and only sporadically caught as bycatch of demersal trawling fleet.

Previous studies pointed out that the aperture of the shell is a highly variable area where sexual dimorphism is expressed. For example, Family Bursidae is characterized by differences in the aperture borders between sexes (Beu 1998). For genera *Buccinum* and *Buccinanops,* differences in size of the aperture were reported between sexes with higher apertures in males than in females (Hallers-Tjabbes 1979; Avaca 2010; Avaca et al. 2013). However, our results did not reveal differences in aperture length and width between sexes, suggesting that such responses may vary according to the family under analysis.

Geometric morphometrics analysis allowed us to separate the individuals from the three populations, being GSM and MDQ the most similar. Main variations were observed in the size and volume of individuals. This result is in agreement with those obtained by traditional morphometric analysis. In general, size was the variable that explained the highest variation (70% of the total variation). When the effects of size and allometry were removed and only shape variation was considered for comparisons, a separation of populations through the principal axis of shape variation was clearly evident. GSM and MDQ showed similar shell shape morphology compared to BSA.

Comparisons between individuals of the same species from different sites or under different environmental conditions, using the combined approach of traditional and geometric morphometrics have been conducted in previous studies. Bigatti and Carranza (2007), studying the effect of the occurrence of imposex in *Odontocymbiola magellanica* from Patagonian waters detected some differences in shell shape and body using both univariate and multivariate approaches. Additionally, shape variations were determined for *Buccinanops deformis* in three populations of Patagonia (Argentina) using both techniques (Avaca 2010). Differences in shell shape were detected using geometric morphometrics that remained undetected by traditional morphometrics in two sympatric ecotypes of *Littorina saxatilis* (Carvajal-Rodríguez et al. 2005). This species also showed a larger aperture on exposed shores and a smaller aperture on sheltered shores in response to predation (Conde-Padín et al. 2009). In the case of *Z. dufresnei*, traditional and geometric morphometrics were useful both to describe and to quantify the shell shape variation observed between populations. These methods were reliable for distinguishing individuals from different locations based solely on their shell shape. Although the two morphotypes were much better separated by geometric morphometrics approach, traditional morphometrics were useful as a complementary technique since it allowed working with a larger number of samples. The number of samples available for geometric morphometrics was limited because it was difficult to access to individuals in good shape condition since samples from MDQ and GSM belonged to fisheries catches.

Our results support the hypothesis of Lahille (1895) who classified the individuals from BSA as a ‘dwarf’ morphotype based on shell morphology, highlighting the need to revise the taxonomic status of *Zidona*. Unfortunately, there are not published genetic data to validate the two species hypothesis from a molecular approach. The marked shell variations detected among populations of *Z. dufresnei* may be driven by several ecological factors other than growth pattern, such as changes in prey availability, presence of predators, and temperature (e.g. Dalziel and Boulding 2005; Doyle et al. 2010). BSA corresponds to an intertidal zone where snails are exposed to highly variable environmental conditions with clines of food availability, wave exposure, desiccation and presence of predators, contrasted with GSM and MDQ (Roche et al. 2011). These environmental pressures (Raffaelli and Hawkins 1999; Chapman 2000) may favor smaller size (i.e. the occurrence of a ‘dwarf’ morphotype population), higher general roundness and relative weight, and also smaller relative aperture in the individuals from BSA.

At the same time, certain characteristics of life history of *Z. dufresnei*, such as direct intracapsular development (Penchaszadeh and De Mahieu 1976; Giménez and Penchaszadeh 2002) and restricted range of spatial dispersion (Penchaszadeh et al. 1999; Pereyra et al. 2009; Roche et al. 2011, 2013) may have resulted in a reduction of gene flow among populations leading to such adaptations to local conditions. Considering that GSM and MDQ individuals were similar in size and shell shape morphology but showed the longest distance between them, ecotypes adapted to different conditions should be maintained as the most probable explanation for the variation between dwarf and normal morphotypes unless new data contradict this. In summary, issues affecting size and shell shape variation in *Z. dufresnei* are multiple and not mutually exclusive. Additional experimental studies are needed to sort out the role of the physical and ecological factors on the shell shape and to test whether this variation has an adaptive value. On the other hand, further investigation is needed to better understand if the phenotypic variation observed in shell morphology is also expressed at genetic level. This is also highlighted in the case of *Z. dufresnei* which is under an increasing fishing pressure.

The authors declare that they have no conflict of interest. No animal testing was performed during this study. All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

The study material is cataloged in the collection deposited at the Laboratory of Benthic Resources. Center for Applied Research and Technology Transfer in Marine Resources Almirante Storni (CIMAS). The data sets generated during and/or analyzed during the current study are available from the corresponding author at reasonable request.

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BACK-CALCULATION OF TOTAL LENGTH OF ARGENTINE SEABASS *Acanthistius patachonicus* USING MORPHOMETRIC RELATIONSHIPS OF BONES AND MEASUREMENTS OF THE BODY

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ABSTRACT. Predictive regression equations were generated to estimate total length of the Argentine seabass (*Acanthistius patachonicus*) using skull and pectoral girdle bones, specific body, and otolith lengths. Regressions of skull and pectoral girdle bones, specific body and otolith lengths were all statistically significant. Generating regressions between specific bones and external characteristics of the body meaningfully increases the ability to analyse the information obtained from studies of stomach contents of predator fish from the Southwestern Atlantic Ocean.

Key words: Diagnostic bones, piscivores, top predators, diet.

INTRODUCTION

Argentine seabass or “mero” *Acanthistius patachonicus* (Jenyns, 1842) is a benthic-demersal fish that inhabits both soft and hard bottoms at depths not exceeding 100 m. Distribution of this species ranges from 30° S (Brazil) to 48° S (Patagonia, Argentina) in the Southwestern Atlantic (SWA) (Cousseau and Perrotta 1998). Argentine seabass comprises an important prey for top predators such as the South American sea lion (*Otaria flavescens*), cooper shark (*Carcharhinus brachyurus*), tope shark (*Galeorhinus galeus*) and grey nurse shark (*Carcharias taurus*) (Koen Alonso et al. 2000; Lucifora 2003; Lucifora et al. 2006).

It is important to determine the role that each species plays within the ecosystem and its position in the trophic network for a better understanding of predator-prey interactions (Pauly et al. 1998b). Interactions between species affect the dynamics of marine fish populations (Alonso et al. 2003), while community structures are strongly influenced by piscivorous predators (Lyons and Magnuson 1987; Tonn et al. 1992; Scharf et al. 1997). On the other hand, studies in trophic

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†Deceased 16 September 2015.

ecology have become relevant in recent years because of their use in the construction of indices for evaluating the health of ecosystems (Pauly et al. 1998a, 1998b). Regarding these indices, the trophic level has been extensively used to evaluate the state of fisheries, as well as to determine the existence of over-exploitation and the sustainability of these fisheries over time (Pauly et al. 1998a, 2001, 2002). Therefore, it is extremely important to accurately achieve great precision in the evaluation of the diet of any predator, including size and weight of the ingested prey, information that is essential to define future management and conservation strategies (Cherel et al. 2000).

Because of the difficulty of directly assessing a predator's diet by field observations, feeding studies are based on the examination of stomach contents that have not been fully digested. Usually, the identification of prey species, as well as the estimation of their length and weight, has been based on the analysis of otoliths. The otolith is a calcified structure that is differentially digested in the stomach of predators, completely dissolved (North et al. 1984; Jobling and Breiby 1986) or significantly eroded modifying their morphology and making measurements and taxonomic identification more complex (Johnstone et al. 1990). Thereby, the presence of certain species could be underestimated or ignored, leading to biased estimates of the original prey sizes and the amount of prey consumed (Jobling and Breiby 1986). Diagnostic bones concerning the body length allow estimating both the ingested biomass as the prey age class in the study of the diet of piscivorous predators (Gosztonyi et al. 2007). Nowadays, skull and shoulder girdle bones are a complement of the use of otoliths in diet studies because of its resistance to digestion (Hansel et al. 1988; Scharf et al. 1997, 1998; Gosztonyi et al. 2007; González Zeballos et al. 2010; Perez Comesaña et al. 2013, 2014).

This paper presents the linear regression and predictive total length equations for *A. patachonicus* based of the length of the cranial bones, scapular bones, otoliths and specific body measurements. These equations constitute a complementary tool to optimize the quantitative studies of the diet of marine piscivorous predators.

MATERIALS AND METHODS

Two hundred specimens of *A. patachonicus* captured by commercial bottom trawl vessels operating at Puerto Quequén, Buenos Aires Province, Argentina (fishing area: 38° 40′ S-39° 50′ S, 57° 68′-60° 08′ W) during 2013, were analysed. Total length, predorsal length, preanal length and head length in centimetres (± 1 mm) were registered (Figure 1) and immediately frozen. Diagnostic bones were selected according to Gosztonyi and Kuba (1996). Fish were placed in boiling water for a period no longer than 2 min, depending on the size of the specimen, to remove bones. Once separated from the soft tissues, bones were measured using a calliper (± 0.05 mm) (Figure 2). Least square regression equations were generated using INFOSTAT/L (Di Rienzo et al. 2010) to predict original total length of *A. patachonicus* based on the predorsal, preanal and head lengths. In addition, skull bones measurements such as hyoid bar length, cleithrum length, dentary length, maxilla length, premaxilla length, opercle length, preopercle length, vomer length, hyomandibula length, parasphenoids length and otolith length have been used (Figure 2). Total lengths were regressed on measurements of the remaining bones.

RESULTS

Total length of Argentine seabass ranged between 207 and 584 mm. Regressions relating body measurements to total length were highly significant ($p < 0.0001$). The coefficient of determination (r^2) related to body measurements took

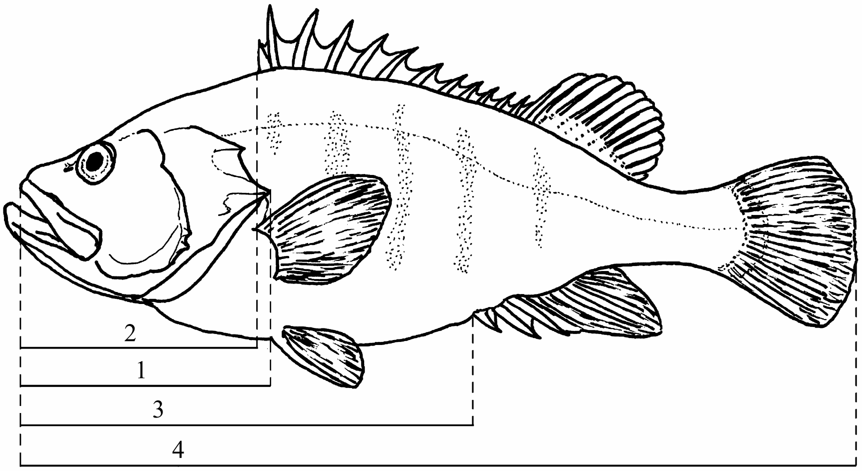

Figure 1. Body length measurements of *Acanthistius patachonicus*. 1: length of the head, 2: predorsal length, 3: preanal length, 4: total length.

values between 0.88 and 0.96, being the preanal length the one that showed a better fit (Table 1). Also, values of the coefficient of determination for the lengths of diagnostic bones varied between 0.90 and 0.96. The best fit was obtained with the preopercle (measure 2, Figure 2) (r^2 = 0.96), slightly higher than those obtained with the opercle, hyoid bar, dentary (measure 1, Figure 2), all of them with r^2 = 0.95, and the cleithrum (r^2 = 0.94), as well as the otolith length also showed a good fit (r^2 = 0.91) (Table 1).

All measurements, whether from diagnostic bones or from body lengths or otoliths, showed significant relationship with total length. Regressions obtained from diagnostic bones, especially preopercle (measure 2), dentary (measure 1), opercle, hyoid bar and cleithrum appear to be reliable predictors of the length of *A. patachonicus*.

DISCUSSION

It is well known that the external morphology of a prey fish can be distorted by the effect of the predator's digestive process, which can lead to biased measurements. If prey was consumed recently, external morphological measurements can be estimated in an accurate way, becoming an appropriate alternative to that of the diagnostic bones, as is the case of the preanal length in the present work. However, back-calculation of the original dimensions of a fish from measurements of diagnostic bones is not as susceptible to error as that taken from external body measurements (Perez Comesaña et al. 2013).

It must also be recognized that reconstruction of the original size of fish prey from diagnostic bones has some limitations. The effect of preservatives on bone size should be taken into consideration if stomach contents are stored in a chemical stabilizer (Hansel et al. 1988; Scharf et al. 1997). Another potential problem is the use of boiling water to facilitate the separation of soft tissue bones. It can cause deformation and contraction of bones if an excessive time elapses between boiling and taking of measurements. These drawbacks were avoided in the present work since individuals were frozen, then thawed and boiled at controlled time intervals and subsequently measured after extraction and separation of bones.

In recent studies of the early development of *A. patachonicus*, preopercle complex has been pointed out as the most important characteristic

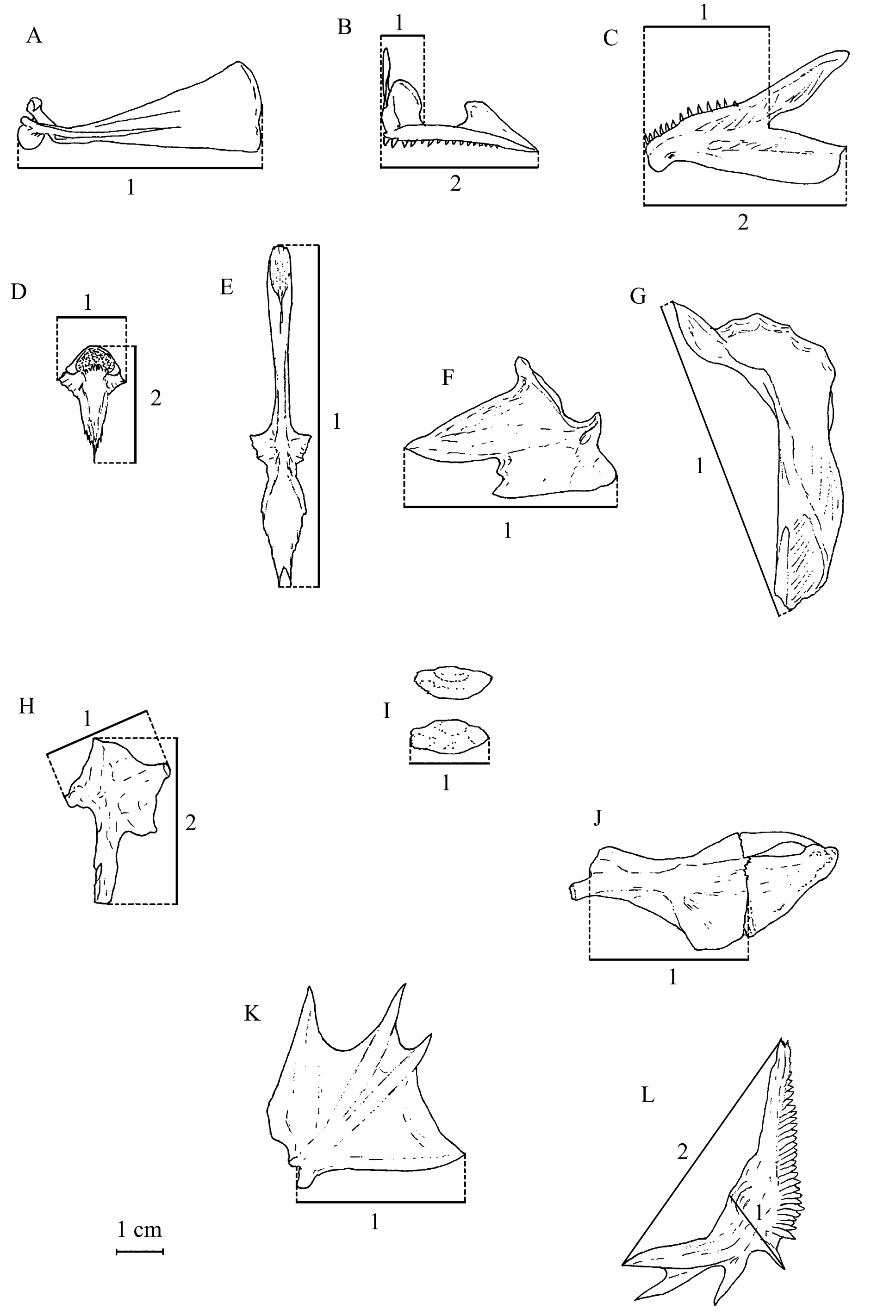

Figure 2. Bones and otolith measurements. A: maxilla, B: premaxilla, C: dentary, D: vomer, E: parasphenoids, F: angular, G: cleithrum, H: hyomandibula, I: otoliths, J: hyoid bar, K: opercle, L: preopercle. Numbers (1) and (2): registered measurements.

Table 1. Estimated parameters of predictive regression equations of data versus total length *Acanthistius patachonicus* (y = a + bx). x: variable in mm, y: total length in mm, n: sample size, r^2: coefficient of determination, SE: standard error, CI: confidence interval. Numbers (1) and (2): measurements illustrated in Figure 2.

Variables (mm)		n	r^2	a ± SE (CI 95%)	b ± SE (CI 95%)
a. Maxilla	(1)	200	0.93	-6.03 ± 6.71 (-19.26 – 7.20)	8.18 ± 0.15 (7.87 – 8.48)
b. Premaxilla	(1)	193	0.92	-12.04 ± 7.80 (-27.42 – -3.34)	49.84 ± 1.08 (47.71 – 51.97)
	(2)	199	0.93	-10.19 ± 6.80 (-23.61 – 3.23)	11.98 ± 0.23 (11.53 – 12.43)
c. Dentary	(1)	197	0.95	-8.46 ± 5.93 (-20.15 – 3.23)	16.78 ± 0.28 (16.23 – 17.33)
	(2)	196	0.90	26.81 ± 7.50 (12.02 – 41.60)	16.78 ± 0.28 (16.23 – 17.33)
d. Vomer	(1)	193	0.93	11.05 ± 6.96 (-2.68 – 24.77)	36.82 ± 0.76 (35.33 – 38.42)
	(2)	191	0.91	-9.28 ± 8.27 (-25.59 – 7.03)	15.48 ± 0.36 (14.78 – 16.19)
e. Parasphenoid	(1)	191	0.92	-30.00 ± 8.22 (-46.22 – -13.79)	6.21 ± 0.14 (5.94 – 6.48)
f. Angular	(1)	197	0.91	-1.10 ± 7.82 (-16.53 – 14.33)	9.34 ± 0.21 (8.93 – 9.75)
g. Cleithrum	(1)	180	0.94	-7.82 ± 7.00 (-21.63 – 5.99)	5.18 ± 0.10 (4.98 – 5.38)
h. Hyomandibula	(1)	197	0.93	0.75 ± 6.95 (-12.97 – 14.46)	16.62 ± 0.33 (15.97 – 17.28)
	(2)	187	0.93	-6.12 ± 6.77 (-19.47 – 7.24)	12.10 ± 0.23 (11.64 – 12.55)
i. Otolith	(1)	197	0.91	-114.94 ± 10.58 (-135.82 – -94.07)	31.30 ± 0.72 (29.89 – 32.72)
j. Hyoid bar	(1)	196	0.95	-19.32 ± 6.04 (-31.24 – -7.40)	12.98 ± 0.21 (12.56 – 13.04)
k. Opercle	(1)	198	0.95	12.77 ± 5.71 (1.50 – 24.04)	11.07 ± 0.19 (10.70 – 11.44)
l. Preopercle	(1)	198	0.90	-17.44 ± 8.81 (-34.82 – -0.06)	19.75 ± 0.48 (18.81 – 20.69)
	(2)	198	0.96	-17.63 ± 5.01 (-27.51 – -7.75)	7.56 ± 0.10 (7.35 – 7.76)
Head length		185	0.89	11.55 ± 8.60 (-5.42 – 28.52)	2.96 ± 0.08 (2.81 – 3.12)
Predorsal length		183	0.88	53.66 ± 8.13 (37.61 – 69.71)	2.95 ± 0.08 (2.79 – 3.11)
Preanal length		185	0.96	24.58 ± 4.84 (15.03 – 34.13)	1.65 ± 0.02 (1.60 – 1.70)

that allowed the reconstruction of the development from larva to adult stage (Villanueva Gomila et al. 2015). Our results showed that two bones from the preopercle complex (preopercle and opercle) are also important as predictors of total length of *A. patachonicus*. Likewise, our results showed as well that dentary, hyoid and cleithrum bar bones, aside from the distance to the anterior insertion of the anal fin, are also good predictors of total length of *A. patachonicus*.

We have found that all measurements of the cranial bones of *A. patachonicus* showed a significant relationship with total length and that regressions obtained from diagnostic bones were reliable predictors of length. Thereby, regression equations calculated from cranial bones and external body measurements presented in this work increased the quali-quantitative potential of the information obtained from the analysis of stomach contents of piscivorous predators of the Southwestern Atlantic Ocean.

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DEVELOPMENT MORPHOLOGY OF *Undaria pinnatifida* SPOROPHYTES (PHAEOPHYCEAE, ALARIACEAE) IN CALETA CORDOVA (CHUBUT, ARGENTINA)

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ABSTRACT. *Undaria pinnatifida* is an invasive brown algae that has been found on the Argentine coast since 1992. This work aims to follow the ontogeny of sporophytes, from egg fecundation to thallus senility, and thereby contribute to information on the development of the species in San Jorge Gulf. Sporophytes obtained in the laboratory were used to study the first stages of development, while samples collected from field population were used to describe advanced stages. Morphological observations were carried out on fronds, stipes, midrib, sporophylls and holdfasts of thalli at different developmental stages, and they was interpreted related to its functionality. Sporophytes described as typical and distant forms were found, and their location in the coastal zone was determined. Primary growth of sporophyte begins in the intercalar meristoderm located between the frond and the stipe. The upper portion of the intercalar meristem produces a row of small pinnules, and its lower portion is the origin of the lateral stipe ribbons. The thallus area and growth in thickness occur through a meristoderm in the frond surface. Characteristic morphological structures such as gland cells, filaments and trumpet cells, and cryptostomata were observed. Some of the gland cells lead to the formation of hair-filled cryptostomata. This work contributed to increase the knowledge of anatomical characteristics of the thallus at different moments of development of this invasive species.

Key words: Morphology, *Undaria pinnatifida*, invasive species, San Jorge Gulf, sporophytes, meristoderm.

INTRODUCTION

Undaria pinnatifida (Harvey) Suringar, 1873 is an invasive brown algae, native from Japan, southern China and Korea (Saito 1975). This species was introduced in several coastal areas and has become established in the Mediterranean Sea, European Atlantic, New Zealand, Australia, Tasmania and Argentina. The arrival of *Undaria* to the Mediterranean coast was reported by Perez et al. (1981), and it is believed that it was introduced along with the Japanese oyster *Cassostrea gigas* for cultivation (Boudouresque et al. 1985; Floc'h et al. 1991). Later, *Undaria* was recorded along the coast of Brittany and was subsequently registered on the Atlantic coasts of England and Spain (Perez et al. 1984; Santiago Caamaño et al. 1990; Fletcher and Manfredi 1995). Numerous works on the introduction and dispersal of *Undaria* on the European coasts (Hay 1990; Rismondo et al. 1993; Salinas et al. 1996; Cecere et al. 2000; Peteiro 2008; Minchin and Nunn 2014; Minchin et al. 2017, among many others), the Northeast Pacific (Silva et al. 2002; Aguilar-Rosas et al. 2004; Thornber et al. 2004; Dietrich and Lonhart 2010) and the Southern hemisphere (Hay and Luckens 1987; Stapleton 1988; Sanderson 1990; Campbell and Burridge 1998) can be mentioned.

In particular, on the Argentine coast (Figure 1) it was first detected in Nuevo Gulf in 1992 (Piriz and Casas 1994; Casas and Piriz 1996). By 1997, the species expanded 4.6 km north and 6.1 km south, while in 1999 it was found 12 km north and 22 km south (Piriz and Casas 2001; Casas et al. 2008). At the end of 2000, *Undaria* was registered on the coast of Camarones Bay (approximately 300 km south of Nuevo Gulf). In mid-2005, *Undaria* was observed for the first time on the shores of Puerto Deseado estuary, 600 km south of the first point of entry (Martin and Cuevas 2006), and since then no records of the species further south have been made. During the first years of the invasion, the species only spreaded to the south, suggesting that Valdés Peninsula represented a natural barrier to its dispersal; notwithstanding it was observed in San José Gulf in 2008. Consequently, it is estimated that its arrival to San Matías Gulf was in 2010 (Pereyra et al. 2014), while its presence on the coasts of Buenos Aires Province (Mar del Plata city) was documented in 2011 (Meretta et al. 2012), thus leading to the speculation that it could reach Uruguay and even southern Brazil (Dellatorre et al. 2014).

The introduction of *U. pinnatifida* can occur accidentally, as in the case of the Mediterranean Sea (Perez et al. 1984), the Venice Lagoon (Curiel et al. 1994), New Zealand (Hay and Luckens

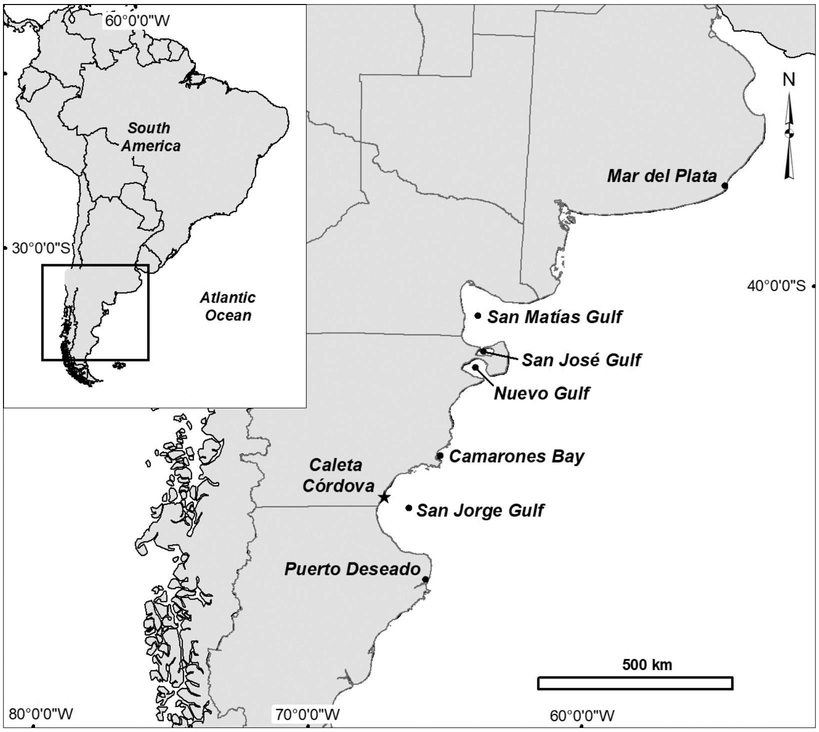

Figure 1. Study area indicating locations in the Patagonian coast of Argentina.

1987) and Argentina (Piriz and Casas 1994), or intentionally for aquaculture. This species was first introduced for culture experiments on the coast of Brittany (Perez et al. 1984; Castric-Fey et al. 1993) and was subsequently introduced in Spain for the same purpose (Perez-Cirera 1997; Peteiro 2001 in García and Peteiro 2015). The most important vector of accidental dispersion is via maritime traffic through fouling on ship hulls, such as gametophytes or small sporophytes, or through spores in ballast water discharge (Williams and Smith 2007). Dispersion through fouling is mentioned by Fletcher and Manfredi (1995) for Southern England, Curiel et al. (2002) for the Island of Venice, and Minchin and Nunn (2014) for Northern Europe, among others. The introduction of *Undaria* through ballast water discharge has been reported for New Zealand, Tasmania and Argentina (Hay and Luckens 1987; Sanderson 1990; Piriz and Casas 1994).

Distribution and reproductive stages of *Undaria* in Argentine coast were analyzed by Casas and Piriz (1996) after its entry into Nuevo Gulf. Subsequently, same authors studied the impact of the species on the environment and how it dispersed (Casas and Piriz, 2001). In the north of Argentine Patagonia, Pereyra et al. (2015) analyzed the expansion of the species in San Antonio Bay.

Macroalgae are characterized by their large-sized thalli, made up of a pinnate frond with a midrib, a stipe that separates the holdfast from the frond and in which the sporophylls develop upon reaching reproductive maturity, and a holdfast that adheres to the hard substrate (Guiry and Guiry 2014). This basic morphology presents an appreciable degree of variability (Yendo 1911; Okamura 1915; Castric-Fey et al. 1999; Cecere et al. 2000; Uwai et al. 2006) which has been thought to have genetic or plasticity components in the face of spatial or seasonal environmental variability. According to different authors (Stuart et al. 1999; Shibneva and Skriptsova 2012), most recognized forms of *U. pinnatifida* sporophytes are: a) Distant form, which corresponds to an elongated stipe, as long as the lamina, with large sporophylls limited to the basal area of the stipe and without proliferations; b) Typical form, with short stipe thalli and comparatively shallow sinuses between adjacent pines, far from the midrib. Upper parts of the sporophyllic zone are formed of large sporophylls (folds) confluent with the base of the frond; and c) Narutensis form (Yendo 1911) (= typical form, Okamura 1915), with very short stipes, slightly folded sporophyll zone, and ligulated proliferations of the sporophyll margins.

This study analyzes the ontogeny of the sporophyte, and aims to describe the developmental stages of *U. pinnatifida*, from egg fertilization to senility of the thallus. It represents a contribution to the knowledge of anatomical characteristics of the thallus at different moments of development of this invasive species, which have not yet been described for Caleta Cordova population (San Jorge Gulf).

MATERIAL AND METHODS

Study area is located in the central zone of San Jorge gulf (Figure 1), where *U. pinnatifida* is present. The coast of Caleta Cordova (45° 44′ 22″ S, 67° 22′ 26.9″ W) is made up of sedimentary rock with tidal pools and channels. Tides are characterized as semi-diurnal with average amplitude of 6 m (Zaixso et al. 2009). Middle and upper mesolithic horizon are covered with mussel *Perumytilus purpuratus*, while in the lower infralittoral zone *Corallina officinalis* can be found together with banks of *Aulacomya atra* and mussel *Mytilus platensis* (Gil and Zaixso 2008).

Morphological and anatomical observations of first stages of thallus development were studied in sporophytes obtained from cultures of gametophyte in the laboratory. More advanced stages were studied in sporophytes collected from field population.

Thalli at different developmental stages were collected randomly each month from lower intertidal and upper subtidal zones of the rocky shore of Caleta Cordova during extraordinarily low tides or through scuba diving when necessary. Sporophytes were collected from April 2017 to November 2017 because of during December to March there are very few sporophytes on the ground, and most of them are senile with damaged structures. A total of 80 observations of *Undaria* thalli were made.

Gametophyte cultures were obtained monthly from spores released by fertile sporophytes. Ten cultures were started each month. Sporophyll materials located on slides were cultured inside glass containers filled with 150 ml of enriched seawater renewed weekly. Gametophyte cultures were maintained in filtered seawater enriched with 1 ml of stock solution (3 g nitrates, 0.3 g phosphates, 0.7 g iron chloride, and 2 g EDTA per liter of seawater). Cultures were maintained between 10-14 °C (taking into account temperatures in natural conditions during harvest months) and irradiation of 40-80 μM $m^2 s^{-1}$ from a 40-Watt fluorescent lamp (Pang and Wu 1996) under a 12:12 light: dark cycle. Development of sporophytes in these cultures continued until the frond reached about 3 mm in length.

In order to understand development stages at tissue level, sections ranging from 2 cm long to fully developed sporophytes were taken, covering the meristematic and mature areas of the frond, midrib, sporophyll, stipe and holdfast of each specimen. Microscopic observations and photographic records of these events were taken. Whole-mount slides, cross sections and longitudinal sections were made by hand with a stainless-steel razor blade. Photographs of unstained sections were taken with a Samsung digital camera and a Zeiss Standard 25 microscope. A sample of specimens was deposited in the Herbario Regional de la Patagonia (HRP) at the Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia (HRP 7480 to HRP 7502).

The development of the sporophyte was divided into stages according to an increasing order of structural complexity with respect to the number of cells (in the embryonic stages), tissue differentiation, presence of structures (such as glandular cells, cryptostomata and trumpet cells), length of the frond, presence of pinnae, and the reproductive state of the thalli. The development of the sporophytes was divided into the following stages:

- Embryonic postzygotic thalli (Figure 2 A).
- Embryonic laminar thalli, initially monolayered, up to 2-3 mm long (Figure 2 B).
- Pre-sporophyllic juvenile thalli, before pinnae differentiation, less than 10 cm long (Figure 2 D).
- Pre-sporophyllic juvenile thalli, with differentiated pinnae, up to 30 cm long (Figure 2 E).
- Thalli, longer than 30 cm, vegetative or reproductive, with an active growth zone between the frond and stipe (Figure 2 G, 2 I and 2 J).
- Senile thalli of variable size with zones between frond and stipe completely filled with well-developed sporophyll, and immature juvenile thalli with blades and stipes damaged by environmental conditions (Figure 2 K).

RESULTS

Embryonic thalli

Two successive embryonic stages were identified. The first one was the postzygotic embryonic thalli, which was monoseriate filament of 2-20 cells long. This stage began with the longitudinal division of the filament apical cell and the development of growth zones along the edge of the tiny frond (Figure 2 A). The second stage was the embryonic laminar thalli with a length of 2-3 mm (Figure 2 B).

Germ tube (Figure 3 A) and first gametophyte cells were produced during the first two weeks after liberation of viable spores. Female gameto-

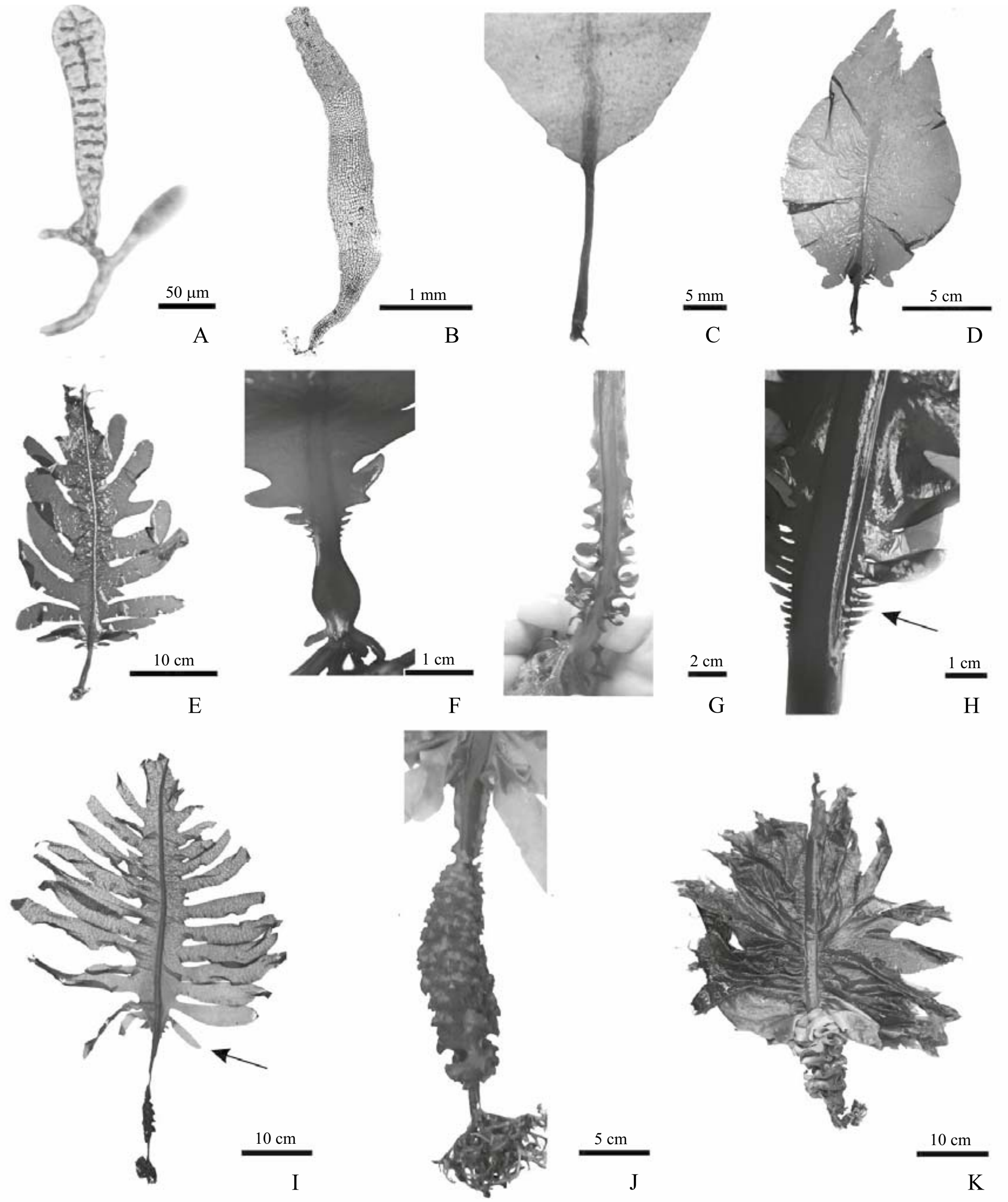

Figure 2. General external development. A) Embryonic post-zygotic thallus. B) Embryonic laminar thallus. C) Stipe before the formation of lateral wings. D) Pre-sporophyllic thallus with entire frond. E) Pre-sporophyllic thallus with pinnae. F) Initial stage of sporophyllic thallus with active growing zone between frond and stipe, and beginning of lateral wings. G) Stipe with folded sporophyll. H) Pinnulae growing into pinnae at the frond base. I) Sporophyll with frills restricted to the basal portion. This sporophyte corresponds to the distant form. J) Sporophyll in a more mature stage. K) Thallus with sporangial sori also developing on the basal portion of the frond without active growing zone remaining between the frond and the stipe. Sporophyte corresponds to the typical form.

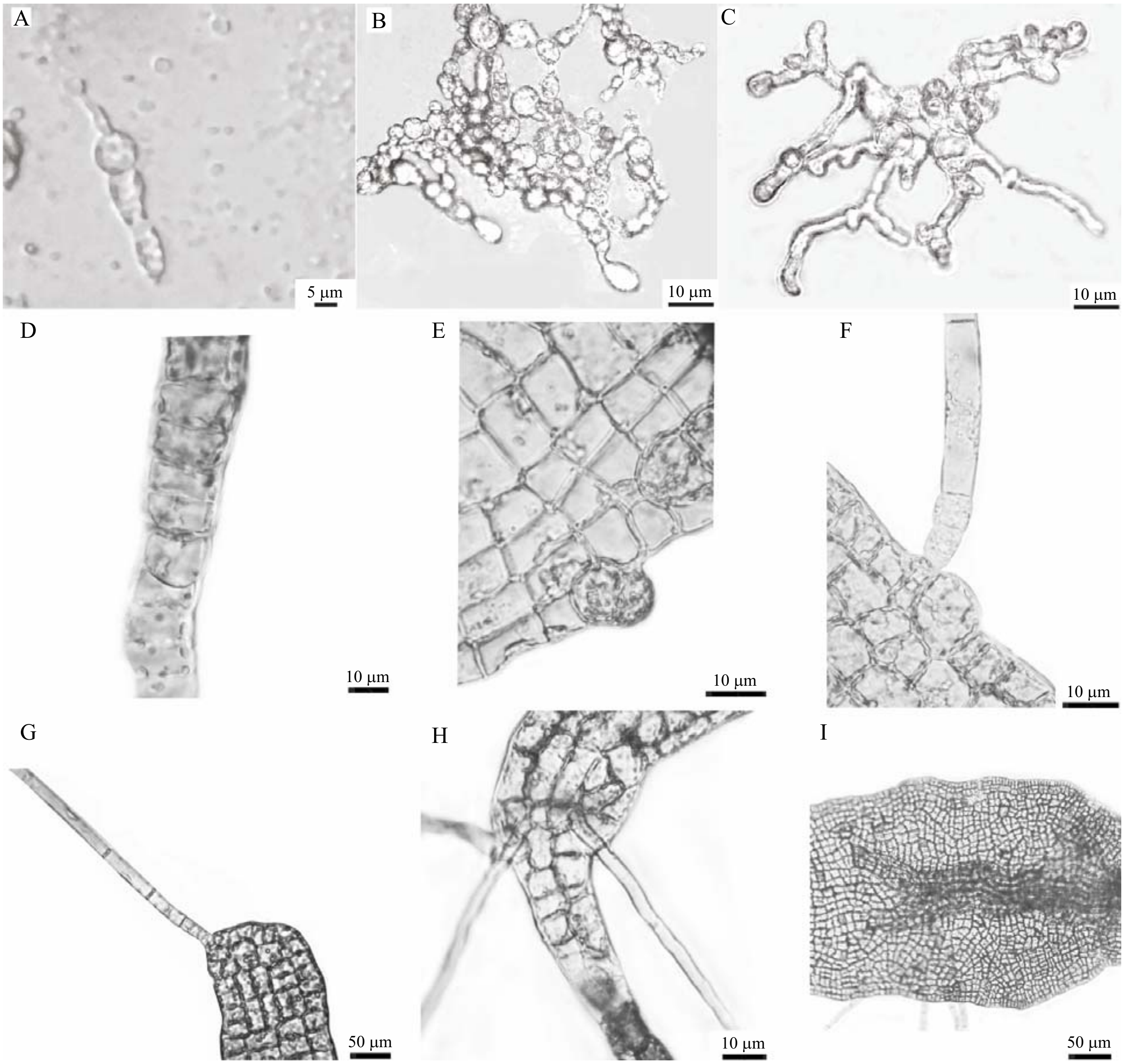

Figure 3. Embryonic thalli. A) Germ tube. B) Female gametophytes. C) Male gametophytes. D) Transversal section of single-layered thallus. E) Hair primordium at the thallus margin. F) Phaeophycean hair. G) Subapical hair. H) Uniseriate rhizoids. I) 'Y'-shaped thickened central ribbon at the base of the embryonic frond.

phytes produced lateral rows of short filaments (Figure 3 B) with apical oogonia. After this, in the same conditions, mature male gametophytes (Figure 3 C) formed spermatangium which released one or more biflagellate anterozoids, that fertilized the oogonium.

Embryonic laminar thalli were initially monolayered (Figure 3 D). Solitary phaeophycean hairs with a basal meristem were seen on the surface or margins of small embryonic fronds less than 1 mm long (Figure 3 E, 3 F and 3 G). These hairs were deciduous and left scars at their insertion points. The presence of these hairs could indicate a nutrient deficit in the culture medium used.

When the frond was about 2 mm long, its lowermost cells elongated and formed the beginning of the cylinder stipe, which adhered to the substrate through a few uniseriate lateral rhizoidal filaments (Figure 3 H). Thalli with this characteristic were collected from intertidal tide pools during autumn. At this stage, the frond was still monolayered and had a margin of small quadrangular cells (Figure 3 G); a region of smaller, apparently meristematic cells between the flattened frond and the cylindrical basal zone was observed. At the basal zone of the most advanced laminar embryonic thallus, a central darker ribbon similar to letter ‘y’ was frequently observed (Figure 3 I).

Pre-sporophyllic juvenile thalli

It was established that the embryonic stage was over and the pre-sporophyllic juvenile stage had started when the layer of meristoderm could be distinguished. Frond midrib began as a central ribbon of cells when the multilayered frond was only a few millimeters long. Meristodermic zone between the frond and the stipe could already be observed when the thallus was a few centimeters long. In this growing zone, short pinnulae were formed along the lower margins of the midrib (Figure 2 H). Later, pinnulae flattened and formed the lateral frond pinnae (Figure 2 I).

The apex of young pinnae had only one meristoderm layer (Figure 4 A); however, a few layers of undifferentiated cells were produced inwardly close to the apex (Figure 4 B), and long medullary cells and a thin cortex of pigmented cells with some young gland cells were also observed. At the center of the fronds, and also along the sinuses of the growing pinnae, subepidermic cells produced some additional filaments which grew inwards and reached the cortex on the other side (Figure 4 C).

In young areas of the frond, the meristoderm with hyaline gland cells, the cortical tissue and the medulla (Figure 4 D) with young trumpet cells in formation could be observed (Figure 4 E). A few intermediate layers of somewhat elongated, less pigmented cells were observed between the outer pigmented cortex and the medulla. Young medulla consisted of trumpet cells that could be differentiated very early on (Figure 4 F), and anticlinal filaments with diameters averaging 10 μm, forming a net, which could be either dense (Figure 4 G) or lax (Figure 4 H).

The external aspect of the surface differed depending on the age of the epidermal tissue, the distance to the growing margin and the presence of gland cells and hair-filled cryptostomata. In the younger zones, each meristodermic cell contained several parietal chloroplasts (Figure 4 I), and as the thallus became older the chloroplasts filled the cell volume (Figure 4 J).

Gland cell and cryptostomata formation

Gland cells differentiated from meristoderm cells at the frond margins. Gland cells were denser (ca. 300 cells mm^{-2}) in young thalli (< 5 cm long) (Figure 5 A and 5 B) and in the apical portions of pinnae in more developed thalli. As the frond grew, gland cells became sparser and were found further from the frond margin. In older thalli, some gland cells could be found in the middle of the frond and the midrib, but never as dense as in young growing zones. Most of gland cells increased in volume and their content became hyaline (Figure 5 B). They were usually very conspicuous because of their larger volume and the purple/burgundy to yellow color (Figure 5 C).

Enlarged cells at the surface were displaced below the meristoderm and became transition cells (TC) (Figure 5 D), which in turn produced the hair-filled cryptostomata. A pore opened in the meristoderm immediately over TC (Figure 5 E). TC developed several outgrowths towards the inside of the thallus (Figure 5 F) and divided into small, lenticular cells with thickened edges

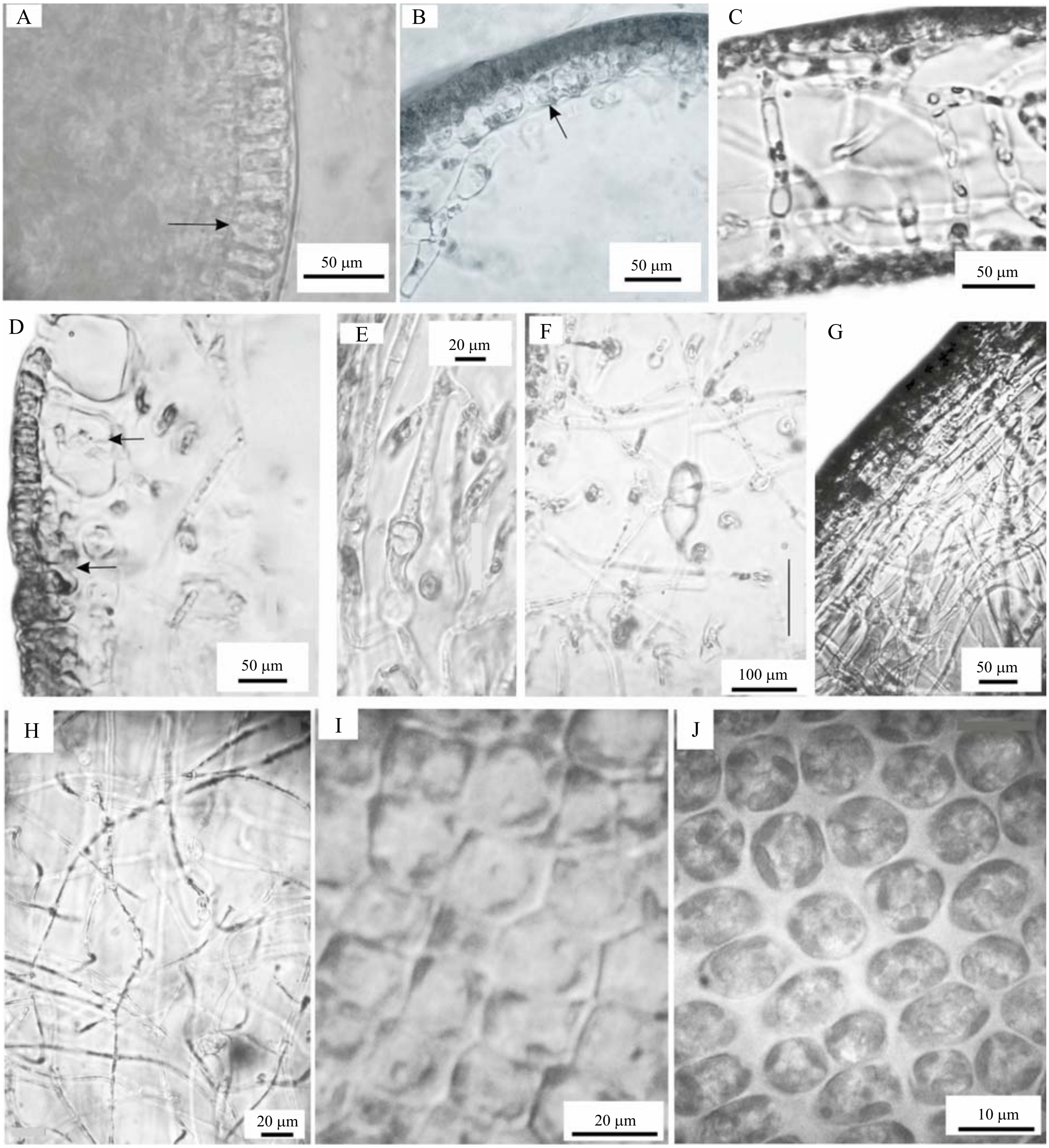

Figure 4. Frond structure. Longitudinal sections at the margin of a very young, monolayered thallus. A) Small meristoderm cells at the lobe apex. B) Single-layered cortex near to the apex. C) Cross section of a young portion of the frond with transverse medullary filaments. D) Cross section showing continuity between cortex and medulla. E) Formation of trumpet cells in the young medulla. F) Trumpet cells in older medulla. G) Cross sections in fully developed frond, compact medulla. H) Lax medulla. I) Surface view of meristoderm cells with chloroplasts. J) Surface view of meristoderm cell with chloroplasts at an older zone.

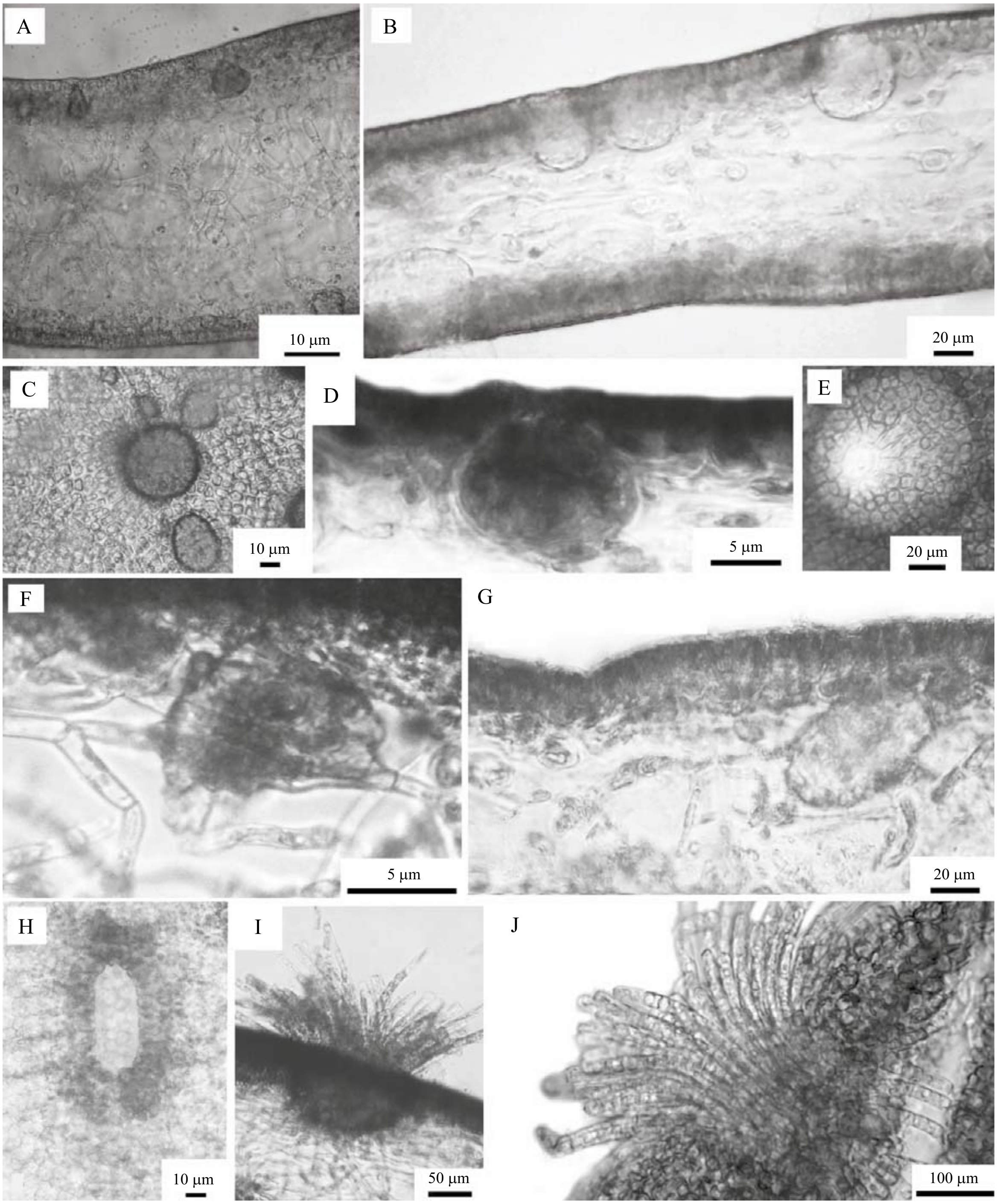

Figure 5. Gland cells and cryptostomata. A) Dark gland cells (GC) in young thalli. B) Hyaline GC in a young frond. C) GC superficial view. D) Transition cell (TC). E) Pore. F) Filaments growing inwards. G) Lenticular cells cross section of TC outer surface. H-J) Formation of cryptostomata.

towards the outer surface (Figure 5 G). The lenticular cells became flat, polygonal with hexagonal outlines (Figure 5 H), which then divided transversely producing the hair primordia at the center of their outer surface. After some elongation, hairs appeared as a tuft through the pore in the meristoderm (Figure 5 I and 5 J). Hairs were firmly anchored into the thallus through the basal filamentous tissue of the crypt. They continued developing until reached several millimeters long and were observed as hyaline spots on the adult thalli at the naked eye.

Midrib and stipe

Sections of the midrib and stipe had a similar structure. Globose cells in the cortex were observed in the cross section of the midrib (Figure 6 A) with the notable presence of a net-like structure of trumpet filaments in the medullary zone (Figure 6 B). In the longitudinal section these cells elongated longitudinally (Figure 6 C). Cross section of the very young stipe had an external layer of strongly pigmented cells, a cortical zone formed of about ten rows of small cells (Figure 6 D) and a filamentous medulla (Figure 6 E). At the end of the pre-sporophyllic stage, the stipe was already compact and cortex cells became transversally globose and somewhat elongated longitudinally (Figure 6 F and 6 G). The medulla was limited to a thin, flat cell layer located in the middle of the frond. In this study, thalli up to 30 cm long remained at the pre-sporophyllic stage. At the end of this stage, two lateral wings were formed along the young stipe (Figure 2 F).

Sporophyllic thalli

Thalli over 30 cm long showed some signs of sporophyll development. This development began at an early stage or just when pinnae could be distinguished on the frond. The lateral ribbon of the stipe generated sporophylls (Figure 2 F and 2 G). The surface of the lateral fringes along the stipe grew faster than the stipe in length, and this difference in growth led to the formation of the adult sporophyll frills. At first, the younger portion of the sporophyll adjacent to the primary meristematic zone was unfolded (Figure 2 G); as it matured (Figure 2 I, 2 J and 2 K) frills were seen along most of the stipe, and the entire length of the stipe was covered with frills when sporophyll development was completed. By this stage, no meristematic zones were left (Figure 2 K).

Specimens with characteristics of Figure 2 I were collected between August and September in the upper subtidal, and these thalli belonged to the distant form. Thalli with characteristics of Figure 2 J were found in tidal pools of the lower intertidal and upper subtidal during spring months. These thalli belonged to the typical form.

Meristoderm, cortical and medullary layers were observed in the transverse section of sporophylls. The most distinctive feature was the presence of sori with unilocular sporangia and paraphyses on both sporophyll surfaces (Figure 6 H, 6 I, 6 J and 6 K). Parparaphyses capped by mucilaginous masses protected the sporangia until the spores were released (Figure 6 J and 6 K).

Senescent thalli

While sporophytes grew, distal zones of the fronds became damaged, and fronds became shorter and wider. In senescent thalli, which had attained full sporophyll development, reproductive sori also developed on the lowest pinnae of the frond (Figure 6 L). At the end of the growth cycle, thalli which have lost the entire frond but still adhered by the holdfast presented remains of the sporophyll. These thalli were observed more frequently at intertidal tide pools or detached from the substrate during the summer.

Adhesion of the adult thalli

The holdfast was formed by dichotomic ramifications or haptera (Figure 7 A, 7 B, 7 C and 7 D). Holdfasts adapted anatomically according to

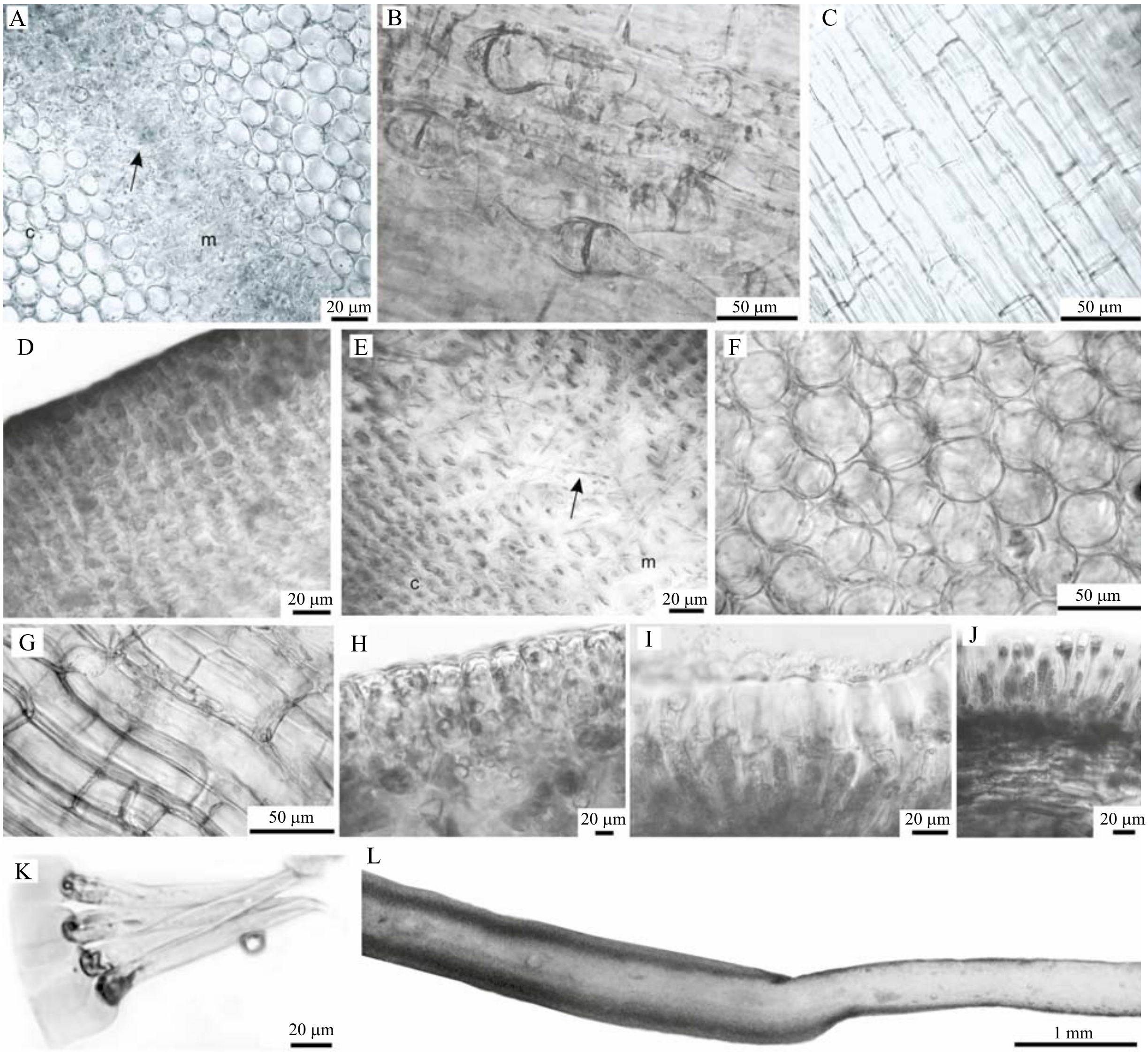

Figure 6. Midrib, stipe and sporophyle. Midrib: cross section (A), detail of medullary filaments (B), longitudinal section of midrib (C). Cross section of a young thallus stipe: cortex (D), flattened medulla (E), cross section with cortex in more developed thallus (F), idem in longitudinal section (G). Successive stages of development of sori: initial stages (H), later stage with gelatinous surface (I), detail of paraphyses with gelatinous distal walls (J), later stage with mature sporangia (K), cross section at the lower portion of the frond in a senescent thallus, partially covered with sori (L). c: cortex. m: medulla.

the substrate. On hard substrates such as rock or encrusting coralline algae, the holdfast of the adult thallus consisted of a few sturdy branches (Figure 7 C). In contrast, haptera were crowded and medium sized on flat fronds, and when they were attached to branches of Corallinaceae, such as *Corallina* sp., haptera usually had several small branches (Figure 7 D). The medullary zone had cylindrical cells in a longitudinal direction, with the absence of trumpet filaments (Figure 7

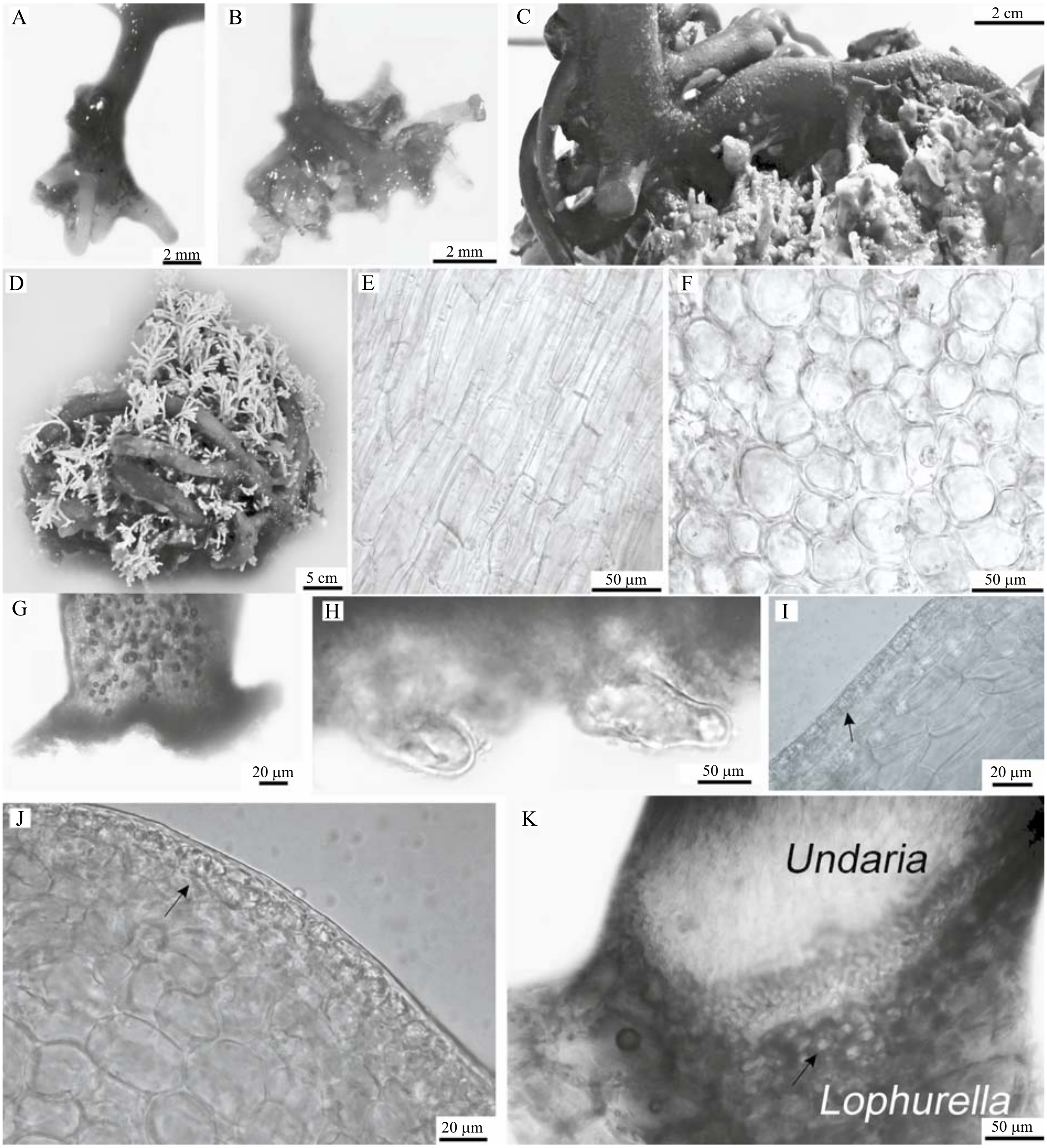

Figure 7. Holdfast. A) Young holdfast with two levels of dichotomy. B) Young holdfast with several levels of dichotomy. C) Adult holdfast with a few branches on encrusting corals. D) Adult holdfast with many branches on *Corallina officinalis*. E) Haptera longitudinal section, cylindrical cells of the medullary zone. F) Haptera cross section, cortical zone. G) Haptera apex detached from the hard substrate. H) Surface between haptera and rocky substrate. I) Haptera longitudinal section with undifferentiated cortical tissue and very thin epidermis. J) Haptera apex with undifferentiated cells. K) Haptera apex in contact with *Lophurella.*

E), while the cortical zone of the holdfast was characterized by the presence of ovoid cells (Figure 7 F). The contact points of the haptera with substrates were apical (Figure 7 G) or in the abaxial zone. On hard rock, haptera surface cells could be globose, hyaline and relatively undifferentiated at the contact points (Figure 7 H). In the cylindrical zones of the holdfast not in contact with the substrate, the haptera was made mostly of longitudinally elongated cells (Figure 7 I) covered by a stratum of flattened superficial cells; this stratum was absent from the zones in contact with the different substrates (Figure 7 J).

When the thalli lived on thin, cylindrical algae, such as *Lophurella hookeriana*, haptera was surrounding their thalli, and somewhat a denser cellular tissue of smaller cells on both surfaces was formed (Figure 7 K).

DISCUSSION

Morphology of *Undaria pinnatifida* has a genetic base and can also be affected by environmental factors (Saito 1972; Stuart et al. 1999; Park 2012). Sporophytes found in *Undaria* population from Caleta Cordova corresponded to those described as typical and distant forms, which matches the findings of Casas (2005) in Nuevo Gulf. Thalli of the distant form were found at greater depths, corresponding to the subtidal level, while thalli of the typical form were found at tidal pools.

Very evident transformations among embryonic stages were observed, in which the thallus consisted of a uniseriate frond adhered to the substrate only through the gametophyte, and adult thallus with different tissues showed marked specialization and complexity. Five main elements can be distinguished in the thallus of *Undaria*: frond, stipe, midrib, sporophyll and holdfast. These elements have been considered here to elucidate the deep transformations from the initial uniseriate filament to the complex adult thallus of *U. pinnatifida*. Developmental differences observed between these portions of the thallus might be related to their distinct functionalities. Descriptions made in this work are comparable with those made by Casas (2005) for specimens from Nuevo Gulf.

Laminariales have a primary intercalary meristoderm that determines the general course of growth (Lee and Yoon 1998; Castric-Fey et al. 1999). In this study, meristoderm was observed between the frond and the stipe in *U. pinnatifida*. In the upper portion a row of small lateral cilia or pinnules was produced, from which the pinnae of the frond was developed. Adult frond morphology depends on the number of pinnules, which presented a very variable trait in samples from Caleta Cordova population. The final area of the frond is attained by the subsequent growth, which takes places through the meristoderm on the surface of the thallus.

Main functions of fronds are photosynthesis and nutrient absorption, both of which depend on the frond surface area. In the frond, the photosynthetic meristoderm gives rise to an inner, colorless layer of larger cells, which in turn produces a lax medullary zone. The loss of the frond apical tissue, observed even in young thalli, is effectively balanced by the pinnae and midrib elongation. This is characteristic of Laminares, in which new tissue formation and distal tissue loss occur at the same time (Larkum 1986; Skriptsova et al. 2004).

Yendo (1909) noted the presence of dark gland cells which were more abundant in very young thalli and young margins of pinnae. Our observations confirmed the greater abundance of gland cells at the growth zones of the fronds. The present study showed that hair-filled cryptostomata originated from gland cells. Pang and Lüning (2004) indicated that the quantity of hairs on the surface of fronds is critical for the quality of commercially harvested *Undaria*. These authors also suggested that the presence of hairs on the fronds was a response to a greater demand for nutrients originated from the expanded surface-volume ratio of the frond. Hairs could also play an important role in the prevention of herbivory (Schaffelke et al. 2005). In Argentina, Teso et al. (2009) registered scraped-off biofouling species on *Undaria* thalli. No signs of herbivory were observed in the present study.

Stipe and midrib of the frond contribute to the flexibility of the thallus and the orientation and movement of the frond. Stipe is longer at greater depths in order to locate fronds in areas with greater illumination (Cremades-Ugarte et al. 2006). These data agreed with observations in the coast of Caleta Cordova, where thalli corresponding to the distant form were found in the subtidal zone exposed to lower light intensity. Saito (1975) reported *Undaria* growing on sites with low to medium exposition to waves, while Russell et al. (2008) note its presence in higher dynamic conditions. In Caleta Cordova and nearby locations inside San Jorge gulf, *U. pinnatifida* populations are found in relatively protected sites, like small bays.

In the midrib and the stipe, the inner cortex is more developed with several colorless cell layers. The medullary zone is reduced to a thin plate, while the multi-layered compact cortex contributes to flexibility and strength, both necessary for withstanding water movements and for nutrient and gas absorption. Stipes maintains it structure until the end of the sporophyte life cycle.

Midrib would have a function similar to that of the sieve tubes of vascular plants due to the presence of structures such as screened plates, filaments and trumpet cells in their medullary zone. This structure is the most important site for the translocation of photoassimilates from the apical area to the basal area of the frond (Wu and Meng 1997).

The folded structure of the sporophyll generates an increase in the surface of the sori, favoring the reproductive capacity of this species, a characteristic of invasive species. The sporophyll structure is similar to the frond but thicker. Fertile sporangia are produced on its surface in an almost continuous layer. Schaffelke et al. (2005) reported that functional zoospores are only liberated from the most mature zones of the sporophyll, far from the meristem. This assertion is true only for younger fertile thalli, since sporophyll development continues until it occupies the entire length of the stipe.

The capacity to adhere to the available substrata is essential for survival in each developmental stage of *Undaria*, and is a characteristic of the opportunistic seaweed able to rapidly colonize new or disturbed substrata and artificial floating structures (Hay 1990; Valentine and Johnson 2003, 2004). *Undaria* can also develop as an epibion of marine invertebrates (Cremades-Ugarte 2006). Embryonic frond is at first adhered through the gametophyte and is later attached by a few, thin, very characteristic lateral filaments. In the juvenile stage, a holdfast primordium is formed, whose haptera later divide dichotomically. The holdfast has a less complex structure than the frond or the stipe, with a single layer of epidermis and a cortex. However, a greater diversity of tissues can be found at the contact points of the haptera with different kinds of substrate.

Morphological structures observed in this study are typical of this species and provide information on the characteristics of the thallus at each stage of development, which will be useful for subsequent analyses.

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MARINE IMPACTS IN THE ANTHROPOCENE

HERMIT CRABS ASSOCIATED TO THE SHRIMP BOTTOM-TRAWL FISHERY ALONG THE PACIFIC COAST OF COSTA RICA, CENTRAL AMERICA

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ABSTRACT. Studies of the bycatch associated to the shrimp trawling fishery in the Pacific coast of Costa Rica do not assess small organisms (< 10 cm TL) and non-dominant species (< 0.1% of total catch). There is a void in assessing the maintenance of the ecology and ecosystem on which the fishery depends. Furthermore, the Constitutional Court of Costa Rica prohibited the renewal of existing and the issuing of new shrimp bottom-trawl licenses, indicating the necessity of more scientific information on the impacts of this fishery. We present the results of a 23-month study of the shrimp bottom-trawl fishery, performed between 50 and 350 m deep in the Pacific coast of Costa Rica. A total of 109 hermit crabs were collected (six species and two families). *Paguristes* cf. *holmesi* was the most common species. Zone II presented the highest species richness and abundance. Most specimens (81.8%) were caught in shallower waters (50-149 m). More than 45% of the trawls presented hermit crabs. It is imperative to further assess the trawling effects on non-commercial benthic fauna and changes on predator-prey relationships, before issuing new shrimp licenses.

Key words: Bycatch, benthos, non-dominant species, deep waters, biodiversity.

INTRODUCTION

Trawling –the dragging of nets across the seabed– can be dated back to 1376, when concerns and complaints were raised by fishermen about the use of beam trawling (‘a new destructive and wasteful fishing habit’) in England (Roberts 2007). Since then, the introduction of steamed vessels and otter trawls has evolved in the adaptation of trawl fishing technology of many species (Gillett 2008). Furthermore, technological development, market demands and overexploitation of shallow water fishing grounds have led the fishing fleet to progressively explore into deeper waters causing the deep water ecosystems to face great threats (Roberts 2002; Morato et al. 2006; Ramírez-Llodra et al. 2011; Norse et al. 2012).

Shrimp fisheries have used many types of gears (beach seines, lift nets, cast nets, tramps, etc.), but the otter trawl is currently the most important commercial gear worldwide (Gillett 2008). In recent decades, the concern over the bycatch of the shrimp trawling fisheries has increased significantly (Dumont and D’Incao 2011; Queirolo et al. 2011; Meltzer et al. 2012; Arana et al. 2013; Villalobos-Rojas et al. 2017; Clarke et al. 2018), and the discard rates of these fisheries has increased significantly (Kelleher 2005; Arana et al. 2013). Moreover, information voids on the biology of both target and non-target species preclude any solid conclusions about the impacts of these fisheries (Bensch et al. 2008; Polidoro et al. 2008; Soykan et al. 2008). Deep water fisheries in Latin America focus mainly on benthic and demersal invertebrates (Arana et al. 2009; Wehrtmann et al. 2012). Detailed information on the composition of shrimp bottom-trawl fisheries' catch in the region is limited to the Chilean nylon shrimp fishery (*Heterocarpus reedi* Bahamonde, 1955), and the northern nylon shrimp (*Heterocarpus vicarius* Faxon, 1893) and kolibri shrimp (*Solenocera agassizii* Faxon, 1893) in Central America and Colombia (Chile: Queirolo et al. 2011; Arana et al. 2013, Colombia: Puentes et al. 2007, Costa Rica: Wehrtmann and Echeverría-Sáenz 2007; Arana et al. 2013; Villalobos-Rojas et al. 2017). Nevertheless, little attention has been paid to hermit crabs caught as bycatch in these fisheries. Puentes et al. (2007) reported *Xylopagurus cancellarius* Walton, 1950, as part of the bycatch of the trawling fishery from the Colombian Pacific, while Wehrtmann and Echeverría-Sáenz (2007) mentioned two species of hermit crabs from shrimp trawls along the Costa Rican Pacific: *Paguristes bakeri* Holmes, 1900 and *Petrochirus californiensis* Bouvier, 1895.

The Costa Rican Pacific waters support a high biodiversity of hermit crabs, comprising currently four families and 34 species (Vargas and Wehrtmann 2009), with 19 of these species reported from waters deeper than 50 m (Vargas and Wehrtmann 2009). Hermit crab taxonomy is presently under review, and a large number of new species have been recently described while others have been re-described for the Eastern Tropical Pacific (Ayón-Parente and Madrid-Vera 2009; Ayón-Parente and Hendrickx 2012a, 2012b, 2013; Ayón-Parente and Wehrtmann 2019). Shrimp bottom-trawl fisheries, thus, represent an excellent opportunity to access biological material from deep waters (> 50 m), especially in countries like Costa Rica, which do not have research vessels. The collected information allows expanding the description of the hermit crab diversity and distribution patterns along the Costa Rican Pacific continental shelf (Wehrtmann and Nielsen-Muñoz 2009; Wehrtmann et al. 2012; Ayón-Parente and Wehrtmann 2019).

In 2013, the constitutional court of Costa Rica prohibited both the renewal of existing and the issuing of new shrimp bottom-trawl licenses, indicating the necessity of more scientific information on the impacts of this fishery (Sentencia No 2013-10540 2013). In order to assess the possible impacts of shrimp trawling on the ecosystem, it is imperative to gather information on the diversity and ecological patterns of deep water species, including the hermit crabs. Therefore, the results of this study provide information necessary for the development of management approaches aimed to secure the sustainability of these deep water resources.

MATERIALS AND METHODS

Specimens were collected during a 23-month period (March 2010-February 2012) along the Costa Rican Pacific continental shelf. The sampling was carried out as part of a project to study the fisheries of commercially important deep-water shrimps (*H. vicarius* and *S. agassizii*). Samples were obtained using commercial shrimp trawlers (22.5 m long, 270 HP) equipped with two standard epibenthic nets (20.5 m length, mouth opening 5.35 width × 0.85 m height, mesh size 4.5 cm, cod-end mesh size 3.0 cm), at a speed of 2.0 knots (~ 3.7 $km \cdot h^{-1}$). The specimens were collected in the framework of scientific sampling programs along the entire Pacific coast of Costa Rica with samples collected between 50 and 300 m, with a total of 179 samples (44.75 h) (Figure 1). The study area was divided into three geographic zones based on oceanographic conditions to analyze the geographic distribution of hermit crabs captured by the shrimp bottom-trawl fishery: Zone I, influenced by a seasonal upwelling in the northern Pacific coast; Zone II, Golfo de Nicoya estuarine system, Central Pacific and Térraba-Sierpe estuarine system; and Zone III, mouth of Golfo Dulce, a tropical fjord with anoxic conditions (Nielsen-Muñoz and Quesada-Alpízar 2006; Cortés and Wehrtmann 2009) (Figure 1). The bathymetric distribution was divided into four depth ranges: 50-99 m, 100-149 m; 150-199 m, and 200-350 m. The collected hermit crabs were stored on board at 0 °C and subsequently transported to the laboratory. All specimens were identified to species level using the available literature (Ball and Haig 1974; McLaughlin 1981a, 1981b, 1982; Lemaitre 1989; Hendrickx 1995; Lemaitre and McLaughlin 1996; Hendrickx and Harvey 1999; Ayón-Parente 2009; Ayón-Parente and Hendrickx 2010; McLaughlin et al. 2010), preserved in 70% ethanol and deposited in the collection of the Museo de Zoología of the Universidad de Costa Rica (MZUCR).

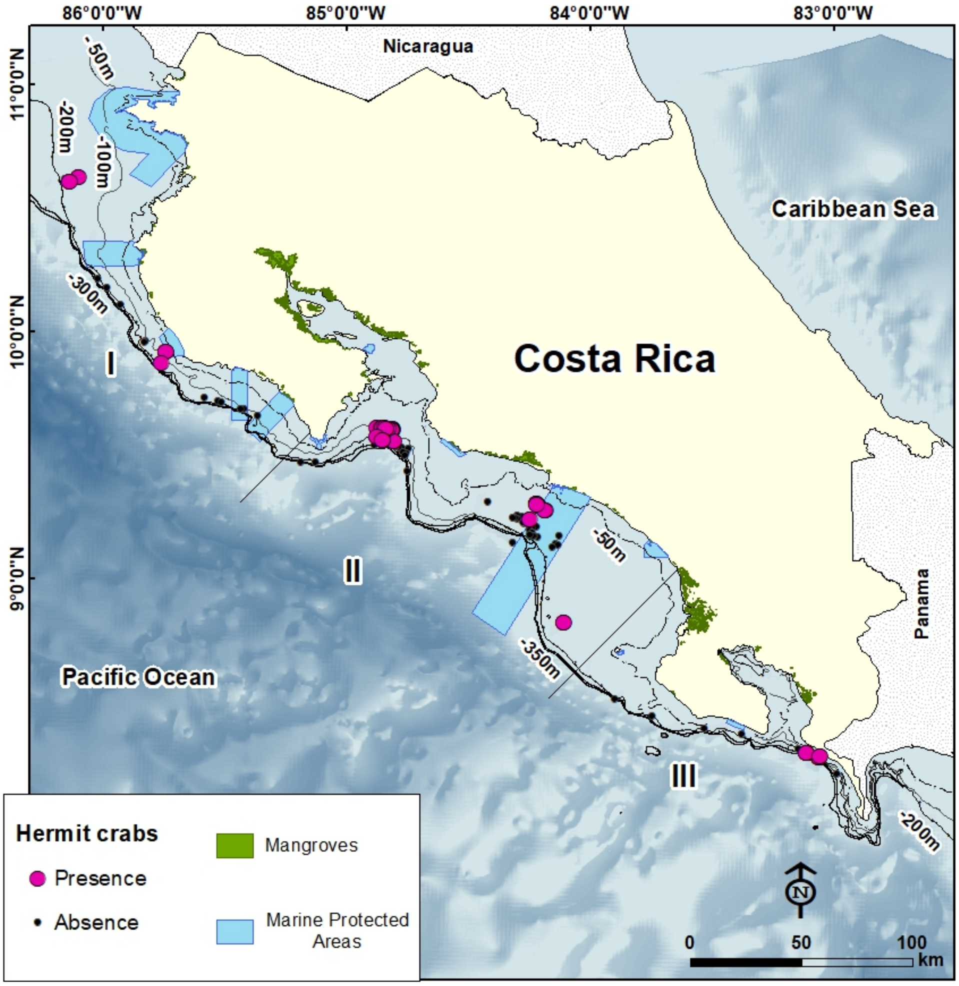

Figure 1. Pacific coast of Costa Rica, Central America, divided into the three zones used in the analyses. The sampling stations indicate the presence (pink circle) or absence (small black circle) of hermit crabs in the bycatch.

Species composition

To compile a species list of hermit crabs we examined both the living specimens collected during our surveys (2010-2012) as well as additionally specimens collected at the same fishing grounds and depths during other shrimp bottom-trawl surveys carried out between 2008 and 2012 with the same methodology. A species accumulation curve was calculated to assess the completeness of the sampling methods used to record the hermit crabs inhabiting the surveyed area (2010-2012), using the 'vegan' library (Oksanen et al. 2016) in the R statistical package v3.1.3.

Morphometric measurements

The cephalothorax length (CL), abdomen length (AL) and total length (TL = CL + AL) of hermit crabs were measured using a caliper (± 0.05 mm) (Figure 2). Additionally, each specimen was weighted (± 0.001 g) and sexed using the location of gonopores at the base of the third (females) or fifth (males) pereiopods (Hendrickx 1995; Hendrickx and Harvey 1999). Photographs of at least one specimen per species were taken with a Canon EOS7D camera equipped with macro lens Canon EF 100 mm and lens Canon MP-E 65 mm. A Chi-square goodness of fit test

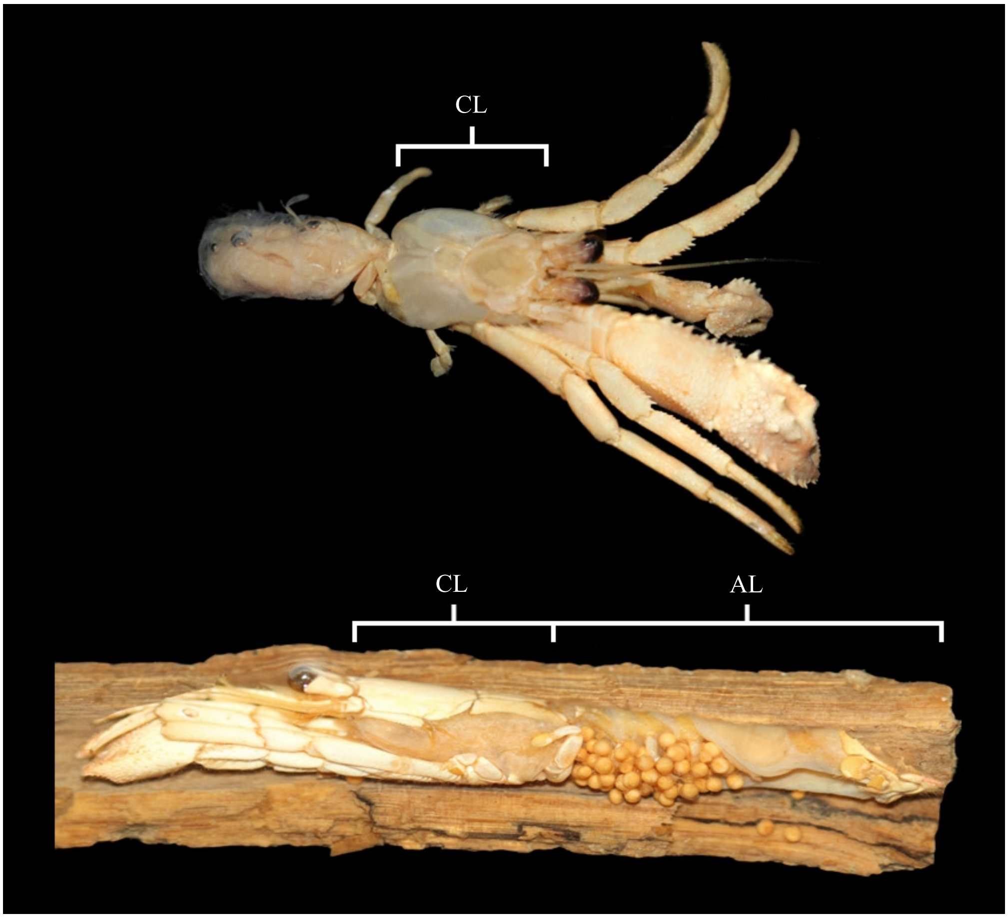

Figure 2. Measurements recorded for hermit crabs collected along the Pacific coast of Costa Rica. CL: carapace length, AL: abdomen length.

was conducted to detect species with sex ratios, which were different from the expected 1:1 ratio (Zar 1999; Hernáez et al. 2012; Villalobos-Rojas and Wehrtmann 2018).

Species geographic and bathymetric distribution

We used a Generalized Linear Model (GLM) with binomial distribution to identify environmental variables influencing the presence/absence of hermit crabs. Seven independent variables were considered for the analysis: (1) geographic zones (I, II, III), (2) depth level (50-99 m, 100-149 m, 150-199 m and > 200 m), (3) seasonality (rainy, transition and dry season; according to Amador et al. 2006), (4) Oceanic Niño Index (ONI categories: cold, normal and warm; NWSCPC 2019), (5) marine bottom substrate (bathyal soft-bottoms, infralittoral hard-bottom and sublittoral lithoclastic mud) as provided by TNC (2008) (6) shortest distance to the closest protected area and mangrove area and (7) sea bottom slope. The shortest distance to the closest protected area and mangrove area were obtained with spatial data from ITCR (2014) and the tool 'Near' of the Analysis toolbox, while sea slope bottom data were obtained using the Digital Elevation Model (DEM) for the Eastern Tropical Pacific (TNC 2008) and the tool 'Slope' of the 3D Analyst toolbox. Slope values for each record were extracted using the tool 'Extract multivalues to points' from Spatial Analyst toolbox. The GIS and all toolboxes used are part of ArcGIS10.4 (ESRI 2019).

Statistical analyses were performed using the 'coin' package (Hothorn et al. 2006) in R v3.1.3. A Tukey *post-hoc* test was applied to determine differences considering the categorical environmental variables that were significant in the binomial-GLM using the 'multcomp' package (Hothorn et al. 2008).

RESULTS

Species composition

A total of 109 specimens were collected, comprising six species, five genera and two families (Table 1; Figure 3). The most common species was *Paguristes* cf. *holmesi* Glassell, 1937 (n = 63), followed by *Areopaguristes praedator* (Glassell, 1937) and *Tomopagurus merimaculosus* (Glassell, 1937) with 15 specimens each (Table 1). *Dardanus nudus* Ayón-Parente and Hendrickx, 2009 and *D. stimpsoni* Ayón Parente and Hendrickx, 2009 were collected only during the additional surveys (between 2008 and 2012) (Table 1). Both *D. nudus* and *D. stimpsoni* are new reports for Costa Rica. Figure 4 shows the species accumulation curve with a relatively low slope and Figure 5 presents the locality of all hermit crabs analyzed.

Morphometric measurements

Table 2 summarizes morphometric measurements obtained from the 109 specimens collected. The largest specimen belonged to *D. stimpsoni* with 83.0 mm TL (29.4 mm CL), whereas in average *D. nudus* presented the largest length (62.6 ± 12.7 mm TL). The smallest specimen was represented by *P.* cf. *holmesi* with a total length of 11.7 mm (8.4 mm CL), whereas in average *A. praedator* comprised the smallest specimens (25.3 ± 5.2 mm TL) (Table 2).

Species geographic and bathymetric distribution

A total of 189 shrimp bottom-trawl surveys were carried out between 2010 and 2012 (Table 3). The Zone II presented the highest sampling effort (32.75 h), with the highest species richness (four) and abundance (n = 60). In all zones, more

Table 1. Species list, number of collected specimens (n), geographic distribution and depth range (m) reported in literature compared to the depth range for the hermit crabs collected as bycatch in the shrimp bottom-trawl fishery along the Costa Rican Pacific (2008-2012).

Species	n	Geographic distribution	Previously reported depth range (m)	Study depth range (m)
Diogenidae				
Areopaguristes praedator (Glassell 1937)	15	Gulf of California to Costa Rica[6]	6-155[6]	93.5-158.9
*Dardanus nudus** Ayón Parente and Hendrickx (2009)	4	Gulf of California-Panamic Region[4]	16-55[4]	41.1-56.1
*Dardanus stimpsoni**, †, ‡ Ayón Parente and Hendrickx (2009)	10	Gulf of California[4, †]	2-144[4]	187‡
Paguristes cf. *holmesi**, †, ‡ Glassell 1937	63	Gulf of California[5, †]	60-150[5]	84.1-187‡
Paguridae				
Tomopagurus merimaculosus (Glassell 1937)	15	Gulf of California to Colombia[2, 3]	35-183[2, 3]	67.3-187
Xylopagurus cancellarius‡ Walton 1950	2	Costa Rica and Colombia[1, 2, 3]	73[1, 2, 3]	93.5‡
Total specimens	109			

*New report for Costa Rica.
†Geographic distribution extension.
‡Depth range extension.
[1] Lemaitre (1995).
[2] Vargas and Cortés (2004).
[3] Vargas and Wehrtmann (2009).
[4] Ayón-Parente and Hendrickx (2009).
[5] Ayón-Parente and Hendrickx (2010).
[6] Ayón-Parente et al. (2015).

than 45% of the trawls presented at least one species of hermit crab. Only *Paguristes* cf. *holmesi* was collected in all three sampling areas.

Most of the specimens (81.8%) were caught in the first two depth levels (50-99 m and 100-149 m). The 50-99 m depth level had the highest sampling effort (15.3 h), the highest percentage of samples with hermit crabs (90.2%), the highest species richness (four), and the highest abundance (n = 55). On the other hand, the 150-199 m depth level had the second highest sampling effort (12.8 h), but less than 40% of the samples contained hermit crabs. The 100-149 and > 200 m depth levels had similar sampling efforts (7.8 h and 9 h); nevertheless, hermit crabs were absent at the deepest level. *Tomopagurus meri-*

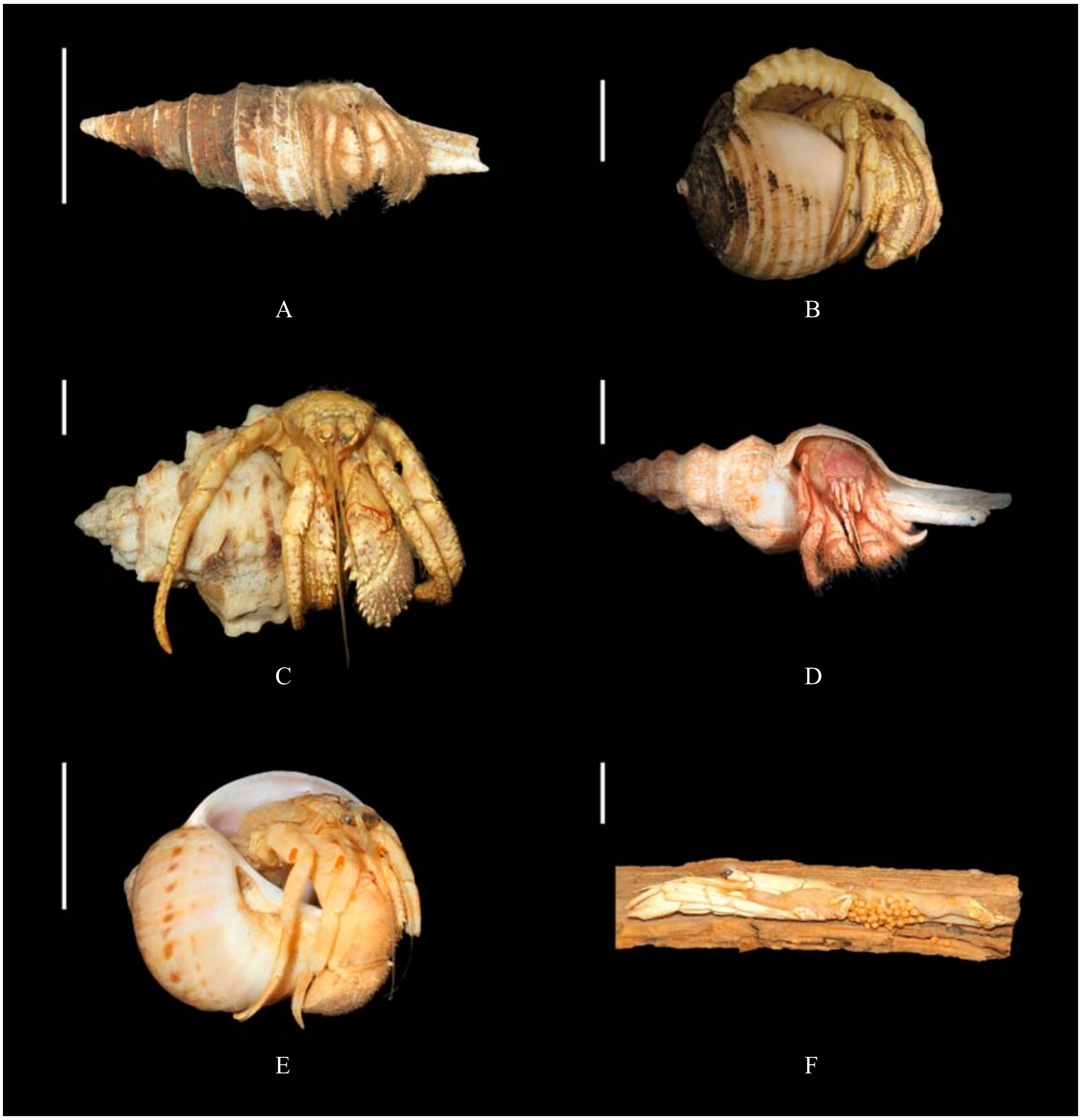

Figure 3. Hermit crabs collected as bycatch in the shrimp bottom-trawl fishery along the Costa Rican Pacific. Diogenidae. A) *Areopaguristes praedator*, 9.95 mm CL (MZUCR 3594-1). B) *Dardanus nudus*, 25.0 mm CL (MZUCR 3537). C) *Dardanus stimpsoni*, 20.5 mm CL (MZUCR 3595-1). D) *Paguristes* cf. *holmesi*, 19.0 mm CL (MZUCR 3593-1). Paguridae. E) *Tomopagurus merimaculosus*, 10.0 mm CL (MZUCR 3595-2). F) *Xylopagurus cancellarius*, 20.3 mm CL (MZUCR 3596-1). Scale bars = 10 mm.

maculosus presented the widest depth distribution range (67-187 m), whereas *Xylopagurus cancellarius* occurred only at 93.5 m depth (Table 1).

The results from the binomial-GLM selected five variables that significantly influenced ($p < 0.05$) the presence of hermit crabs: (1) depth level, (2) ONI categories, (3) marine bottom substrate (4) sea bottom slope, and (5) geographic coordinates. The GLM (hermit crab presence ~ depth + ONI + marine bottom substrate + sea bottom slope

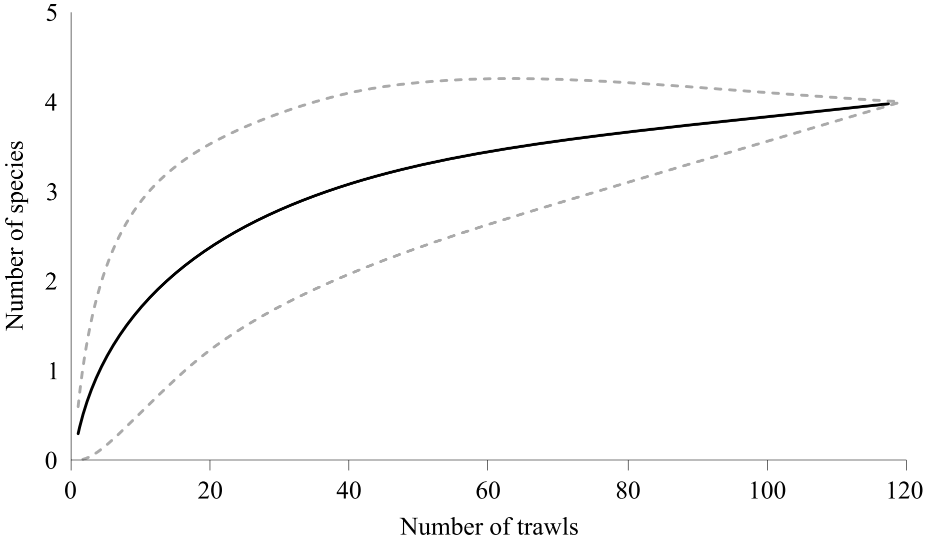

Figure 4. Number of hermit crab species accumulated by number of shrimp bottom-trawls carried out between 2010 and 2012 along the Pacific coast of Costa Rica, Central America.

+ geographic coordinates) explained 72.4% of the observed variance. Additionally, the Tukey *post-hoc* test revealed significant differences between the factors of the categorical variables according to the probability of presence of hermit crabs: depth level (50-99 m > 100-149 m, 150-199 m and > 200 m, $p < 0.01$), marine bottom substrate (lithoclastic mud > bathyal soft-bottoms; $p < 0.01$) and ONI categories (cold > normal). Although no significant differences were detected between the geographic zones (I, II and III), a significant tendency to find more hermit crabs in higher longitudes was determined ($p > 0.05$) Table 4.

DISCUSSION

The hermit crab fauna from the Costa Rican Pacific is currently comprised by 34 species; including the two new records obtained by the present study (*Dardanus nudus* and *D. stimpsoni*: 1 sp. of Coenobitidae, 14 spp. of Diogenidae, 17 spp. of Paguridae and 2 spp. of Parapaguridae). Nineteen of these species are distributed deeper than 50 m: 7 spp. of Diogenidae, 10 spp. of Paguridae, and 2 spp. of Parapaguridae (Vargas and Cortés 2004, Vargas and Wehrtmann 2009). The six species found in our study represent 31.6% of hermit crabs fauna reported at these depths.

Published information on the hermit crabs associated to the Costa Rican shrimp bottom-trawl fisheries is scarce. Campos (1986) reported ‘crustaceans in gastropod shells’ representing 0.0006% of total capture of shrimp trawls between 27 m and 238 m deep, but no species identification was provided. Wehrtmann and Echeverría-Sáenz (2007) reported *Paguristes bakeri* as rare (< 15% of hauls) and *Petrochirus californiensis* as occasional (15% of hauls) fauna in the northern nylon shrimp (*Heterocarpus vicarius*) fisheries of Costa Rica, collected at 273 m and 293 m deep, respectively. Therefore, there are a total of seven hermit crab species associated to the Costa Rican shrimp fisheries since the *P. bakeri* found by Wehrtmann and Echeverría-Sáenz (2007) is probably *P. holmesi* found and identified in our study.

All six species found in our study were previously documented for the Panamic Region

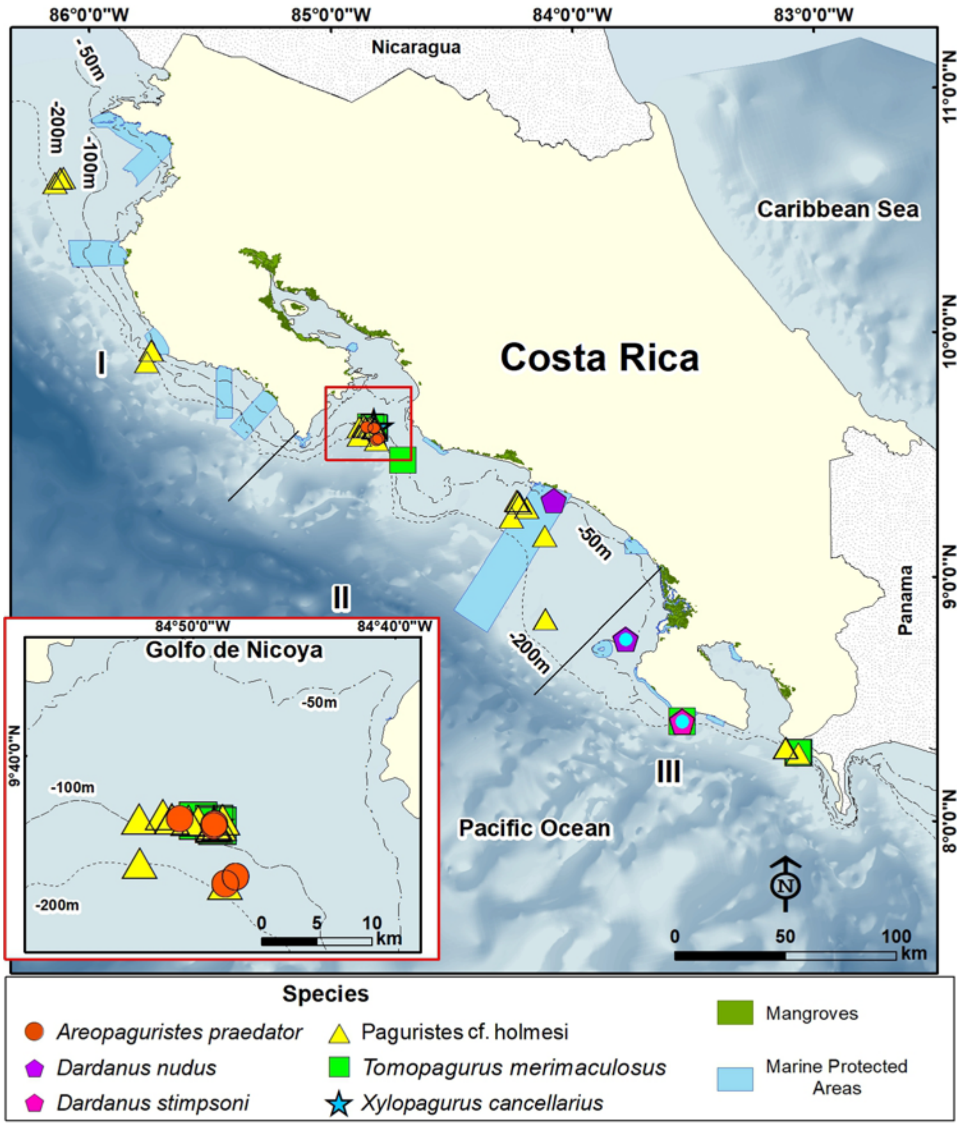

Figure 5. Presence of hermit crab species associated to the shrimp bottom-trawl fishery from 2010 to 2012 along the Pacific coast of Costa Rica, Central America. The close-up shows the distribution of hermit crab species collected in the entrance of the Golfo de Nicoya.

(Ayón-Parente and Hendrickx 2010). Nevertheless, here we present the first report of two hermit crab species: *Dardanus nudus* and *Dardanus stimpsoni* for the Costa Rican Pacific. Our records expand the depth range for *D. stimpsoni* down to 187 m (both were previously reported at 144 m) (Ayón-Parente and Hendrickx 2010). Three of the other collected species have been previously reported: *Areopaguristes praedator*, *Tomopagurus merimaculosus*, and *Xylopagurus cancellarius* (see Lemaitre 1995; Vargas and Cortés 2004; Vargas and Wehrtmann 2009; Ayón-Parente et al. 2010, 2015). Nevertheless, our data extend the depth range for *X. cancellarius* from 73.1 m deep (Vargas and Wehrtmann 2009) down to 93.5 m.

Table 2. Measurements and sex ratio of hermit crabs collected as bycatch in the shrimp bottom-trawl fishery along the Costa Rican Pacific (2008-2012). SD: standard deviation, n: number of specimens analyzed, F: females, M: males.

			Carapace length (mm)		Total length (mm)		Weight (g)	
Species	n	Sex ratio (F/M)	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Diogenidae								
Areopaguristes praedator (Glassell 1937)	15	0.9	8.13 ± 1.6	5.6-10.5	25.3 ± 5.2	15.45-32.1	0.43 ± 0.3	0.1-0.9
Dardanus nudus Ayón-Parente and Hendrickx (2009)	4	0.0	20.9 ± 4.0	16.0-25.6	62.6 ± 12.7	48.7-79.2	8.4 ± 4.8	4.69-15.1
Dardanus stimpsoni Ayón-Parente Hendrickx (2009)	10	0.6	16.1 ± 5.6	9.8-29.4	47.6 ± 14.6	29.8-83.0	4.0 ± 4.8	0.4-16.7
Paguristes cf. holmesi Glassell 1937	63	0.4*	15.3 ± 3.8	8.4-25.6	43.6 ± 12.6	11.7-75.7	3.19 ± 2.5	0.2-11.8
Paguridae								
Tomopagurus merimaculosus (Glassell 1937)	15	0.3*	13.6 ± 2.4	9.65-18.55	36.8 ± 6.7	12.15-50.2	2.3 ± 1.3	0.9-55.9
Xylopagurus cancellarius Walton 1950	2	1.0	17.3 ± 4.2	14.3-20.3	52.7 ± 19.1	39.2-66.2	3.0 ± 2.7	1.1-4.9
Total specimens	109							

The specimens of *Paguristes* cf. *holmesi* were identified as *confer* because its taxonomy is still under revision in the Eastern Tropical Pacific (M. Ayón-Parente, pers. comm). This species was previously synonymized with *Paguristes bakeri* Holmes, 1900 (Haig and Hopkins 1970). Afterwards, Moran and Dittel (1993) reported specimens of *P. holmesi* from material collected in Costa Rica. Nevertheless, Hendrickx and Harvey (1996) indicated that the material mentioned by Moran and Dittel (1993) could not be located in the Los Angeles County Museum of Natural History where it was allegedly deposited. Recently, Ayón-Parente (2009) examined additional material from the Mexican Pacific and found enough morphological differences for them to be considered as a separate species. Consequently, it is possible that the species identified as *Paguristes bakeri* by Wehrtmann and Echeve-rría-Sáenz (2007) is *Paguristes* cf. *holmesi*. Therefore, our study reports five additional species associated to shrimp bottom-trawl fisheries to the previous study (Wehrtmann and Echeverría-Sáenz 2007).

Regarding the geographic distribution of the species, results indicated a tendency to find more hermit crabs in higher longitudes. For example, although Zones I and III had similar sampling efforts, higher abundance was found in Zone I.

Table 3. Number of species, number of individuals, percentage of samples with hermit crab, and total number of samples by geographical area and depth range associated with shrimp bottom-trawl fisheries along the Costa Rican Pacific (2010-2012).

	Geographic area			Depth range (m)			
Species	I	II	III	50-99	100-149	150-199	> 200
Diogenidae							
Areopaguristes praedator	-	15	-	8	5	2	-
Paguristes cf. *holmesi*	9	40	10	39	6	14	-
Paguridae							
Tomopagurus merimaculosus	9	3	-	6	6	-	-
Xylopagurus cancellarius	-	2	-	2	-	-	-
Number of specimens	18	60	10	55	17	16	0
Number of species	2	4	1	4	3	2	0
Samples with hermit crabs (%)	69.2	45.8	45.5	90.2	54.8	31.4	0
Number of samples	26	131	22	61	31	51	36
Sampling effort (h)	6.5	32.75	5.5	15.3	7.8	12.8	9

Nevertheless, additional studies with a higher sampling effort are required to confirm this tendency.

Our results suggest that the probability of finding hermit crabs is higher at shallower waters (50-99 m) and decreases towards deeper waters (> 200 m). A similar pattern was observed for hermit crabs of the family Diogenidae in the Eastern Pacific, where the species richness was highest at shallower waters (Ayón-Parente and Hendrickx 2010). Our results follow the general distribution pattern of marine benthic invertebrates (Sanders 1963). Therefore, shrimp fisheries carried out in shallower waters (< 100 m) will have a greater impact on the hermit crab community than deep-water shrimp fisheries. In Costa Rica, the shallow-water shrimp fishery has focused on seven Penaeidae species (*Litopenaeus vannamei*, *L. stylirostris*, *L. occidentalis*, *Xiphopenaeus riveti*, *Trachypenaeus byrdii*, *Farfantepenaeus brevirostris*, and *F. californiensis*) and was carried out between 5 and 120 m deep (Álvarez and Salazar 2010). In the case of the trawling shrimp fisheries will be reinstalled in Costa Rica, the monitoring program should include identifying hermit crab species.

The probability of finding hermit crabs off the Costa Rican Pacific is higher during cold Oceanic Niño Index (ONI) than during normal ONI conditions Hermit crabs are affected in different ways by temperature changes (Briffa et al. 2013; Gilland 2017). For example, Gilland (2017) suggested that changes in temperature levels affect the ability of tide pool hermit crabs to occupy high quality shells that will protect them from predators and desiccation, as well as decrease growth rate and increase energy usage. To our knowledge there are no studies associating deep water hermit crabs with temperature, however, our results suggest that temperature could be affecting their distribution, which might be important considering the different climate change scenarios (Gorman et al. 2018).

In our study, hermit crabs were caught on soft bottom sediments (lithoclastic mud and bathyal

Table 4. Generalized Linear Model for the presence of hermit crabs associated with shrimp bottom-trawl fisheries along the Costa Rican Pacific (2010-2012).

Coefficients	Estimate	Standard error	z	Pr(>|z|)
(Intercept)	296.3248	857.9968	0.345	0.729818
Depth 100	2.8904	0.7457	-3.878	0.000225*
Depth 150	-2.8904	0.7349	-4.439	0.000252*
Depth 200	-20.847	2467.13	-0.008	0.992546
Depth 250	-20.847	3400.71	-0.006	0.994615
Depth 300	-20.847	5377	-0.004	0.996911
Latitude	-68.0098	51.0083	-1.33	0.1824
Longitude	12.6376	6.5037	1.943	0.049*
Latitude × Longitude	-0.8824	0.6107	-1.445	0.1485
ONI cold category	-1.61E+00	7.62E-01	-2.113	0.0346*
ONI normal category	-1.34E-01	8.76E-01	-0.152	0.8789
Sea bottom slope	-1.56E+00	3.99E-01	-3.921	0.0000884*
Marine bottom substrate	1.5444	0.6524	2.367	0.0179*

$^*p < 0.05$.

GLM (hermit crab presence ~ depth + ONI + marine bottom substrate + sea bottom slope + geographic coordinates, family = binomial, link = logit).

Null deviance: 121.901 on 112 degrees of freedom.

Residual deviance: 33.679 on 85 degrees of freedom.

AIC: 89.679.

soft-bottoms), due to the characteristics of commercial shrimp trawling. Most hermit crabs were captured in trawls taken on the lithoclastic mud bottom, which were covered by fine grain to very fine sediments (SINAC 2008). Sediment particle size (Stanski et al. 2016) and sediment organic-matter content (Fransozo et al. 1998; Frameschi et al. 2014; Stanski et al. 2016) has been correlated to the abundance species of hermit crabs.

Impact of shrimp trawling fisheries

Few studies assessing the fauna associated to bottom-trawl shrimp fisheries have considered its impacts on small and non-dominant species (< 0.1% of total catch) (Branco et al. 2015; Villalobos-Rojas et al. 2017). In fact, hermit crabs have been rarely identified when monitoring the bycatch present in shrimp bottom-trawl fisheries (Branco et al. 2015; Gimenez-Hurtado et al. 2016). Non-dominant species, however, can have important ecological functions in the community. For example, hermit crabs have been reported as important allogenic ecosystem engineers in marine habitats and to have a large number of symbiotic relationships (Gutierrez and McDermott 2004; Pretterebner et al. 2012).

The impact of shrimp trawling on hermit crabs has been poorly studied (Ramsay et al. 1996; Groenewold and Fonds 2000; Stanski et al. 2016). Ramsay et al. (1996) suggested that some scavenging hermit crabs could migrate to recently trawled areas to feed on the damaged or disturbed fauna affected by trawling. Although trawling can lead to these shortcuts in trophic relationships and enhance secondary production, the direct importance of the additional food resource for populations of scavengers is considered to be relatively small (Groenewold and Fonds 2000).

Trawling is known to impact the structure and functioning of benthic ecosystems (Alverson et al. 1994; Collie et al. 2000; Hinz et al. 2009; Hiddink et al. 2017). The pressure of constant extraction can damage the maintenance of populations as it impacts recruitment, reproduction and growth of specimens (Stanski et al. 2016). The constant trawling impact on non-commercial species can change the predator-prey relationships due to the loss of biological diversity, disturbance or elimination of local species and can jeopardize the balance of the marine ecosystem (Stanski et al. 2016). Taking into account that surveys had a ~ 20 min duration and that commercial trawls last between 2 and 6 h (Álvarez and Salazar 2010; Marín-Alpízar et al. 2019) an increase in the abundance of hermit crabs in these nets is expected due to mesh plugging and reduction of selectivity (Stanski et al. 2016). According to Marín-Alpízar et al. (2019) trawls for fisheries focused on *Solenocera agassizii* and *Farfantepenaeus brevirostris* should have a maximum duration of two hours so that the mesh will not become obstructed and increasing the bycatch. Nevertheless, these authors did not provide information on non-dominant species or small invertebrates present in these two fisheries. Therefore, the possible impact of the suggested two-hour trawls still needs to be investigated.

In order to attain a sustainable and democratic fishery it is indispensable to consider the sustainability of exploited fish stocks, the maintenance of the ecosystem on which the fishery depends, and an effective and responsible management of the fishery (Pacheco-Urpí et al. 2012; Baigún 2013). Due to the decision taken by the Constitutional Court of Costa Rica (Sentencia No 2013-10540 2013), studies have aimed to assess the fishery and reduce the abundance of the bycatch associated to shrimp trawling fishery at the Pacific coast of Costa Rica (AJDIP/336-2018 2018; AJDIP/498-2018 2018, Marín-Alpízar et al. 2019). The majority of the results in these studies has not been officially published and do not assess small organisms (< 10 cm TL) such as gastropods, bivalves and hermit crabs. Therefore, there is a clear gap of information assessing the maintenance of the ecology and ecosystem on which the fishery depends. Considering that more than 45% of the survey trawls contained hermit crabs, it is imperative to assess the trawling effects on both non-commercial benthic fauna and changes on predator-prey relationships, before insinuating the possibility of obtaining a sustainable fishery. In case that the trawling shrimp fisheries will be reinstalled in Costa Rica, monitoring programs need to be installed to accompany these fisheries, and special attention should be given to the shallow-water fishery bycatch (< 100 m), which should include the identification of hermit crab species and other small invertebrates (< 10 cm TL).

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NOTE

MATING BEHAVIOR OF PATAGONIAN OCTOPUS (*Octopus tehuelchus*) UNDER LABORATORY CONDITIONS

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ABSTRACT. Patagonian octopus (*Octopus tehuelchus*) is a species that holds an artisanal fishery in the northern area of the Argentine Patagonian coast and has a potential for aquaculture development. This work aimed to characterize the mating behavior of four pairs of Patagonian octopuses under laboratory conditions. Results showed that this species has a complex reproductive behavior. Remarkably, female remained inside her shelter during pre-copula, copulation and intercourse events. Male and female faced by the oral face during sexual intercourse, which lasted 3 to 5 min. The observations will contribute to the better management of the reproductive specimens of the species in captivity.

Key words: *Octopus tehuelchus*, aquaculture, copula, hectocotyle.

Mating in cephalopods has been analyzed in the natural environment (Boletzky and Hanlon 1983) as well as in the laboratory (Wood et al. 1998; Gutiérrez et al. 2012), observing complex behaviors between male and female during courtship (pre-copulation) and copulation (Huffard et al. 2008). This complexity has consequences at the individual, population and productive systems levels (Sims et al. 2001). In addition, marked separation by age, size or proportion of individuals during reproduction in different octopus species have been described (Sims et al. 2001).

Patagonian octopus *Octopus tehuelchus* (Orbigny, 1834) (Cephalopoda: Octopodidae) is an endemic, semelparous, small-sized species (< 150 g) inhabiting the Southwestern Atlantic Ocean, from south of Brazil (16° S) to the northern part of the Argentine Patagonia (44° S). It is found in rocky substrates from low intertidal to the shallow subtidal zone, up to 100 m depth (Iribarne 1991; Ré 1998; Narvarte et al. 2006; Storero et al. 2010; Ré and Ortiz 2011) (Figure 1). Females fix egg clutches to a hard substrate, usually a hole in the rock, empty shells or artificial shelters. In this way, embryos are safe from predators, oxygen level is high by fanning water currents, and incubation area is free from dead embryos and debris (Ré 1998). This species is caught by an artisanal fishery community in the northern Patagonian coast of Argentina (Iribane 1991; Ré 1998; Narvarte et al. 2006) and it has been the subject of biological and fishery studies in the last decades

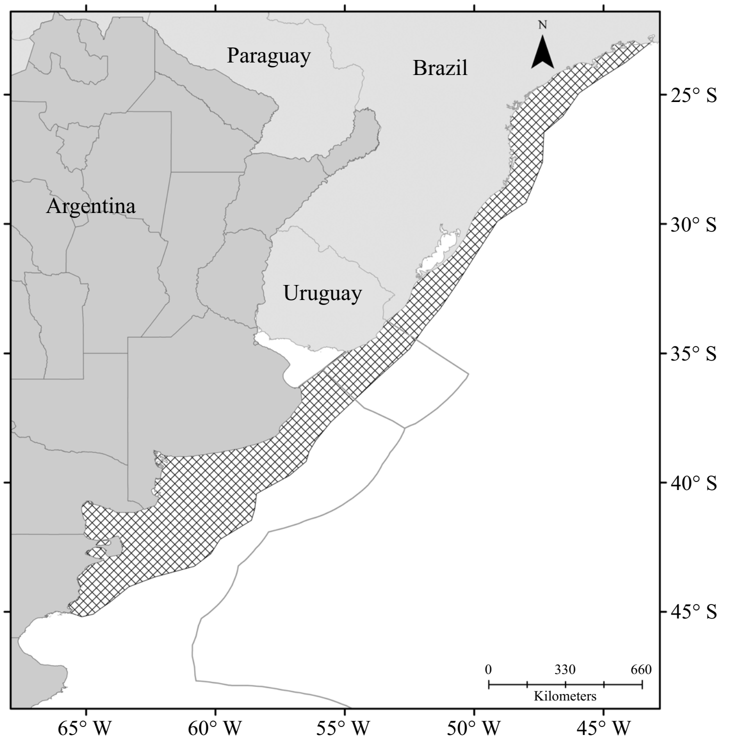

Figure 1. Geographic distribution of *Octopus tehuelchus* in the Southestern Atlantic Ocean (Ré 1998, 2008).

(Pujals 1982; Narvarte et al. 1996, 2007; Storero et al. 2012; Fassiano et al. 2017). Recently *O. tehuelchus* has been considered as a potential aquaculture resource (Berrueta et al. 2018a, 2018b), but the lack of understanding of some aspects of reproductive behavior useful for developing an incubation plant, hinders the development of mass cultivation technology of this species. The objective of this work was to describe male-female interactions during mating of *O. tehuelchus* under controlled aquarium conditions.

Octopuses hatched in captivity at the Estación Experimental de Maricultura, Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). They were maintained individually in 30 l aquaria connected to a recirculation aquaculture system (RAS). Seashells were provided as individual shelters. Photoperiod was set at 12:12 h (light : dark). Water quality parameters were monitored daily and maintained at 15.5 ± 1.1 °C (Earth Industries heater/cooler, Japan), pH 7.7 ± 0.2 (Oakton pH/temperature Series110 RM232), salinity 34 ± 1 (Tanaka NewS-100 light refractometer), and total ammonia concentration 0.0 ± 0.5 mg NH_4^+ L^{-1} (Merck colorimetric kit). Four pairs (male-female) of adult octopuses (nine-month-old) were used to record the events during the mating courtship. Prior to weighting and handling, individuals were anesthetized with 2.5% ethyl alcohol in sea water, following bioethical guidelines by Fiorito et al. (2014) and Butler-Struben et al. (2018). Total weight was registered by using a Mettler Toledo PB 602-S. Initial weight range was 100-125 g and 38-48 g for females and males, respectively. Each couple was placed in an 80 l aquarium with seashells and fed *ad libitum* with fresh shrimp (*Artemesia longinaris*). Male-female interactions were recorded during daytime hours. Mating behavior of Patagonian octopus was classified following the criteria proposed by Huffard et al. (2008), Rodrigues et al. (2009) and Caldwell et al. (2015), which were described as pre-copulatory (swimming, display, and contact) and copulatory behavior. Once the mating was over, male and female were left in the mating tank until the experience ended. After intercourse, females were sedated and examined to verify the presence of spermatophores in the distal oviducts. Octopus behavior in each aquarium was recorded and photographed daily with a Sony Lens G camera.

Three pre-copulatory events (male display, female display, and contact) and one copulatory behavior (intercourse) were observed. Male exhibited an intense and changing reddish color during the display, moving around female's shelter (Figure 2 A) and also returning back to his own shelter. Female exhibited a pale and homogeneous coloration, remaining inside the shelter and displaying her arms outside and directs them towards the male (Figure 2 B). Contact event consisted of touching each other with one or more arms for short intervals of time (5-10″) (Figure 2 C). During copulation male moved towards the female and partially or totally surrounded her with his arms (Figure 2 D). Female remained in her shelter exposing her oral surface with her arms folded towards her mantle while male performed the insemination process by intruding the hectocotylized arm into the female's mantle accompanied by occasional changes in body coloration patterns (Figure 2 E and F). The approximate duration of the copula was 3 to 5 min. After that, male returned to his shelter. Copulation event was repeated 2 to 3 times during the same day, always preceded by the display of the female and the contact of the arms. Couples remained together (from a few days to weeks) in the same tank until female's aggressive behavior towards the male was observed, including the removal of male's shelters. Coincidently with this behavior, egg clutches were found in female's shelters in all cases and males were consequently removed from the mating tanks.

Courtship is an important mechanism in the couple's choice (Krebs and Davies 1993). Huffart et al. (2008) reported a pre-copulatory behavior characterized for a recognition interaction at species and sex level during the onset of courtship in *Abdopus aculeatus*. Gutierrez et al. (2012) indicated that a pre-copulatory behavior in *Enteroctopus megalocyathus* begun with the approach without physical contact followed by three consecutive events: swimming, exhibition and contact. In the present work, both male and female exhibited display behaviors, remarkable changes in coloration and contact between the arms, confirming that a pre-copulatory behavior was present.

Copulation mode and chromatic changes varies significantly in cephalopods (Mangold 1987; Hanlon and Messenger 1996). In squids like *Sepioteuthis lessoniana* and *S. australis* mating position is called 'head to head', where male holds the female with the arms (Boal and Gonzalez 1998). In sepiolids, however, the copulatory strategy observed is the so-called 'male to female neck', accompanied by intense color patterns characteristic for each sex (Moynihan 1983; Nabhitabhata et al. 2005; Rodrigues et al. 2009). Mangold (1987) observed two mating positions in specimens of Family Octopodidae: the 'distance position' in which male and female remain separated during the copulation (only joined by the hectocotyle), and the 'close position' in which the male rides the female. In both cases, the interactions can last from a few minutes to hours. Authors such as Hanlon and Messenger (1996) and Wells and Wells (1972), determined that copula positions in octopuses are of 'distance' or 'assembly', or an intermediate positions between the two. Oral surface of female *O. tehuelchus* faces out of the shelter while the mantle looks towards the eggs during parental care. This mating position was described previously as 'beak to beak' by Caldwell et al. (2015) for the Great Pacific Striped Octopus (LPSO). The same authors indicated that, unlike the 'distance' and 'assembly' positions observed in other types of

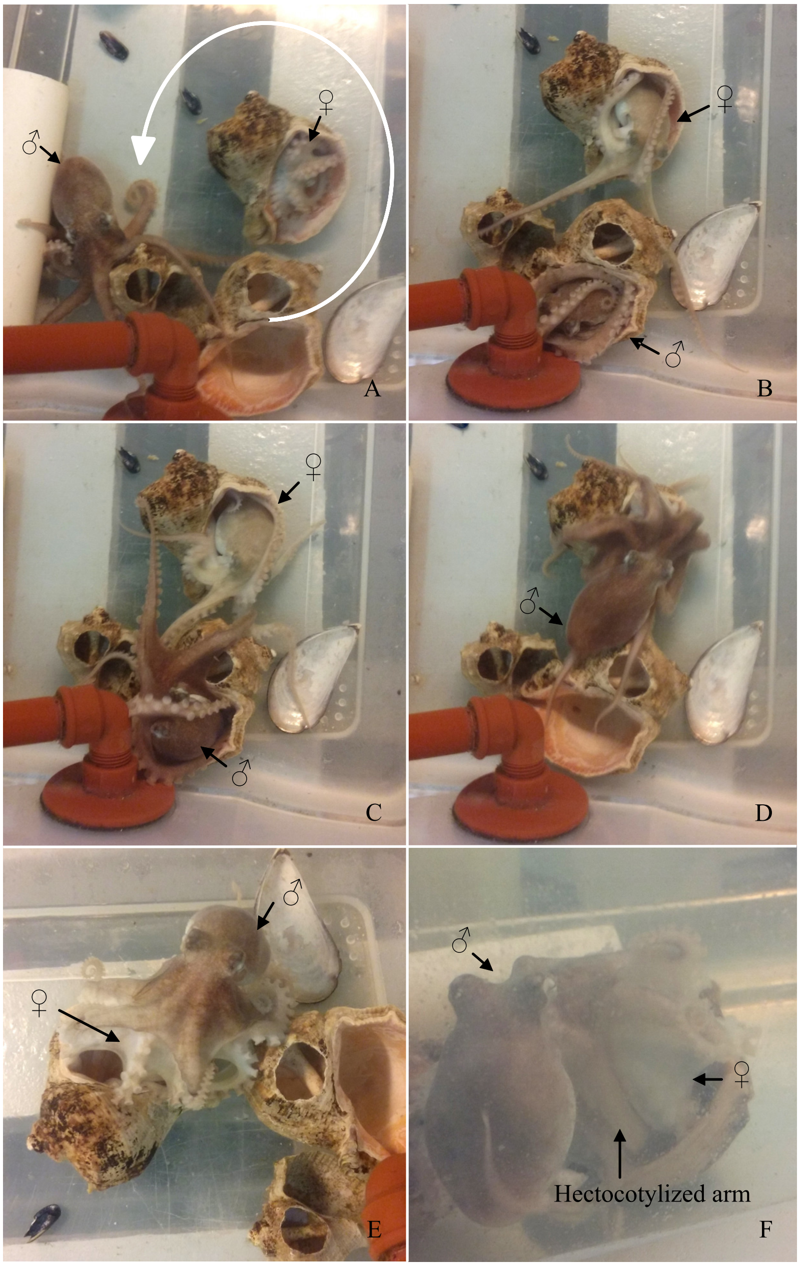

Figure 2. Detail of mating events of Patagonian octopus *Octopus tehuelchus*. Precopulatory behavior: male display (the arrow indicates the movement of the male) (A), female display (B), contact (C). Copulatory behavior: copula (D-F).

octopus, the 'beak to beak' mating implies an effective grip and allows a complete wrapping of the male over the female's oral region, as well as conferring specific advantages such as protection of eggs clutches by female. Generally, in octopuses that have other mating positions such as *O. cyanea* (Tsuchiya and Uzu, 1997), *Vulcanoctopus hydrothermalis* (Rocha et al. 2002), *O. kaurna*

(Norman 2000) and *O. bimaculoides* (Hanlon and Messenger 1996) females can mate with several males simultaneously.

Although many aspects of the mating behavior of *O. tehuelchus* are similar to those reported for LSPO, including the ‘beak to beak’ mating position, it should be noted that female Patagonian octopus remains in the shelter during the pre-copula and copula events. The observations obtained during the present work showed complex behaviors between males and females during mating events, such as a protective behavior of the putting in parallel with the rejection of the already copulated male by female. In this sense, and from a zootechnical point of view, these data are highly relevant for the handling of specimens during reproductive conditioning of *O. tehuelchus* in the laboratory.

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NOTE

NEW OCCURRENCE OF *Mendosoma lineatum* Guichenot, 1848 IN CENTRAL PATAGONIA, ARGENTINA, WITH COMMENTS ON THE ROCKY REEF COMMUNITY

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ABSTRACT. A new record of *Mendosoma lineatum* has been made in central Patagonian waters. This record is the second mention after one specimen was caught in the north of San Jorge Gulf in 2012. It was proposed that the specimen arrived from the Antarctic Circumpolar Current and this hypothesis is now reinforced with this new record. The number of species that make up the rocky reef community of central Patagonia is also extended here. At present, eight species have been recognized as part of this environment, and in this paper the number is extended to fifteen with seven new species identified.

Key words: Telescope fish, Latridae, Argentine Patagonia, rocky reef fishes.

The Subantarctic Zone (SAZ) is the region delimited by the Subtropical Front to the north and the Subantarctic Front to the south (SAF). Strongly influenced by the cold water coming from the southern oceans, SAZ has a circumpolar distribution in the Southern Hemisphere with its northern limits in the Atlantic Ocean. The Malvinas Current originates in the SAF in the Drake Passage and flows northward over the Argentine continental slope (Knox 2007; Herraiz-Borreguero and Rintoul 2011; Artana et al. 2018). Coastal reef fish fauna appears to have a similar composition along the circumpolar distribution of SAZ. One characteristic is the low number of species and abundance with nototheniids making up an essential part of the fish community and other groups making regional differences (Kingsford et al. 1989). For example, in the Auckland Islands three out of twelve species were nototheniids, in Navarino Island nine out of eighteen species were nototheniids, and in Beagle Chanel this proportion is seven out of eighteen. However, in the islands of Tristan da Cunha and Gough no nototheniids were registered (Moreno and Jara 1984; Kingsford et al. 1989; Andrew et al. 1995), but other species groups are common to these sites, such as the families Latridae, Bovichthidae, Moridae and Sebastidae.

In the northern part of Argentine Patagonia, the rocky reef fish community is dominated by warm-temperate fauna with twenty-one families recognized in Nuevo and San José gulfs on reefs up to 30 m depth, including most of those mentioned for SAZ. Toward the south, in the Beagle Chanel, the fish community associated with the kelp (*Macrocystis pyrifera*) forest up to 6 m depth is typical of subantarctic waters, with five families and only eleven species, of which the Nototheniidae family is one of the most important. However, scarce information for central

Patagonia coastal rocky reef is available (Galván et al. 2005, 2009; Irigoyen et al. 2005; Vanella et al. 2006; Venerus et al. 2008, 2014).

Waters of Argentine Patagonia are influenced by Malvinas Current, and from central Patagonia southwards, the rocky reef fish community seems to have a similar composition to that described above for subantarctic waters. Nototheniids are an important component of this community, but other groups are shared with southern South America, Southeast Atlantic islands and New Zealand islands. In this context, the telescope fish *Mendosoma lineatum* Guichenot, 1848 is a species that appears in the Southeast Pacific (Pequeño et al. 1980), Southeast Atlantic (Gon and Heemstra 1987) and New Zealand (Kingsford et al. 1989), but it has only one record in the Southwest Atlantic (Bovcon et al. 2017). The aim of this paper was therefore to add another record of *M. lineatum* and to extend the number of fish species observed in rocky reef of central Argentine Patagonian coast.

Two telescope fish (Figure 1) were caught between October 28th and November 1st 2019 at ‘La Tranquera’ beach, a coastal rocky reef off central Patagonia, Argentina (46° 02′ 36″ S, 67° 35′ 49″ W; Figure 2), between 3 and 10 m depth. Fish were caught by spearfishing. Gut and other organs were removed and then frozen by the fisherman. Once in the laboratory, specimens were fixed in 10% formaldehyde, identified, and morphometric measurements and meristic counts

Figure 1. Specimens of *Mendosoma lineatum* Guichenot, 1848 caught in San Jorge Gulf, central Patagonia. A) Specimen 1. B) Specimen 2.

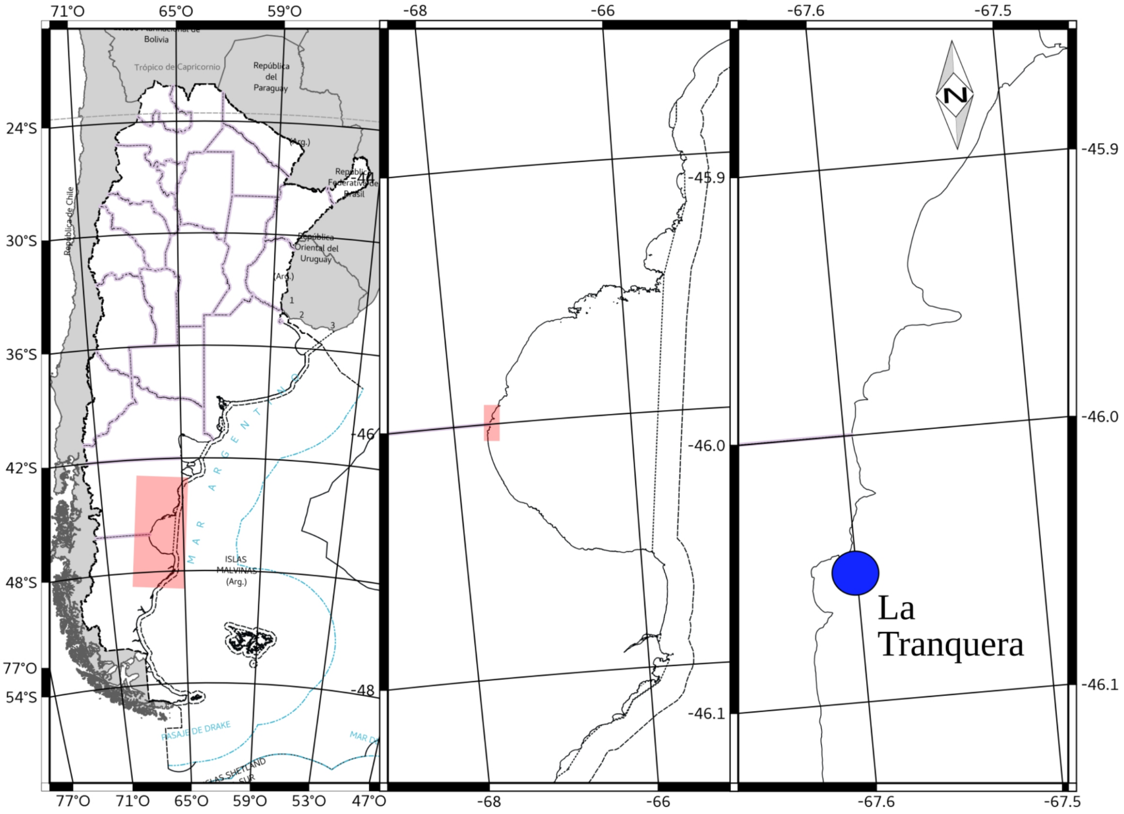

Figure 2. Collection site of *Mendosoma lineatum* Guichenot, 1848.

were made following Pequeño (1980) and Bovcon et al. (2017). *M. lineatum* specimens were deposited in the Ichthyological Collection of the Instituto de Diversidad y Evolución Austral (IDEAus-CENPAT-CONICET) under the following numbers: CNPICT 2019/32 and CNPICT 2019/33 for specimens 1 and 2, respectively. All measurements were made to the nearest millimeter. Exploratory surveys of rocky reef fish were performed by underwater observation conducted by the author and scuba divers over several years.

Morphometric measurements (Table 1) and meristic counts (Table 2) of *M. lineatum* were in accordance with those taken by Pequeño (1980) in Corral Bay (Chile), Gon and Heemstra (1987) in Gough Island (South Atlantic Ocean), and Bovcon et al. (2017) in the north of San Jorge Gulf (Argentine Patagonia). According to the fisherman, fish were in the rocky reef, swimming outside but near the shelter, along with several other fish that he recognized as the same species coming in and out from other shelters. Table 3 show the list of species observed in coastal rocky reef of San Jorge Gulf.

One specimen of *M. lineatum* was observed for the first time in Argentine waters in 2012 and it was proposed that it could have arrived from the northern branch of the Antarctic Circumpolar Current, the Malvinas Current (Bovcon et al. 2017). This paper records another occurrence of two specimens caught and several others observed in the study area, and it is possible that they arrived in the same way. As previously mentioned, the rocky reef fish community of sub-antarctic waters is characterized by having few, low abundance species, of which an important

Table 1. Morphometric measurements of the two specimens of *Mendosoma lineatum* Guichenot, 1848. Measured length and proportion with respect to the standard length or head length are shown.

	Specimen 1		Specimen 2	
Measures	Length (mm)	%SL	Length (mm)	%SL
Total length	314	-	321	-
Standard length (SL)	264	-	275	-
Head length (HL)	74	28.0	71	25.8
Pre-anal length	184	69.7	189	68.7
Predorsal length	76	28.8	87	31.6
Dorsal-fin base	163	61.7	175	63.6
Anal-fin base	47	17.9	50	18.2
Caudal peduncle maximum height	23	8.7	21	7.6
Pectoral-fin length	56	21.2	56	20.4
Pelvic-fin length	40	15.2	40	14.5
	Length (mm)	%HL	Length (mm)	%HL
Orbital diameter	16	21.6	15	21.1
Inter-orbital space	22	29.7	21	29.6
Preocular distance	22	29.7	23	32.4
Postocular distance	38	50.7	35	49.3
Maxilla + premaxilla length	26	35.1	27	38.0

number are nototheniids (Moreno and Jara 1984; Kingsford et al. 1989). Many sites in SAZ share species from the Latridae, Bovichthidae, Moridae, Sebastidae and Nototheniidae families (Moreno and Jara 1984; Kingsford et al. 1989; Andrew et al. 1995; Vanella et al. 2006). With the exception of Latridae, the other families have well-established populations in the waters of central Argentine Patagonia. Since both the oceanographic characteristics of SAZ are similar in all the oceans that it covers, and that many fish families are well adapted to this water mass, the establishment of a telescope fish population could be possible. However, with only two records so separated in time, a population analysis over time would be needed to test this hypothesis.

Nine species were mentioned for central Patagonia as part of the rocky reef community (Galván et al. 2009), and in this paper the number of species was extended to fifteen. Only one species mentioned above, *Pinguipes brasilianus* Cuvier, 1829, was not found, and a second record of *M. lineatum* was made. Compared with description of northern Patagonia made by these authors, most of the families are shared, except for Zoarcidae, Syngnathidae and Latridae (Galván et al. 2009). The Latridae Family is represented by *M. lineatum* and was seen on one occasion; the Syngnathidae Family is represented by the pipefish, well known in San Matías Gulf (Luzzato and Estalles 2019). It is a highly cryptic species and that is possibly why Galván et al. (2019) could not

Table 2. Meristic counts for the two specimens of *Mendosoma lineatum* Guichenot 1848.

	Specimen 1	Specimen 2
Dorsal-fin rays	XXIII-24	XXIII-26
Anal-fin rays	III-16	III-18
Pectoral-fin rays	16	16
Pelvic-fin rays	I-5	I-5
Lateral-line scales	71	78
Scales between the origin of the dorsal fin and lateral line	5	6
Scales between the origin of the anal fin and lateral line	15	16

Table 3. List of species observed in the rocky reef of San Jorge Gulf, including information on species recorded by Galván et al. (2009) in northern Patagonian gulfs (NPG).

Family	Species	NPG
Nototheniidae	*Patagonotothen brevicauda* (Lönnberg 1905)	*
	Patagonotothen cornucola (Richardson 1844)	
	Notothenia angustata Hutton 1875	*
Bovichtidae	*Bovichtus argentinus* MacDonagh 1931	*
	Cottoperca trigloides (Forster 1801)	
Eleginopsidae	*Eleginops maclovinus* (Cuvier 1830)	
Zoarcidae	*Austrolycus laticinctus* (Berg 1895)	
Moridae	*Salilota australis* (Günther 1878)	*
Sebastidae	*Sebastes oculatus* Valenciennes 1833	*
Pinguipedidae	*Pseudopercis semifasciata* (Cuvier 1829)	*
Cheilodactylidae	*Nemadactylus bergi* (Norman 1937)	*
Tripterygiidae	*Helcogrammoides cunninghami* (Smitt 1898)	
Congiopodidae	*Congiopodus peruvianus* (Cuvier 1829)	*
Syngnathidae	*Leptonotus* sp.	
Latridae	*Mendosoma lineatum* Guichenot 1848	

observe it. Perhaps the most important difference is made by Zoarcidae family, which is well represented in southern Patagonia (Gosztonyi 1977; Vanella et al. 2006). On the other hand, compared with the Beagle Channel, three of the five families found in the south are shared: Nototheniidae, Zoarcidae and Bovichtidae (Vanella et al. 2006).

This study was carried out in San Jorge Gulf, which is an intermediate zone with a mixed fish community, some shared with northern Patagonian gulfs, and others with Beagle Channel. It has a moderate number of species, lower than north of Patagonia and higher than Beagle Channel, but corresponding to that seen in the subantarctic reef.

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NOTE

SEA GRASSES, A NEW UNREPORTED HABITAT FOR THE HETEROBRANCH MOLLUSK *Umbraculum umbraculum* IN THE CARIBBEAN REGION

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ABSTRACT. Herein, a new habitat for the heterobranch mollusk *Umbraculum* is described. One specimen was found on a *Thalassia testudinum* bed at Taganga Bay at 3 m depth, a buffer area of the Tayrona National Park, Colombian Caribbean. To the best of our knowledge, these mollusks have not been previously reported in this kind of habitat. Seagrasses may provide protection and possibly serve as areas for its reproduction.

Key words: Heterobranch, habitat, *Thalassia testudinum*, Colombian Caribbean.

INTRODUCTION

Among Caribbean gastropods, heterobranchs are an uncommon sight due to their low local abundances. Except for some local population pulses of aplysiids (sea hares), heterobranchs are largely overlooked as a group (Diaz and Puyana 1994). *Umbraculum* (Mollusca: Gastropoda: Heterobranchia: Umbraculida: Umbraculidae) has a cosmopolitan distribution in warm tropical and temperate waters (Wägele et al. 2006a).

Umbraculum umbraculum has been given different names at various geographic regions (Sankar et al. 2011). The species was recently reported at the Bay of Biscay, eastern Atlantic Ocean (Arias and Crocetta 2016). The local seawater temperature generally ranges from 12-13 °C in winter (January-February) to 21-22 °C in summer (July-August). However, a generalized sea surface warming (an upward trend of the sea surface temperature series) and intensification in the upwelling intensity during the summer months has been registered off the Santander and Bilbao coast during the last two decades (Bode et al. 2013). This increase in temperature influences significant changes in the local faunal composition (Bode et al. 2013) and may be considered an indication of a tropicalization of the area, a pattern that has also been shown in coral replacement of kelps in southern Japan (Vergés et al. 2014).

Morphologically, *U. umbraculum* is characterized by its long foot and a flat shell covering its body (Mikkelsen 2002). It has a deep orange color and a mantle covered with pustules. As other members of the Order Umbraculida, *Umbraculum* spp. are specialist predators on a wide array of sponges (Willam 1984; Avila et al. 2018). Heterobranchs are well known for sequestering, transferring and even modifying metabolites from their diet for defensive purposes (Faulkner and Ghiselin 1983; Cimino et al. 2001). These compounds may be released via mucus or concentrated in the mantle dermal formations or other glandular structures (Wägele et al. 2006a). The only metabolites from *U. umbraculum* known to date are two diacylglycerols and a fatty acid ester probably produced by the sponge *Geodia cydonium* in the Mediterranean where the mollusk was collected (Cimino et al. 1988, 1989). Until now, little is known about the ecology of heterobranchs such as *U. umbraculum*, even though its presence is recognized in the Caribbean region. Information about habitat preferences, food and reproduction patterns is scarce. This note describes a recent finding of this mollusk on a previously unreported habitat, which may provide shelter during various stages of its life cycle.

Habitat characteristics

A solitary specimen of the heterobranch mollusk *Umbraculum umbraculum* was found on March 1, 2018 at a *Thalassia testudinum* bed at Taganga bay, a buffer area of the Tayrona National Park, Colombian Caribbean (11° 16′ 16.1″ N-74° 11′ 54.1″ W; Figure 1 A) at 3 m depth. The area is affected by local coastal upwelling from December to March. In these months, seawater temperature may drop to 20-25 °C (Diaz-Pulido and Garzon-Ferreira 2002; Bayraktarov et al. 2012). The seagrass bed where we found the specimen was located on a muddy sand substrate at the leeward side of the bay (Figure 1 B). We carried out some preliminary evaluations to assess the conservation state of this seagrass bed in particular. In an area of 100 m^2, we measured parameters such as shoot density, growth rate and overall biomass. We determined that this bed has a rather low density (88 shoots m^{-2}, each bearing two to five short leaf blades, 15 cm long, growing from a basal meristem). The calculated growth rate was of 0.8 cm day^{-1}, yielding an overall biomass of 5.04 g m^{-2} and reaching a productivity of 0.15 g m^2 day^{-1}. These biological features, together with rather intense tourist activity in the area, and ecosystem risk analysis (Bland et al. 2016) allow us to consider that this seagrass bed is in a poor conservation state, and possibly in Critical Risk of collapse according to IUCN categories.

Specific habitat preferences for *U. umbraculum* have not been well documented to date. The species has been only reported at shallow sandy bottoms in Greece (Wägele et al. 2006b; Sankar et al. 2011). In Colombia, a specimen (Catalog number INV MOL-1595; MAKURIWA-Marine Natural History Museum of INVEMAR; http://siam.invemar.org.co/buscador) was collected on soft bottoms (70 m depth) at Cabo de la Vela (Marcus and Marcus 1967) in the upwelling area of the Guajira (12° 12′ 15.7″ N-72° 10′ 59.4″ W) and also seen at Tayrona National Park (Ardila et al. 2007).

To the best of our knowledge, there are no previous reports of *U. umbraculum* thriving in *Thalassia testudinum* beds. As with other heterobranchs, *U. umbraculum* might gain protection from predation among the seagrass blades and may also find suitable food sources, once, in our field evaluations, we found several specimens of *Agelas* spp. and other sponges. Additionally, the animal observed was in reproductive mode since upon collection it released copious amounts of sperm (Figure 1 C and 1 D), which suggest that *U. umbraculum* uses the upwelling season (January to March) to migrate to shallow water and reproduce as others mollusks do at Taganga Bay such as *Octopus hummelincki* (Adam, 1936) and *Aplysia dactylomela* (Rang, 1828) (Jürgen Guerrero-Kommritz, Pers. Observ.).

Habitat and water quality in Taganga bay have diminished over the last four decades. The bay is

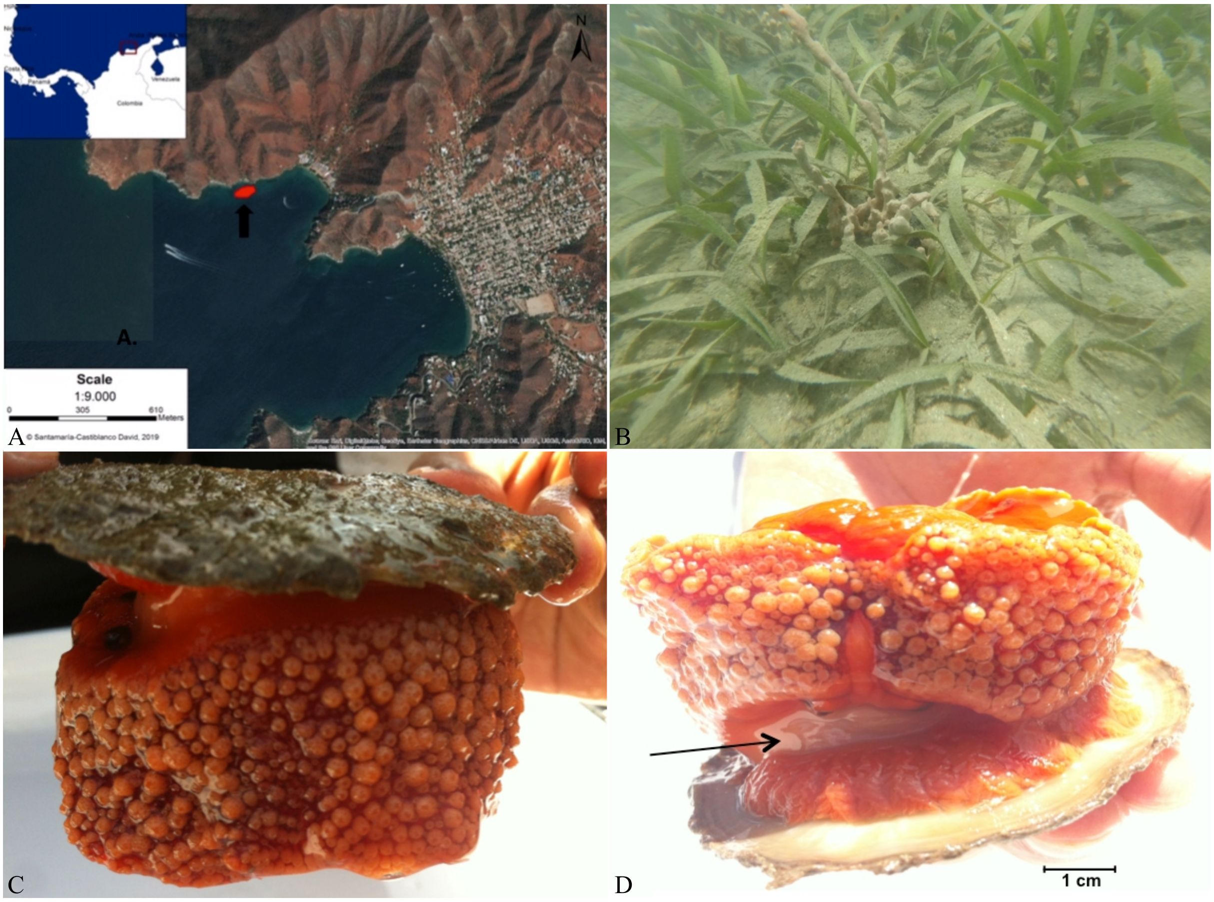

Figure 1. A) Map of the seagrass bed where the specimen of *Umbraculum umbraculum* was found (red dot) at Taganga Bay, Colombian Caribbean. B) Detail of the seagrass habitat, with profuse growth of sponges that could potentially be a food source for this opisthobranch. Seagrasses could also be an important breeding habitat for this mollusk. C-D) Live specimen of *U. umbraculum* collected; note the sperm released by the individual (arrow).

subject to high sedimentation rates coming directly from local sources (the Manzanares and Gaira rivers as well as seasonal stream flows into Playa Taganga) and indirectly through the Magdalena river plume, particularly after heavy rains. The fact of finding this specimen suggests two possible scenarios: the first one is that seagrasses may be a suitable habitat for this species, where potential predators such as fishes and crabs are significantly diminished due to overfishing. Alternatively, the presence of this mollusk species might represent a threat for other animals such as sponges upon which they prey upon. Overall, we believe that the seagrass bed at Taganga bay may provide food and shelter for many invertebrate species and possibly vertebrates as well, from adjacent rocky shores, reef formations and soft bottoms (Pawlik 1998; Pawlik et al. 2018).

While brief, this report is of great interest to gain some further insights on the distribution and ecology of this uncommon mollusk. It also raises new questions concerning its potential vertical migration, as well as food and habitat preferences. Further research should provide more insights on the life habits of *U. umbraculum* in the Caribbean region.

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