UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA

Programa de Doctorado en Acuicultura Sostenible y Ecosistemas Marinos
Escuela de doctorado

Tesis Doctoral

Bioecología de *Sepia bertheloti* d'Orbigny, 1835 en la costa noroccidental africana

Airam Manuel Guerra Marrero

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Fotografía portada***: Eye of cuttlefish in the spotlight with a blac background. Stocktrek, Inc./ Alamy Stock Photo.***

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INFORMA,

De que la Comisión Académica del Programa de Doctorado, en su sesión de fecha .... tomó el acuerdo de dar el consentimiento para su tramitación, a la tesis doctoral titulada **"Contribución a la ecología de la sepia africana *Sepia bertheloti* en el oeste de África**" presentada por el doctorando D. Airam Manuel Guerra Marrero y dirigida por el Dr. José Juan Castro Hernández y la Dra. Catalina Perales Raya.

Y para que así conste, y a efectos de lo previsto en el Artº 11 del Reglamento de Estudios de Doctorado (BOULPGC 04/03/2019) de la Universidad de Las Palmas de Gran Canaria, firmo la presente en Las Palmas de Gran Canaria, a...de...de dos mil............

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA

ESCUELA DE DOCTORADO

Programa de doctorado Acuicultura Sostenible y Ecosistemas Marinos.

Título de la Tesis

BIOECOLOGÍA DE *SEPIA BERTHELOTI* D'ORBIGNY, 1835 EN LA COSTA NOROCCIDENTAL AFRICANA.

Tesis Doctoral presentada por D. Airam Manuel Guerra Marrero

Dirigida por el Dr. D. José Juan Castro Hernández
Codirigida por el Dra. Dª. Catalina Perales Raya

Las Palmas de Gran Canaria, a 11de noviembre de 2022

El Director,	La Codirectora	El Doctorando,
(firma)	(firma)	(firma)

A mis padres,
A mi hermana y cuñado,
A Mateo.

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Agradecimientos

Creo que es de bien nacidos ser agradecidos, por lo que es mi deber que a los primeros que rinda el agradecimiento sea a mis padres, Ramona y Manolo, ya que sin su inestimable apoyo esta tesis no habría sido posible. He de agradecer toda la confianza puesta en mí desde que inicié mi andaduría en la investigación, donde su motivación ha hecho que hoy este terminando esta tesis doctoral tras 5 largos y duros años. No puedo olvidarme de mi otra parte, Lucia, que, aunque ahora mismo junto a mi cuñado Héctor me han convertido en el tío más feliz del mundo por la llegada de Mateo, quiero reconocerle su carisma, su curiosidad y su apoyo continuo para que trabaje en aquello que más me apasiona, el mar. Agradecer a mis abuel@s, mis tí@s, a toda mi familia su apoyo incondicional no solo durante estos años, sino por estar siempre ahí.

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Resumen

La costa noroccidental africana es uno de los sistemas pesqueros más productivos del mundo, abarcando desde el estrecho de Gibraltar hasta Guinea-Bissau. Esta área forma parte de lo que se conoce como gran ecosistema marino de la Corriente de Canarias (CCLME), cuya característica más destacable son los diversos sistemas de afloramientos responsables de la alta productividad primaria, sostenida por masas de agua profundas, frías y cargadas de nutrientes, que ascienden a la superficie impulsadas por el transporte generado por la corriente y la intensidad de los vientos alisios. Esto hace que la diversidad de cefalópodos conocida para la CCLME, según su última actualización, esté conformada por 65 especies pertenecientes a 23 familias. Por su interés pesquero o comercial, destacan unas pocas especies tales como *Octopus vulgaris, Loligo vulgaris, Sepia officinalis, Todarodes sagittatus*, *Alloteuthis africana*, *Todaropsis eblanae, Illex coindetti y Sepia hierreda,* aunque algunas de estas, al igual que otras muchas, no son registradas de manera individualizada en las capturas, registrándose como *Loligo* spp*.,* *Omastrephidae* spp*. o Sepia* spp*.* Esto también se debe a que los estudios biológicos y pesqueros de estas especies "secundarias" son escasos o ausentes, ya que el mayor esfuerzo científico se ha centrado en O. *vulgaris, S. hierreda, S. officialis* y *T. sagittatus.*

En 2019 las capturas de cefalópodos en el área FAO 34 fue de 158.494 t, el 27% de las cuales fueron de sepias (también denominados chocos). Curiosamente, bajo la denominación de *Sepia* spp*.* se englobó el 99% de las capturas de choco en ese mismo año, abarcando especies como *Sepia hierreda, S. bertheloti, S. elegans* y *S. orbingyana.* Por ello, el objetivo de esta tesis doctoral es ampliar la información biológica y ecológica de una de estas especies "ocultas" en las estadísticas pesquera

del área, concretamente de la sepia africana, *Sepia bertheloti,* con la finalidad de proporcionar información biológica que permita mejorar su conocimiento biológico y de su dinámica poblacional en la costa noroccidental africana. Para ello, se analizaron muestras de sepia africana procedentes de la pesca comercial en dos áreas, una de la costa norte (Marruecos) y la otra de la zona sur (Guinea-Bissau).

Dentro de los objetivos específicos, se analizó la estimación de edad y su validación en sepias, con el propósito de confirmar la interpretación de la edad y del crecimiento en *Sepia bertheloti*, ya que estos parámetros son necesarios describir la dinámica poblacional de la especie y por tanto para mejorar la gestión de la pesquería. Además, se analizó la dieta y estrategia alimentaria de la especie a través de análisis de contenidos estomacales, para establecer las preferencias tróficas, las interacciones de la especie dentro del ecosistema. Finalmente, en esta tesis doctoral se analiza el sepión, ya que es una estructura resistente y que comúnmente se suele encontrar en las artes de pesca como residuo de la depredación. El sepión es una estructura útil para conocer el sexo de los individuos que han sido predados, pero también para realizar estimaciones de biomasas, al servir como predictor de la talla o peso de estos animales.

En cuanto al material analizado, se obtuvieron un total de 1124 individuos de *Sepia bertheloti* para las dos áreas de estudio citadas. En Marruecos se obtuvieron 499 individuos mientras que de Guinea-Bissau fueron 625. Los ejemplares en Marruecos se obtuvieron de capturas realizadas entre julio-septiembre 2018 y enero 2020, mientras que en Guinea-Bissau las sepiolas se obtuvieron en capturas realizadas en julio 2019 y enero 2020. Los ejemplares se mantuvieron congelados desde la captura hasta su análisis en el laboratorio de la ULPGC. Los ejemplares de Marruecos presentaron un rango de tallas que osciló entre 50 y 138 mm de Longitud Dorsal del Manto (LDM), y un peso comprendido entre los 18,94 y los 206,98 gramos. En Guinea-Bissau, los ejemplares mostraron tallas más grandes, con una LDM comprendida entre los 32 y176 mm y un peso que osciló entre los 20,03 y los 456,61 gramos. La proporción de sexos fue de 1:0,27 en las muestras procedentes de Marruecos y de 1:0,45 en aquellas llegadas desde Guinea-Bissau, con un claro predominio de los machos en ambas áreas.

Para la estimación de la edad se utilizó la mandíbula (pico), ya que estudios previos en cefalópodos bentónicos han demostrado su utilidad frente a otras estructuras como los estatolitos, cristalinos o sepión. Estas tres últimas estructuras se analizaron para ver su utilidad, aunque su patrón de incrementos observado no presentaba la suficiente constancia y consistencia para su uso en la determinación de la edad de la especie. Por ello, la mandíbula fue la estructura finalmente seleccionada, concretamente la mandíbula inferior por mostrar mejor visibilidad y constancia en el patrón de deposición de los incrementos (o marcas) de crecimiento de forma similar a los resultados validados en otros cefalópodos bentónicos.

En primer lugar, para poder validar la periodicidad de deposición de los incrementos y, por tanto, de las edades estimadas en *Sepia bertheloti,* se utilizaron juveniles de sepia común (*Sepia officinalis*) de edad conocida para establecer una relación entre la edad real y las marcas de crecimiento en la zona del rostro de la mandíbula (Capitulo 2). El estudio se realizó cultivando los ejemplares a dos temperaturas distintas (18 y 21ºC), con objeto de estimar la posible influencia de la temperatura en la deposición de las marcas de crecimiento. Los individuos se cultivaron hasta los 31 días de vida. En este experimento se concluyó que en número de incrementos observados en el rostro de los juveniles se corresponde con la edad real (días de vida desde la eclosión) a ambas temperaturas, sin que se observaran cambios influenciados por este factor.

El siguiente paso consistió en utilizar esta técnica para la estimación de la edad y crecimiento de adultos de *Sepia bertheloti* en las dos áreas de estudio (Capitulo 3). En el caso de los adultos, la técnica para la observación se modifica, ya que la mandíbula es mucho mas consistente y necesita ser cortada y pulida para una correcta observación de los incrementos. El área del pico analizada en adultos fue la misma que en juveniles (rostro), para así poder afirmar la deposición diaria de los incrementos. En este estudio se estimó la esperanza de vida de *Sepia bertheloti* en 14 meses. Las sepiolas procedentes de Marruecos presentaron una edad máxima estimada de 419 días, mientras que en aquellas provenientes de Guinea-Bissau la longevidad alcanzó los 433 días. En ambas, estas sepias presentaron un crecimiento alométrico negativo, y el modelo de crecimiento que mejor se adaptó para definir el desarrollo del conjunto de la población fue el modelo exponencial, aunque los patrones de crecimiento difirieron entre áreas. Los individuos procedentes de Guinea-Bissau presentaron curvas de crecimiento de mayor pendiente que las sepiolas capturadas en aguas de Marruecos. A su vez, los machos de cada área crecen más rápidos que las hembras.

En el siguiente apartado se analizó la estructura del sepión de *Sepia bertheloti*, a través de su estudio morfométrico tradicional, con objeto de identificar posibles diferencias entre sexos y la viabilidad del uso de este órgano como estimador de biomasa (Capitulo 4). Para ello, únicamente se utilizaron los sepiones de individuos capturados en aguas de Marruecos, ya que los sepiones de los ejemplares procedentes de Guinea-Bissau no proporcionaron un numero viable como para obtener resultados satisfactorios en esa área. Esto se debe a que el sistema de pesca y/o procesado de las muestras a nivel comercial es muy agresivo, produciendo en más del 90% de los sepiones fracturas que imposibilitaban la obtención de las medidas necesarias para el análisis morfométrico. Así, en los sepiones de los ejemplares capturados en Marruecos, se tomaron un total de 8 medidas morfométricas. En términos generales, las hembras de *Sepia bertheloti* mostraron un sepión más ancho en relación con los machos. Gracias al índice gonadosomático, se pudo interpretar que las hembras adaptan su cuerpo para el desarrollo gonadal, y un sepión más ancho permite que la gónada femenina ocupe un mayor espacio en la cavidad paleal, con mayor capacidad para alojar los huevos. Para la estimación de biomasas, se aportan las ecuaciones potenciales de las 8 variables morfométricas analizadas respecto a la LDM, gracias a las cuales podremos estimar el peso de los individuos a partir de las dimensiones del sepión.

El último apartado planteado en la tesis fue la determinación de la dieta y la estrategia alimentaria de *Sepia bertheloti* en ambas áreas de estudio (Capitulo 5). Aunque se dispuso de 1124 ejemplares, en el estudio de la dieta se utilizaron 1114. Esto se debe a que 10 de los individuos capturados mostraron su cavidad gástrica rota debido al sistema de pesca, descartándose estos ejemplares del análisis para evitar una malinterpretación de los resultados.

El método finalmente utilizado fue el análisis visual de los contenidos estomacales. Los ejemplares de Marruecos mostraron una dieta compuesta por un total de 65 taxones, mientras que en aquellos de Guinea-Bissau solo se identificaron 49. En ambos casos el número de estómagos analizados fue suficiente para describir la dieta, tal y como indican las respectivas curvas acumulativas de especies. La dieta se ha descrito a través de la frecuencia de ocurrencia de las presas, su importancia numérica y su importancia gravimétrica. No se encontraron diferencias significativas en las categorías de las presas identificadas entre sexos o áreas de estudio, aunque sí se observaron diferencias en la riqueza, diversidad y abundancia de especies. Los individuos procedentes de Marruecos mostraron una media de 3,19 presas en los contenidos estomacales, mientras que en los estómagos analizados de sepiolas de

Guinea-Bissau la media fue de 1,43 presas por estómago. En relación a grandes grupos taxonómicos, las presas más abundantes fueron los crustáceos seguido de los peces y cefalópodos. Los anfípodos gammaridos mostraron la mayor importancia de ocurrencia en ambas áreas de estudio. Además, en este apartado se analizó el espectro de su nicho ecológico, a través del índice de Levin’s y el grafico propuesto por Amundsen, y se define a *Sepia bertheloti* como especie omnívora con una dieta heterogénea, sin una estrategia alimentaria marcada como generalista o especialista. En función de la frecuencia de ocurrencia de las presas, la especie puede clasificarse como un consumidor segundario, ya que su nivel trófico medio fue 3,63 en Marruecos y 3,60 en Guinea-Bissau.

CAPÍTULO 1

Fotografía portada Capítulo 1: *Sepia officinalis,* Bas Kers (NL) vía Flickr [CC BY-NC-SA 2.0]

Capítulo 1

INTRODUCCIÓN GENERAL

1.1. Los cefalópodos

Los cefalópodos (clase Cephalopoda Cuvier, 1979) son el grupo más complejo del Phylum Mollusca desde el punto de vista anatómico, fisiológico y comportamental, pero también en cuanto a su capacidad sensorial y desarrollo de su sistema nervioso, habitando solamente el medio marino (Guerra, 1992). Su primera aparición data del Cámbrico superior (alrededor de 500 millones de años; Jereb & Roper, 2005), donde su origen se relaciona con los Monoplacophora (Fig 1, Dzik, 1981,). Se conocen más de 9000 formas fósiles (Mangold et al., 1989) y actualmente hay 860 especies vivas reconocidas (Luna, 2021).

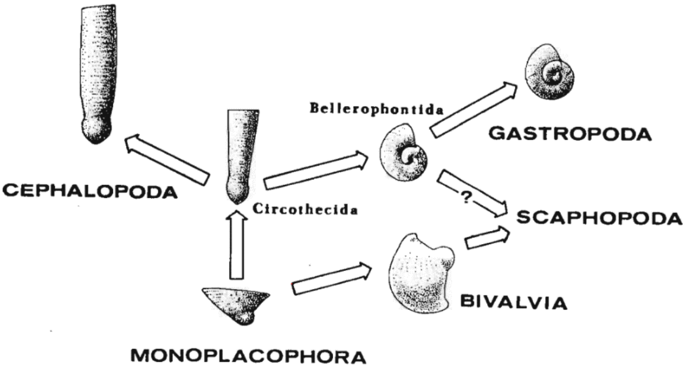


Figura 1.- Evolución de la concha de los moluscos más primitivos (Extraído de Dzik, 1981).

La clase Cephalopoda se encuentra divida en dos subclases, la Nautiloidea Blainville 1825 y la Coleoidea Bather, 1888. De la primera clase existen más de 2500 especies fosilizadas, aunque actualmente solo encontramos vivos dos géneros: *Nautilus Linnaeus, 1758* y *Allonautilus Ward & Saunders, 1997*. De la subclase Coleoidea, actualmente se conocen dos superódenes, los Octopodiformes Berthold & Engeser, 1987 y los Decapodiformes Leach, 1817. Los Octopodiformes se dividen en dos órdenes: Octopoda Leach, 1818 y Vampyromorpha Robson, 1929, estando los octópodos representados por dos subórdenes, mientras que en el orden

Vampyromorpha Robson, 1929 solo encontramos la familia Vampyroteuthidae Thiele in Chun,1915. Por otro lado, los Decapodiformes están representados por 41 familias, que incluyen todas las potas, calamares y sepias (Fig. 2). Los coloideos a diferencia de los nautiloideos, han reducido considerablemente e internalizado el caparazón, generando un manto que utilizan para la locomoción y respiración (Strungnell et al., 2009)

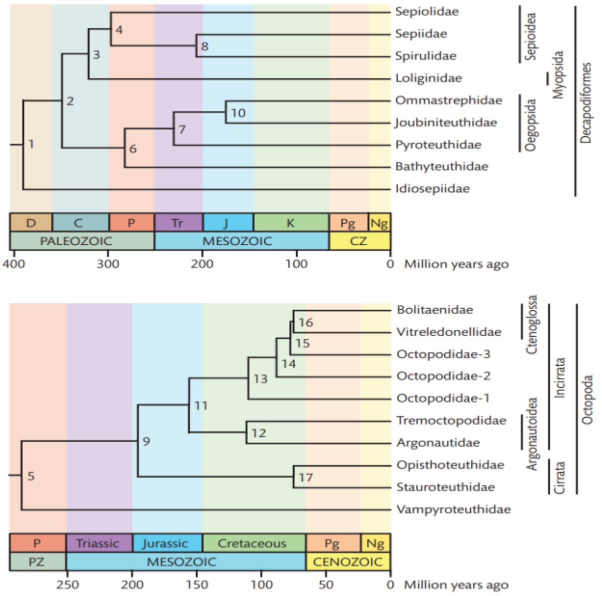


Figura 2.- Dendograma de los moluscos cefalópodos: Decapodiformes y Octopodiformes. C: Carbonífero, CZ: Cenozoico, D: Devónico, J: Jurásico, K: Cretácico, Ng: Neógeno, P: Pérmico, Pg: Paleógeno, PZ: Paleozoico y Tr: Triásico. Octopodidae1: Octopus, Hapalochlaena; Octopodidae 2: Benthoctopus, Enteroctopus, Octopodidae 3: Adelieledone, Pareledone. (Imagen extraída de Strungnell et al., 2009).

Los cefalópodos habitan todos los océanos y son especies que a pesar de su baja diversidad ocupan roles clave en muchos ecosistemas marinos, desde las zonas costeras hasta profundidades abisales superiores a los de 5000 metros (Jereb & Roper, 2010). Actualmente, se conoce un relativo bajo número de especies (aproximadamente 845, Hoving et al., 2014), a pesar de la gran cantidad de estudios destinados a conocer la diversidad faunística, y de que existen áreas que son consideradas "hotspots" de riqueza de cefalópodos (Laptikhovsky et al., 2017; Escánez et al., 2020). Esta baja diversidad en determinadas familias (e.g. Vampiroteuthidae) se debe también a la dificultad de obtención de las muestras, por lo que es necesario un mayor esfuerzo en la obtención de información taxonómica, biológica, ecológica que ayuden a comprender mejor la distribución, comportamiento y papel de los cefalópodos dentro de los ecosistemas marinos.

La presente tesis aborda el estudio de la biología y ecología de la sepia africana, *Sepia bertheloti* d'Orbigny, 1835*,* capturadas en dos áreas del norte y centro de la costa atlántica de África (Marruecos y Guinea-Bissau).

1.2. La especie: *Sepia bertheloti*

Sepia bertheloti d'Orbigny, 1835 (Fig. 3) es un cefalópodo Decapodiforme que pertenece a la familia Sepiidae y al género Sepia (Fig. 2; Mangold and Young, 2012).

Figura 3.- Espécimen de *Sepia bertheloti* capturado en Guinea-Bissau ©IEO

Se caracteriza por tener un manto cuyo margen dorsal se proyecta hacia delante de forma pronunciada con un ángulo agudo (Jereb & Roper, 2005; Guerra et al. 2014). El color de esta especie tiene un característico tono púrpura, como se aprecia en el ejemplar recién capturado de la Figura 3. El 4º par de brazos (pareja ventral) es más largo que el resto. Los tentáculos son retractiles y se encuentran dentro de dos pequeñas bolsas a cada lado de la cabeza. Los tentáculos son delgados y presentan dos quillas en la base (Fig. 4B). Las ventosas en la maza tentacular están distribuidas en 8 filas transversales oblicuas, son pequeñas y todas ellas de similar tamaño (subiguales), aunque la tercera fila se muestra ligeramente más grande (Fig.4 B).

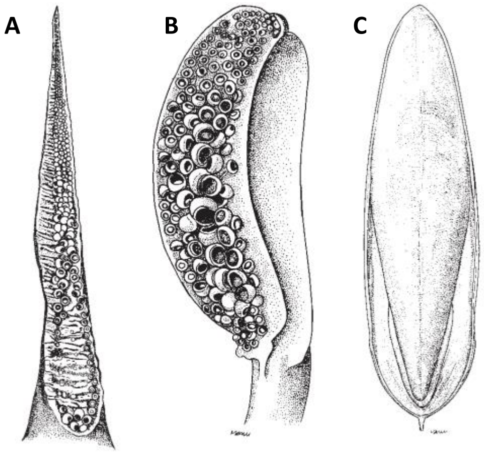


Figura 4.- A. Brazo hectocotilizado, **B.**maza tentacular y **C.**sepión de *Sepia bertheloti*. (imagen extraída de Jereb & Roper(2005))

La familia Sepiidae se caracteriza por la presencia de una concha calcárea, comúnmente conocido como sepión. En el caso de *Sepia bertheloti*, este tiene forma oval (Fig. 4C, Guerra-Marrero et al., 2019) y se caracteriza por la presencia de una espina de longitud moderada. Los machos maduros presentan el brazo ventral izquierdo hectocotilizado (IV brazo izquierdo, Fig. 4A). En el dicho brazo una o dos filas de estas ventosas se mantienen en tamaño normal, mientras que de 9 a 13 filas reducen su tamaño a la mitad, y las dos series dorsales y las 2 ventrales son desplazadas lateralmente dejando un espacio entre ellas, adaptándose para actuar como órgano copulador (Fig. 4A). Esta característica demuestra el dimorfismo sexual en los individuos maduros, pero existen otras para definirlo a lo largo de su ciclo de vida.

El manto es relativamente más ancho en las hembras que en los machos, mientras que los machos son más largos. Los brazos son mucho más largos en los machos que en las hembras. Esta característica es propia también de *Sepia officinalis*, aunque *S. bertheloti* presenta una maza tentacular mucho más pequeña (Jereb & Roper, 2005).

Sepia bertheloti se distribuye por el Atlántico oriental, desde la costa norte de África (Tánger) hasta Angola (Jereb & Roper, 2005) habitando desde los 20 a unos 160 m de profundidad. En verano muestran un comportamiento más costero que en invierno, coincidiendo con la época de reproducción (entre verano y otoño, Hernández-García & Castro, 1994).

La correcta identificación de *Sepia bertheloti* es esencial para poder evaluar el estado de sus poblaciones. Comercialmente se registran como *Sepia* spp. en los registros oficiales de captura, mezclada con juveniles y adultos pequeños de *S. officinalis y S. hierreda* (especies objetivo de la flota en África noroccidental) que no presentan la talla ideal de comercialización. En este grupo además hay que incluir otras sepias de menor tamaño como son *S. elegans* y *S. orbingyana*.

La singularidad de esta especie y centrar los estudios en ella no es casual, ya que a pesar de su pesca e interés comercial (Jereb & Roper, 2005), la actividad extractiva sobre la misma se realiza sin el seguimiento específico de sus descargas, careciendo de registros oficiales de captura individualizados para esta especie (FAO, 2021). Esto se debe a que tanto en su captura como en su comercialización se reportan mezcladas con otras sepias que son las especies objetivo de la flota (principalmente S. *officinalis* en el norte y *Sepia hierreda* en el centro de África). Como consecuencia, la contribución a las capturas de *S. bertheloti* se encuentra incluida junto con las especies citadas como *Sepia spp.*, donde aparecen además las capturas de otras especies accesorias de menor tamaño como *Sepia orbingyana* y *Sepia elegans*.

1.3. Área de estudio

Los ejemplares analizados para la realización de esta investigación fueron capturados en la costa atlántica de África, específicamente en aguas de Marruecos y Guinea-Bissau (Fig. 5), donde existe una gran actividad extractiva debido a la productividad de la zona.

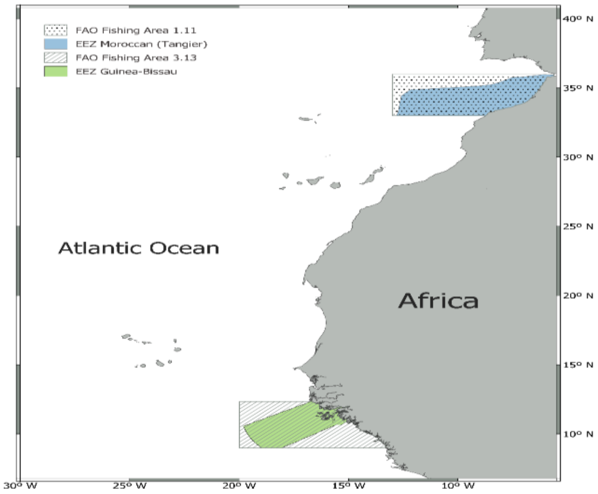


Figura 5.- Mapa en el que se muestra las zonas donde fueron capturadas las muestras de *Sepia bertheloti* en Marruecos y Guinea-Bissau

La costa atlántica del centro y norte de África se caracteriza por la presencia importantes sistemas de afloramientos, conformando lo que se conoce como "*Canary Current Large Marine Ecosystem"* (CCLME), muy relacionados con la orografía del fondo, la geomorfología de la costa y su interacción con la Corriente de Canarias, y muy dependientes de la intensidad de los vientos alisios (Bas et al., 1995). La influencia de estos vientos hace que las masas de aguas profundas, frías y ricas en nutrientes asciendan a superficie, enriqueciendo las capas superficiales costeras, que asociado a la luz solar, generan un crecimiento exponencial de la productividad primaria (Demarcq & Somoue, 2015). Los vientos alisios desplazan las aguas costeras superficiales hacia mar abierto, permitiendo el ascenso de las masas de aguas profundas (Bas et al., 1995). Estas surgencias de aguas profundas debido al desplazamiento de las aguas costeras por los vientos son conocidas como afloramientos, siendo responsables de la gran productividad de la costa oeste de África (Arístegui et al., 2009). Esta gran productividad del área (Watson et al., 2014) además viene influenciada por parámetros oceanográficos anómalos para el área, como son la temperatura ambiental, la cual supera ~2ºC a la esperada para ubicación geográfica, el aporte de agua fría proveniente de la corriente de Canarias y las anomalías atmosféricas debido al ciclón ecuatorial y el anticiclón de las Azores (Arístegui et al., 2009). Todas estas variables son las causantes de la gran productividad del sistema y por consecuente una de las áreas con mayor productividad pesquera (Bas et al., 1995).

La zona de Marruecos se encuentra influenciada por el afloramiento permanente que existe entre el estrecho de Gibraltar y Cabo Blanco, donde dominan los vientos alisios durante casi todo el año. Aunque en esta zona, del norte de África (entre el estrecho de Gibraltar y Cabo Blanco) el afloramiento sea continuo durante todo el año, su mayor o menor intensidad es de carácter estacional, debilitándose entre el invierno y la primavera, mientras que aumenta su intensidad en verano y otoño

(Aristegui et al., 2009). Esto se debe la entrada de flujos polares, los cuales debilitan el afloramiento (Hernández-Guerra et al., 2002). Por otra parte, en Guinea-Bissau, a diferencia de Marruecos, presenta un afloramiento estacional solo en invierno y primavera (Ingham, 1970). Esto se debe a que los vientos ascendentes paralelos a la costa de Guinea-Bissau ocurren más del 30% de los días entre diciembre y abril, mientras que el periodo de repetición disminuye a un 10% entre noviembre y mayo (Ingham, 1970).

La zona con mayor riqueza y recursos pesqueros, el Banco Sahariano, donde el afloramiento muestra una mayor intensidad durante todo el año (Arístegui et al., 2009; Pelegrí et al., 2017), no pudo incluirse en este estudio debido a que no hubo posibilidad de acceder a muestras biológicas capturadas allí. Según indican los pescadores, la sepia africana se descarta porque no tiene un valor económico significativo a diferencia de las otras especies de cefalópodos objetivo de la pesquería, como son el pulpo *Octopus vulgaris*, el calamar *Loligo vulgaris, la sepia común* Sepia *officinalis* o la sepia gigante africana *Sepia hierredda..*

1.4. Bioecología de la especie

La compresión y los avances que se generen de *S. bertheloti* en aspectos bioecológicos básicos como son su esperanza de vida, crecimiento, reproducción o alimentación, permitirá disponer de la información biológica necesaria para conocer la dinámica de sus poblaciones y poder regular las capturas, eludiendo en lo posible su sobreexplotación. Esta información biológica pasa por conocer su ciclo vital, y para ello la determinación de la edad y el crecimiento, y otros aspectos esenciales como alimentación y biología reproductiva constituyen conocimientos esenciales para poder realizar una adecuada gestión y monitoreo del recurso (Guerra-Sierra & Sánchez-Lizaso, 1998).

Existen diversas metodologías para realizar estimaciones de **edad y crecimiento**, agrupándose en métodos directos o indirectos. Dentro de los métodos indirectos, encontramos los análisis de progresión modal o frecuencia de tallas. Esta metodología es cuestionada para su uso en cefalópodos por numerosos autores (Keyl et al., 2008, Arkhipkin et al., 2021 entre otros), ya que las ratios de crecimiento pueden ser muy variables, y en estos modelos no se contempla factores como son la migración. Además, tampoco contempla que existan poblaciones con cohortes interanuales separadas en el tiempo, como es el caso de las sepias o el pulpo, en las que se ha determinado que pueden coexistir dos cohortes intra-anuales (Hernández-García et al., 2002; Grass et al., 2016). La esperanza de vida de los cefalópodos también es un hándicap en este modelo, ya que se estima entre 1 y 2 años, y tras su única época reproductiva mueren masivamente (Guerra, 1992). Esta mortalidad masiva, contribuye a que este método indirecto de estimación de edad, donde los parámetros se alteran considerablemente, no sea de utilidad.

En cuanto a los métodos directos, los más utilizados son los basados en las estructuras duras presentes en los cefalópodos, como son los estatolitos, picos, conchas (plumas de calamares, sepiones de chocos, estiletes de pulpos) y cristalinos o lentes oculares (Guerra, 1992; Arkhipkin et al., 2018; Xavier et al. *in press*). Estas estructuras han mostrado ser útiles para la estimación de la edad y poder extrapolar los resultados a la población, aunque algunas de ellas no son eficientes dependiendo de la especie que analicemos (Arkhipkin et al., 2018). En el caso de las sepias, las estructuras disponibles son los estatolitos, el sepión, las lentes oculares y los picos.

Los estatolitos, al igual que las lentes oculares, muestran ciertas complicaciones para realizar estudios de estimación de edad en sepias (Perales-Raya et al., 1994; Bettencourt & Guerra, 2001; Perales-Raya, 2001). En el caso de los estatolitos, estos presentan una alta cristalización

(Fig. 6A), haciendo que la metodología pueda crear sub o sobre estimaciones de la edad (Bettencourt & Guerra, 2001), por lo que algunos autores recomiendan utilizar otra estructura para la estimación de edad (Arkhipkin & Shcherbich, 2012). En el caso de las lentes oculares o cristalinos, las marcas de crecimiento presentan un patrón que inicialmente (cercano al núcleo, Fig.6B) se asemeja a la disposición de los anillos de crecimiento observados en el domo lateral de estatolitos, aunque los incrementos determinados no corresponden a la edad estimada (e.g. *Sepia berhteloti* o *Sepia officinalis;* Bettencourt & Guerra, 2001).

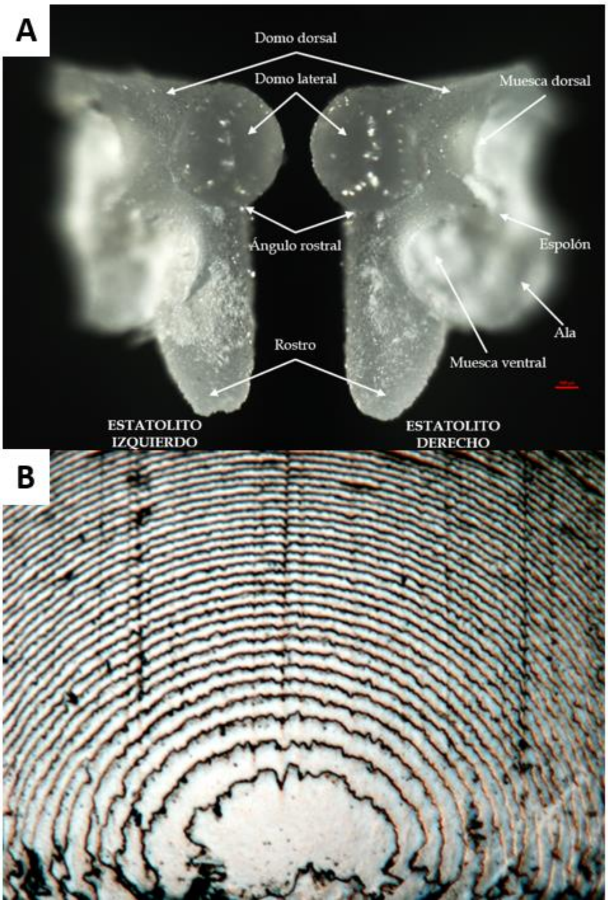


Figura 6.- A. Estatolitos y **B.** marcas de crecimiento en cristalino de *Sepia bertheloti.*

En cuanto al sepión (Fig. 5C), existen controversia en los estudios ya que varios autores demostraron que el número de lamelas contadas no correspondían con la edad real (Ré & Narciso, 1994; Le Goff tal., 1998; Bettencourt & Guerra, 2001), aunque recientemente Nabhitabhata et al. (2022) reevaluaron esta técnica obteniendo datos más favorecedores que permiten una estimación de edad en especies neríticas que habitan en sistemas con unas condiciones ambientales estables.

Finalmente, los picos son estructuras muy útiles, de fácil extracción, y la más precisas actualmente para la estimación de la edad en especies del género Sepia (Arkhipkin & Shcherbich 2012*;* Xavier et al., *in press*). Esta estructura se ha utilizado en diversas especies desde que en los años 60 se observaran por primera vez incrementos o anillos en picos de *Onykia ingens* (Clarke, 1965). Posteriormente, Perales-Raya & Hernández-González (1998) introdujeron una nueva técnica utilizando cortes sagitales para *Octopus vulgaris*, confirmándose posteriormente la deposición diaria a través de la validación de la edad en paralarvas con individuos cultivados (Hernández-López et al., 2001), y finalmente en todo su rango ontogenético (Perales-Raya et al., 2014b). La validación de la edad en cautividad o mediante marcado-recaptura es necesaria para poder afirmar que cada incremento observado en el pico corresponde con un día de vida (Arkhipkin et al., 2018), y así verificar la utilidad de la metodología empleada para la especie estudiada (Campana, 2001).

En esta tesis los picos fueron las estructuras seleccionadas para realizar las estimaciones de edad debido a los inconvenientes que pueden generar el resto de estructuras disponibles. Debido a la dificultad de acceso a ejemplares vivos de *Sepia bertheloti* para realizar la necesaria validación de edad (Campana, 2001), el estudio de validación se llevó a cabo a partir de puestas de *Sepia officinalis*, con el fin de validar la periodicidad diaria utilizando sepias de edad conocida*. Sepia officinalis* es una especie de interés pesquero alto (Denis & Robin, 2001; FAO, 2021) distribuyéndose desde el mar de Norte hasta su Mauritania y Senegal, incluyendo áreas como el Mediterráneo, Canarias, Madeira y Azores (Boletzky, 1983). Se seleccionó esta sepia por su disponibilidad inmediata y de fácil acceso para el área donde se desarrolló el trabajo de la tesis (Canarias, España) y por compartir parte de su rango de distribución con *S. bertheloti*. Además, la disponibilidad de bibliografía sobre *S. officinalis* (como especie modelo del género Sepia) y su especie simpátrica *S. hierredda* (considerada durante mucho tiempo subespecie de *S. officinalis*) permitiría establecer conclusiones más robustas (Boucaud-Camou & Boismery 1991; Perales-Raya et al. 1994; Perales-Raya 2001; Bettencourt & Guerra, 2001; Mion et al. 2014; Nabhitabhata et al., 2022, Lishchenko et al. 2021 entre otros).

Además de la edad y el crecimiento de la especie, los estudios de **alimentación** constituyen elementos esenciales para el conocimiento de la especie en el medio natural. El comportamiento oportunista de los cefalópodos ha sido demostrado en numerosos estudios sobre alimentación a nivel mundial, donde en términos generales se alimentan principalmente de peces, crustáceos y cefalópodos (Rodhouse & Nigmatullin, 1996). Los estudios tradicionales se basan en análisis de contenidos estomacales, aunque desde hace años se han incorporado a ellos los análisis a través de isótopos estables (Ibañez et al., 2021). Este último, es un análisis que surgió para evaluar las estructuras de las cadenas tróficas a través de elementos como el carbono y el nitrógeno, los cuales son útiles para estimar el nivel trófico de los organismos analizados (Layman et al., 2012).

Los análisis de contenidos estomacales aportan información sobre cómo interactúan las especies dentro de los ecosistemas, y conocer cuáles son las poblaciones en las que incide cada especie. De esta forma es posible aclarar los complejos modelos predador-presa y aportar información que permite entender las conexiones de las comunidades, así como los flujos de energía que existen dentro del sistema (Jara-Marini et al., 2009). Los análisis de contenidos estomacales permiten determinar la composición de la dieta en el momento de la captura, mientras que los isotopos estables expresan una dieta a corto o largo plazo, ya que aportan información de los nutrientes asimilados (Walker & Macko, 1999; Gong et al., 2020). Esto permite conocer los componentes ecosistémicos de la comunidad estudiada y el nivel trófico al que pertenece cada organismo. Son dos sistemas de evaluación que se complementan, pero no deberían sustituirse. Los métodos tradicionales aportan información de las especies predadas, por lo que se pueden estimar biomasas consumidas, y por ende establecer aproximaciones de mortalidad natural por depredación (Rodhouse & Nigmatullin, 1996; Renones et al., 2002). Los isotopos estables permiten caracterizar el ecosistema y los niveles tróficos, pero no la diversidad de especies, abundancia, riqueza y dominancia de las mismas en la dieta, la cual se estima mediante análisis tradicionales de contenido estomacal.

El primer capítulo de esta tesis doctoral se centra en validar la deposición temporal de los incrementos de crecimiento en los picos de sepia, usando para ello a *Sepia offcinalis* como modelo de estudio, mientras que el segundo capítulo aplica esta metodología en adultos para estimar la edad y el crecimiento de *Sepia bertheloti* en el medio natural para las dos áreas citadas del Atlántico oriental. En el tercer capítulo se muestra la utilidad del sepión para diferenciar sexos y estimar biomasa, con el fin de mostrar el papel ecológico que juega la sepia africana. El cuarto capítulo se centra en la ecología trófica describiendo su dieta y estrategias alimentarias.

1.5. Objetivo de la tesis

Las capturas de cefalópodos en el área 34 de FAO en el año 2019 alcanzaron 158.494 t (FAO, 2021), siendo las especies bentónicas aproximadamente el 83% de las capturas. Dentro de estos cefalópodos bentónicos, el pulpo con 81.212 t y las sepias con 42.866 t, son las principales especies objetivo de la flota comercial. Tal y como se ha indicado con anterioridad, las capturas desembarcadas de *Sepia bertheloti* no se registran de manera individualizada, sino que se englobada bajo el calificativo *Sepia spp.,* mezcladas con ejemplares pequeños de *S. hierreda, S. bertheloti,* y especies de pequeño tamaño como *S. elegans* o *S. orbingyana*. La única sepia que se registra de manera individualizada es la sepia común o *Sepia officinalis,* cuya captura está regulada y controlada, aunque oficialmente sólo se reportan a alrededor de 1% de las capturas globales de sepias en el área 34 (FAO, 2021). Esto se debe a que se no se identifican correctamente las especies, y es por ello oficialmente *S. officinalis* solo muestra un total de 352 t para 2019 y *Sepia spp*. 42.514 t. Esta falta de control de las capturas de manera individual se debe, a parte de la baja abundancia de determinadas sepias o la mala identificación de las sepias con importancia comercial, a la falta de estudios biológicos, ecológicos y pesqueros de las especies de sepias que representan el 99% restante de las capturas. Es por ello, que la presente tesis tiene como objetivo ampliar la información biológica y ecológica disponible de *Sepia bertheloti,* para identificar su papel dentro de los ecosistemas bentónicos de la costa centro-norte atlántica africana y así poder facilitar su la gestión sostenible de sus poblaciones. La información que aporta esta tesis doctoral se centra en algunas características biológicas relacionadas con la estimación de la edad, el crecimiento, la dieta y su estrategia alimentaria.

CAPÍTULO 2

Fotografía portada Capítulo 2: A small cuttlefish *Sepia officinalis* still in its egg, about 1 cm whole size. David Salvatori/ VWPics/Alamy Stock Photo

Capítulo 2

VALIDACIÓN DE LA EDAD

Age validation in early stages of *Sepia officinalis* from beak microstructure.

Airam Guerra-Marrero, Catalina Perales-Raya, Fedor Lishchenko, Ana Espino-Ruano, David Jiménez-Alvarado, Lorena Couce-Montero and José J. Castro.

2.1 Introduction

Since Young (1960), hard structures have become a routine tool for age estimation of cephalopods (Arkhipkin et al. 2018). However, despite the fact that in 1965 Clarke observed the growth lines in *Moroteuthis ingens* beaks (*Moroteuthopsis longimana*, as it was confirmed later by Cherel 2020), statoliths have been the most frequently used hard structure for ageing cephalopods (Jereb et al. 1991; Morris 1988; Rodhouse & Hatfield 1990; Šifner 2008; Arkhipkin & Shcherbich 2012). Perales-Raya & Hernández-González (1998) suggested that beak sections of *Octopus vulgaris* are suitable for age estimation, and Hernández-López et al. (2001) improved Clarke's method (1965) by counting increments on the inner surface of the lateral wall of the lower jaw, confirming daily periodicity in octopus paralarvae up to 30 days of age. Both methods were later compared and improved (Perales-Raya et al. 2010), although the daily deposition of beak increments across the entire age range of the species in both the lateral wall surfaces (LWS) and sections was not validated until several years later (Perales-Raya et al. 2014b), confirming later the first increment using embryos and new hatchlings (Armelloni et al. 2020). Moreover, Liu et al. (2015) concluded that beaks present greater advantages in age studies than statoliths, due to the relative simplicity of this processing method. After validation in *O. vulgaris*, the beaks have been used for age estimation in a number of cephalopod species, mainly squids and octopuses (e.g. Fang et al. 2016; Liu et al. 2017; Donlon et al. 2019; Jin et al. 2019; Schwarz et al. 2019, Batista et al. 2021).

Daily growth increments in other structures such as stylets or statoliths have been validated for several benthic cephalopod species, including *Octopus vulgaris* (Hermosilla et al. 2010); *O. pallidus* (Leporati et al. 2008), and *O. maya* (Rodríguez-Domínguez et al. 2013). With regard to neritic/pelagic cephalopods as loliginids (Jackson 1990; Lipinski et al. 1998; Cordella de Aguiar et al. 2012; Hoving & Robison 2017) and Oegopsida squids (Hurley et al. 1985; Nakamura & Sakurai 1991), statoliths were the validated structures, although gladius and beaks were cross-verified by comparing their counts with those from statoliths (Arkhipkin & Bizikov 1991; Hu et al. 2016, among others).

The common cuttlefish, *Sepia officinalis* (Linnaeus 1758), is a target species in many industrial and artisanal fisheries in the Eastern Atlantic and the Mediterranean Sea (Boletzky 1983; Denis & Robin 2001), and frequently reported as a by-catch of bottom trawling (Rathjen & Voss 1987; Jereb et al. 2015). Age determination is essential for cuttlefish population dynamic modelling, and therefore for the assessment and management of its fisheries. However, according to Jackson and Moltschaniwskyj (1999), age estimation methods must be accurate and precise and not laborious or very time-consuming. Most of *Sepia officinalis* age estimation studies have been based on polymodal decomposition of length frequencies (Boucaud-Camou & Boismery 1991; Mion et al. 2014), the analysis of statolith microstructure (Perales-Raya et al. 1994; Bettencourt & Guerra 2001) or the cuttlebone (Nabhitabhata et al. 2022) although limited estimations have been obtained.

The beaks in sepiid species were tested in adults of *Sepia apama* (Hall et al. 2007), and more recently in *S. officinalis* by Lishchenko et al. (unpublished results), but validation is still necessary. The aim of the present study is to estimate, for the first time, the ages of the juveniles in sepiid species by counting the growth increments observed in the beaks, to validate daily deposition and the age of the first increment in known-age cuttlefishes reared in captivity.

2.2 Material and Methods

A total of 159 spring hatchlings of *Sepia officinalis* were obtained from fertilized eggs collected in shallow waters off Gran Canaria (Tufia;

27º57’N, 15º22’W). The eggs were attached to a rope at 7 meters depth in a sandy bottom. They were collected in a single batch and the water temperature was 20.4 ºC. Eggs and newly hatched juveniles were reared at similar water temperature (21 ºC), and also at 18 ºC (as a small reduction within the “conventional” rearing temperature of 20±2°C described by Iglesias & Fuentes, 2014; Table I) to evaluate the effect of small changes in temperature in the pattern of growth increments on beaks. The study was carried out in two phases. Phase I addressed two issues: (a) testing the hypothesis of 1 day = 1 increment, and (b) evaluating the impact of the temperature on the increment deposition rates. After Phase 1, Phase II consisted of replicating Phase I and standardizing the methodology used for the newly hatched *Sepia officinalis*. In this phase, all cultures were carried out at 21 ºC.

Table I. Data summary of juveniles of *Sepia officinalis* analysed for each age group and temperature (T^{a}). n: number of individuals; DML: dorsal mantle length; WRA: width of the reading area; Mean CV (%): mean of coefficient of variation; mean values of DML and WRA in brackets.

Age group (Days)	**T^{a} (ºC)**	**n**	**DML (mm)**	**WRA (µm)**	**Mean CV (%)**
0	18	2	5.70 – 5.80[5.75]	40,32-47.85[44.09]	0.000 ± 0.000
	21	8	5.08 – 5.72[5.43]	35.12-58.57[43.27]	0.000 ± 0.000
1	18				
	21	19	5.6-7.01[6.45]	42.52-141.23[97.23]	2.717 ± 1.492
2	18	2	6.96-7.01[6.98]	158.26-186.25[172.25]	0.000 ± 0.000
	21	10	6.27 – 7.20[6.87]	140.25-170.24[153.63]	1.288 ± 0.859
3	18	6	6.98-7.70[7.36]	180.24-241.23[219.72]	1.464 ± 0.900
	21	27	6.85– 7.32[7.08]	138.55-242.12[184.18]	2.024 ± 0.571
4	18	13	6.99 – 7.78[7.52]	200.02 – 261.24[241.27]	1.152 ± 0.501
	21	46	6.54 – 7.99[7.20]	158.07-281.23[211.36]	2.018 ± 0.395
5	18				
	21	8	7.28-8.89[7.79]	222.35-323.27[269.92]	1.461 ± 0.553
6	18	4	7.75-7.89[7.82]	301.95-321.24[298.21]	1.336 ± 0.772
	21	2	7.60-7.77[7.69]	344.56-355.25[349.91]	0.000 ± 0.000

After sacrifice, the dorsal mantle length (DML) of each individual was measured to the nearest 0.1 mm. DML ranged from 5.08 mm to 8.89 mm, and their total weight varied from 0.1098 to 0.2712 g (Table I). A total of 127 and 32 lower jaws of *Sepia officinalis* reared in the laboratory at 21 ºC and 18 ºC, respectively, were analyzed for age determination following the methodology of Perales-Raya et al. (2018) in octopus paralarvae.

2.2.1. Rearing conditions

The eggs development occurred in the natural environment, collecting the eggs in the organogenesis period (Lemaire, 1970). Then, the eggs were incubated in our lab under natural conditions (water temperature around 19–21 ºC, photoperiod of 14 h L / 10 h D, and a salinity of 36 PSU). All juveniles were reared with the aim of sacrificing them randomly to validate the daily deposition in beaks.

Newly hatched individuals were reared inside the laboratory in 25 transparent 10-L square glass tanks (20x20x25, densities not greater than three individuals per tank), with aeration, recirculating seawater at a natural photoperiod. No artificial shelters were provided to hatchlings, their feeding was performed *ad libitum* (3 times per day) with live *Artemia salina* on a daily basis. Thirty-two individuals were reared at 18 ºC, while 127 were kept at 21 ºC. In Phase I, 112 individuals were cultured, of which 32 were reared at 18 ºC and 80 at 21 ºC. There were differences in the number of specimens cultured at each temperature, but the total number of specimens cultured at each temperature condition was enough to check the significance of differences between temperatures. In Phase II, 47 individuals were cultured at 21 ºC. No individuals were cultivated at 18 ºC because in Phase I differences between those cultured at 18 ºC and 21 ºC were no significant. The specimens were euthanized by anesthetic overdose (clove oil, following Ayala-Soldado 2014) and dissected fresh.

Animal rearing was performed in compliance with Spanish law 53/2013 within the framework of the European Union's adopted directive 2010/63/EU regarding animal welfare for the protection of animals employed for scientific purposes, following the *Guidelines for the Care and Welfare of Cephalopods in Research*, as proposed by Fiorito et al. (2015). The present study was also approved (register document OEBA-ULPGC 04/2019R1) by the Ethics Committee for Animal Research (Comité Ético de Experimentación Animal of the University of Las Palmas de Gran Canaria, CEEA-ULPGC, Spain).

2.2.2. Beak extraction, preparation and analysis

The beaks were extracted, cleaned, labelled and stored in distilled water at 5 ºC, as recommended by Perales-Raya et al. (2014b, 2018) for *Octopus vulgaris* paralarvae. Previously, it had been observed that the conservation of the beaks in 70% ethanol resulted in a low visibility of the growth increments. Upper and lower jaws were tested for age estimation. Each jaw was placed whole, without cutting, in the ventral position (convex side up) on a drop of water. It was then covered with a coverslip left tilted until the jaw was positioned correctly. Once its position was secured, some pressure was exerted on the coverslip to ensure fixation of the jaw and obtain standardized images (see Armelloni et al. 2020) (Fig. 1a). Image acquisition was carried out according to Perales-Raya et al. (2014b, 2018) and Armelloni et al. (2020).

After the correct placement, two areas of the jaws – the LWS and the rostrum surface – were explored to select the one that showed higher viability for age estimation. The increments were finally counted on the surface of the pigmented area (rostrum) of the lower jaw under transmitted light with a Nikon Microscope Multizoom AZ100 (400x magnification). The system is equipped with a differential interference contrast attachment

(DIC-Nomarski) that creates a 3-dimensional image of the rostrum surface, where the sequence of micro-increments is revealed. The regions of the jaw were identified, as well as the first increment (hatching; Fig. 1b), to standardize the reading methodology.

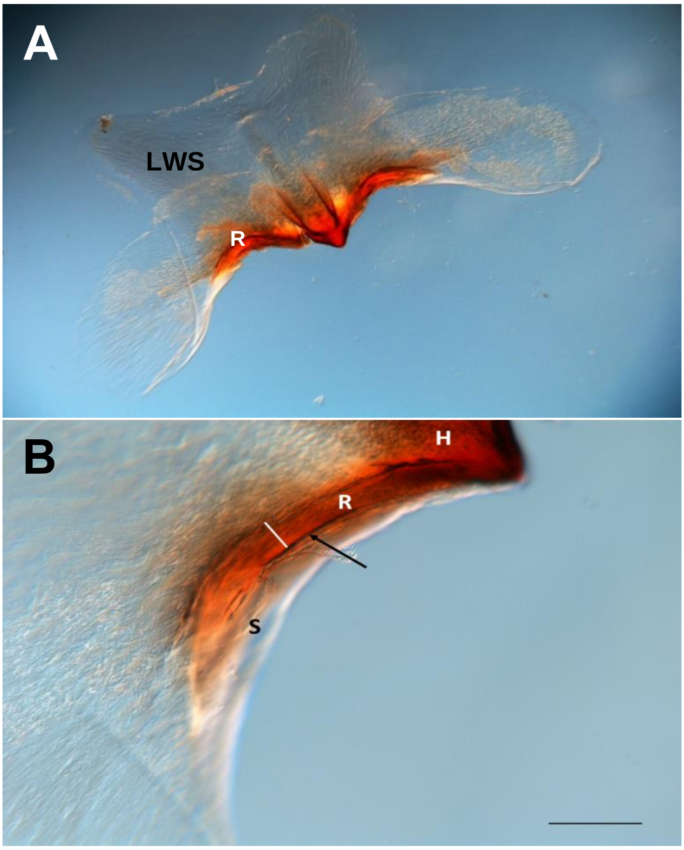


Figure 1. Lower jaw in *Sepia officinalis* juvenile **(a)**. Anterior region of the lower jaw: Location of the main parts **(b)**. R: rostrum, H: Hood, S: Shoulder, LWS: Lateral Wall Surface. The black arrow indicates the first increment, and the white segment indicates the width of the reading area (scale bar = 100 μm).

The increments were counted twice by the same trained reader. The coefficient of variation (CV) was calculated for each specimen to determine the precision (reproducibility) of the counts:

$$\mathrm{CV}(\%) = \frac{100\ x\ \sqrt{(R1-R)^2 + (R2-R)^2}}{R}$$

where R1 and R2 were the mean number of increments from the first and the second reading, respectively; R was the mean number of increments for both readings (Perales-Raya et al. 2018). The sample was classified into 7 age groups (Table I): Group 0: 0–2 days; Group 1: 3–7 days; Group 2: 8–12 days; Group 3: 13–17 days; Group 4: 18–22 days; Group 5: 23–27 days; Group 6: 28–31 days. To avoid any bias by age groups, the CVs were averaged for each age group, and CVs<7.6% were taken as valid (Campana et al. 2001). The mean CV was then calculated for each temperature group to assess and compare the precision of their readings. The number of increments was compared with the true age. The width of the reading area (WRA) was measured (μm) in the widest region of the reading area, where the increments were counted, in accord with Perales-Raya et al. (2018) (Table I).

2.2.3. Statistical analysis

All statistical analyses were carried out using R v-4.1.1 (R Core Team 2021). A general linear model (GLM) was used to test the effect of the temperature, the age, and the interaction of age with temperature on increment numbers following Perales-Raya et al. (2018). ANOVA of the GLM fits was carried out to analyze the possible significant differences in relation to the variables described (Blanca-Mena et al. 2017; Foster 2021). In the same way, ANOVA was used to observe differences in the growth of the WRA between both cultures. The function “glm” was used under the package ‘stats v.4.0.3’ (R Core Team 2021).

2.3. Results

The lower-jaw rostrum shows clear and continuous deposition of the growth increments on its surface, in a way similar to that described in Perales-Raya et al. (2014b; 2018) and Arkhipkin et al. (2018) for the upper-jaw rostrum of *Octopus vulgaris* paralarvae. The DIC-Nomarski technology facilitated image analysis thanks to differential interference contrast, highlighting the deposited daily increments. Our examination of both jaws in *Sepia officinalis* did not reveal any teeth but the rostral area showed a strong pigmentation, which apparently allows a better reading of the growth marks. Regarding the upper jaws, the observed increments did not present a clear sequence of deposition in the rostrum. For this reason, and because the increment deposition was observed more clearly in the lower jaws, they were selected for ageing *Sepia officinalis*. Our exploration of LWS showed unsatisfactory results with no clear pattern of increments for age estimation. Moreover, the observed increments could often be confused with the roughness of the structure due to their poor definition in some areas and the low pigmentation of the lateral walls.

The first increment (hatching) in the rostrum surface of the lower jaw was located in the anterior border of the reading area, and the day of death is the latest increment (posterior border) of the reading area (Fig. 1b). We observe a translucent region that extends to the anterior border of the jaw. This area was identified as a developing shoulder (Fig. 1b), as described by Perales-Raya et al. (2018) for the *Octopus vulgaris* paralarvae. Increments in the rostrum of lower jaws were clear (Fig. 2). Nevertheless, from the culture at 21 ºC, only 121 of the 127 collected beaks

(95.28%) were suitable for age estimation. In the case of cuttlefishes reared at 18 ºC, 29 beaks of the 32 collected (90.63%) were readable.

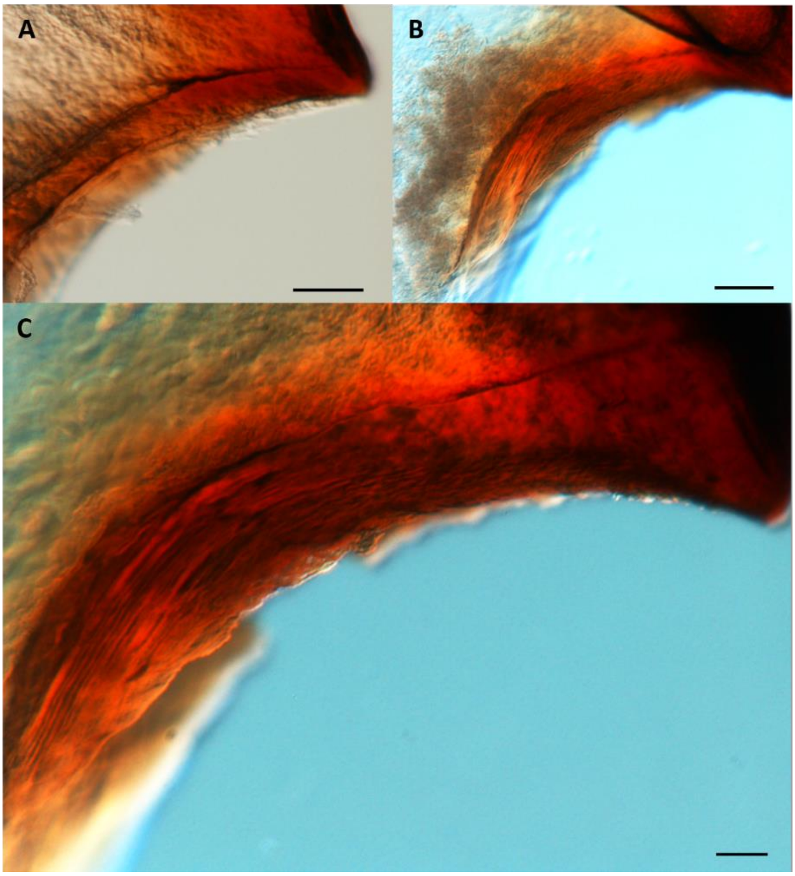


Figure 2. Beaks of *Sepia officinalis* individuals reared for this study at **A.** 0 days old (hatching day), **B.** 15 days old and **C.** 20 days old (scale bar= 50 μm).

Mean reading precision (CV) of readings in the rostral surface of *S. officinalis* was 2.95 ± 5.98 % for all individuals. Mean values of CV for each age group were lower than the usual adopted value of 7.6% for annual and daily structures (Campana, 2001; **Table I**), and therefore no additional individuals were discarded based on the CV. The CV in individuals cultured at 21 ºC (n=120) was 3.26 ± 6.75%, and 2.01 ± 2.47% for those cultured at 18 ºC (n=27). The age assigned to each individual was the average of the two readings.

The relationship between the number of increments and the true age (**Fig**. **3**) in newly hatched cuttlefish at both temperatures showed a linear trend (**Table II**). The regressions between age and number of increments shown in Table II confirm daily deposition of increments in juveniles of *S. officinalis* at 18ºC and 21ºC. In Phase I, ANOVA of the GLM fit showed no significant differences in the increment deposition determined by the temperature alone or the factor Age x Temperature (Table IIb). The same results were obtained for WRA growth, with no significant differences between cultures at different temperatures (ANOVA, $p>0.05$). Phase II results are shown in Table III.

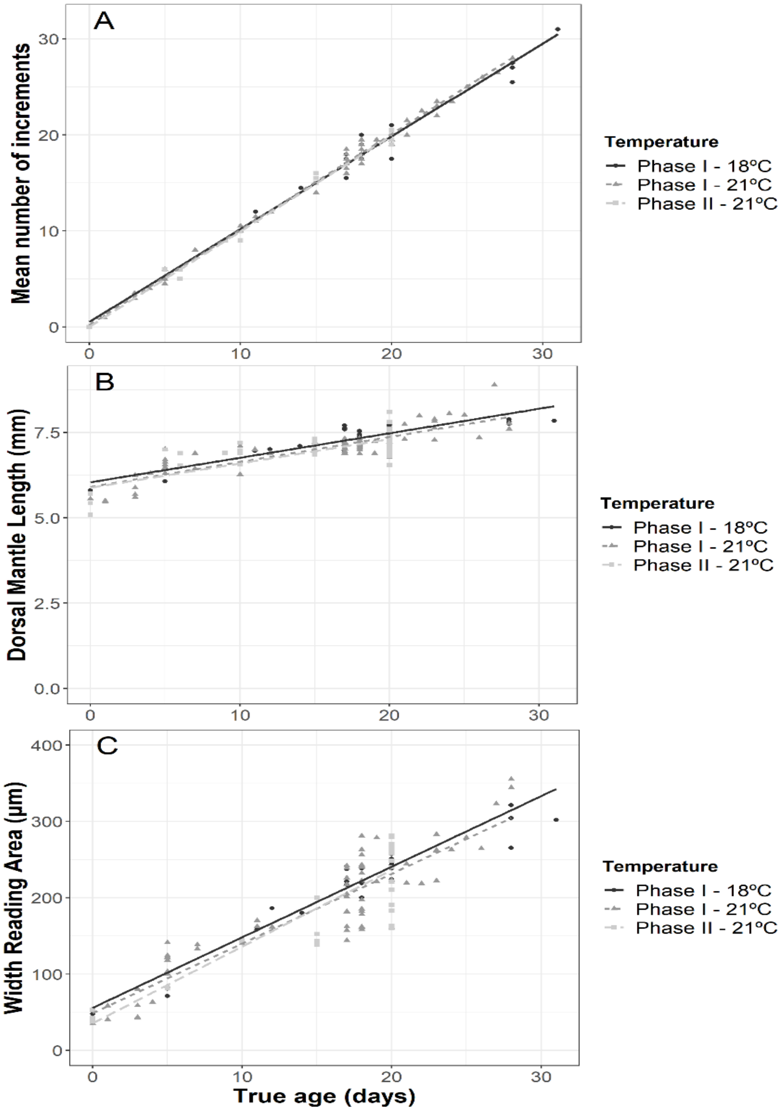


Figure 3. Growth of cultured newly hatched *Sepia officinalis*: **(a)** Relationship between the mean number of increments counted in the lower jaw and the true age; **(b)** Dorsal Mantle Length and the true age; **(c)** Lower jaw growth (width of the reading area; see Fig. 1) with true age. Data grouped by temperature in the different phases.

Table II. Results of: (a) lineal regression analysis for the number of growth increments (NI), the age (days from hatching) and width of the reading area (WRA) by rearing temperature (21 ºC or 18 ºC) in Phase I. (b) General lineal model (GLM) coefficients; ***$p<0.001$.

(a) Regressions	**Intercept**	**Slope**	**n**	r^2	***P***
Age – NI 21º	-0.092	0.998	73	0.992	<0.001
Age – NI 18º	-0.2341	1.016	29	0.982	<0.001
NI – WRA 21º	47.481	1.435	68	0.858	<0.001
NI – WRA 18º	53.217	1.544	29	0.947	<0.001
Age – WRA 21º	48.783	1.445	68	0.863	<0.001
Age – WRA 18º	55.733	1.566	29	0.954	<0.001

(b) GLM coefficients	**Estimate**	**SE**	***t***	***p* (>|*t*|)**
Intercept	91.49176	108.88807	0.840	0.403
Age	7.36607	5.96327	1.235	$<2 \text{ x } 10^{-16}$ ***
Temperature	-2.03376	5.36685	-0.379	0.770
Age x Temperature	0.08407	0.29585	0.284	0.777

Table III. Results of lineal regression analysis for relationships between the number of growth increments (NI), age (days in cultured individuals) and width of the reading area (WRA) at 21 ºC in Phase II.

Regressions	**Intercept**	**Slope**	**n**	**r^2**	***p***
Age – NI 21º	-0.030	0.998	48	0.997	<0.001
NI – WRA 21º	43.296	1.719	35	0.896	<0.001
Age – WRA 21º	44.041	1.730	35	0.902	<0.001

2.4. Discussion

This is the first time that the beak microstructure of *Sepia officinalis* has been shown in its early stages, where the visualization and the count of growth increments in the lower jaw's rostrum was relatively easy. In contrast to the hatchlings of *Octopus vulgaris*, newly hatched *Sepia officinalis* showed no teeth as well as higher and wider pigmentation in the rostrum of lower jaws. This pigmentation in the reading area of the lower jaws probably allowed a better estimation of the true age, while for *O.*

vulgaris the visibility of increments is much better in the upper jaws (Perales-Raya et al. 2014b; Armelloni et al. 2020). The lower jaws of *O. vulgaris* have a narrower and less pigmented rostrum, with deeper teeth and fewer increments visible compared with the upper jaws. It should also be noted that the upper jaws of *S. officinalis* juveniles are harder than those of *O. vulgaris* paralarvae, which complicates their manipulation and increase the risk of damaging them.

Regarding the LWS of *S. officinalis* beaks, they showed unclear growth marks that could be confused with roughness of the structure. Additionally, and according to Armelloni et al. (2020) for *O. vulgaris* paralarvae, the LWS in cuttlefish did not show highly developed pigmentation during these early stages and, consequently, some of the observed marks could be false increments. On the other hand, the rostral surface, which is already pigmented at hatching, showed a continuous sequence of growth increments in *S. officinalis*, making it possible to identify the age of the first increment. It is mandatory for correct validation of the methodology (Campana 2001).

The sizable agreement among readings indicates a high precision of readings in the rostral surface of *Sepia officinalis*. The reading precision (estimated using CV) was high because the readings differed with a maximum of ± 2.95%, although the variability of CV was high too (± 5.98), which is probably related to the complexity of the structure (Perales-Raya et al. 2018). The juveniles used in the present study were fed with soft diet but feeding may erode the beaks and careful should be taken to avoid age underestimations.

The GLM analysis showed that our results support the validation of this methodology for age estimation using beak microstructure as has been shown in other benthic species such as *Octopus vulgaris* (Hernández-

López et al. 2001; Perales-Raya et al. 2014b, 2018; Armelloni et al. 2020) and *O. maya* (Rodriguez-Domínguez et al. 2013; Villegas-Bárcenas et al. 2014). The present study is the first validating the daily deposition of increments in early stages and the age of the first increment in the beaks of *Sepia officinalis.*

Ageing cuttlefish using the beak rostrum seems a suitable method for these species, in comparison with other commonly used methodologies, which are length-frequency analysis and direct ageing methods using statoliths and cuttlebones. Length-frequency distributions have some problems because the age of cohorts are not independently validated, the cephalopods show a high inter-individual variability, and modelling methods ignore variable growth rates which are influenced by environmental conditions (Semmens et al. 2004; Arkhipkin et al. 2021). Jackson et al. (1997) compared this methodology against the use of statoliths, since several authors used length-frequency analysis to analyze growth rate and growth forms (e.g. Jereb & Ragonese 1995; Mohamed, 1996 among others). Jackson et al. (1997) concluded that length-frequency analysis should not be used for these age determinations, being the statoliths the promising technique at that time. As for statolith-based age determination, it is relatively laborious involving the extraction, handling, storage, mounting, both-side grinding and polishing, and counting under a microscope (Arkhipkin & Shcherbich 2012). In addition, its application is limited in cuttlefishes due to the complex crystalline structure of their statoliths (Natsukari & Tashiro 1991; Perales-Raya et al. 1994). Using the sequence of increments observed in the lateral dome (Perales-Raya et al. 1994), Bettencourt & Guerra (2001) validated increment deposition till 240 days of age in *S. officinalis*; but in older specimens the age was underestimated due to the poor resolution of newer increments. Regarding the internal shell (cuttlebone), it has been used since the 1960s in several sepiid species, but formation of the shell stripes, or lamellae, is determined by physiological and environmental conditions (Yagi 1960; Choe 1963;

Richard 1969; Ming-Tsung & Wang 2013, among others). It has also been used in *S. officinalis* (Richard 1969; Re & Narciso 1994, among others) and *Sepia hierredda* (Perales-Raya 2001). The absence of a daily deposition in the cuttlebone of *S. officinalis* was also described by Ré & Narciso (1994) and Le Goff et al. (1998) where they conclude that the cuttlebone lamellae should not be used for age estimation. The number of lamellae does not correspond to the true age and the temporal periodicity can be defined only if the temperature where the animal lives is considered (Bettencourt & Guerra 2001). The internal shell was recently analysed in several loliginid and sepiid species of known age by Nabhitabhata et al. (2022), reevaluating the accuracy in the neritic species living the tropical zone where environmental conditions are more stable. Moreover, some studies proposed to use the concentration of lipofuscin, a pigment that accumulates in tissues, as a proxy of age (Gras et al. 2016), but this method is considered complex and inaccurate (Doubleday & Semmens 2011). The use of these methodologies for age estimation were promising, although biological factors (length-frequency analysis) and morphological factors of the analysed structures (statolith and cuttlebone analysis) may influence the under- or over-estimation of age.

Using the rostrum surface of juveniles to determine age is equivalent to using rostrum sagittal sections in adults, as demonstrated in *Octopus vulgaris* (Perales-Raya et al. 2018, Lishchenko et al unpublished results). Their similarities indicate that both structures are equivalent and suitable for *S. officinalis*. Cuttlefish beaks, once validated in adult stages, could be a promising method to determine the age of cuttlefishes.

The water temperature seems to be one of the most powerful factors influencing cuttlefish growth in cultured conditions. Domínguez et al. (2006) compared wild and reared *Sepia officinalis* observing that temperature and culture space play an important role in the growth of individuals. In the case of *Octopus vulgaris*, Perales-Raya et al. (2018) showed that the readings in octopuses cultured at 14 ºC and 21 ºC differed in width, whereas octopuses cultured at 21 ºC had a bigger reading area than octopuses reared at 14 ºC. Moreover, octopus paralarvae reared at 14 ºC showed apparent compaction of increments in the beaks and growth slowed or stopped at that temperature, thus affecting increment depositions (Perales-Raya et al. 2018). However, in our study, cuttlefishes reared at 18 ºC and 21 ºC did not show significant differences in the WRA. This could be due to the experimental temperatures, since they were both within the optimal range for *S. officinalis*, and this seems irrelevant for the increase in rostrum width during the first month of life. Nevertheless, temperature impact on the structure size was observed in other hard structures of cephalopods, such as statoliths. In particular, Villanueva (2000) reported that the size of the statoliths of *Loligo vulgaris* is determined by the temperatures at which the animal grows.

In conclusion, our results proved the validity of using the rostrum surface of beaks for age estimation in the early stages of *S. officinalis* and show that this methodology (using the microstructure of the beak rostrum) can be promising, once validated in adult stages, to determine the age in cuttlefishes since other structures such as statoliths or cuttlebone have limitations for a routine ageing method. The feeding factor should also be evaluated in future studies to estimate how much it might affect eroding the beak rostrum to avoid age underestimation. This study confirms the daily deposition in the first 31 days of life, fulfilling the initial hypotheses of one increment per day, but it is necessary to validate the age estimation of beaks in the full ontogenetic range of the species.

CAPÍTULO 3

Fotografía portada Capítulo 3: The beak or bill of a large cuttlefish, *Sepia officinalis*, caught in The English Channel, Dorset England. www.pqpictures.co.uk/Alamy Stock Photo

Capítulo 3

EDAD Y CRECIMIENTO

Age, growth and population structure of the African cuttlefish *Sepia bertheloti* based on beak microstructure.

Airam Guerra-Marrero, Aurora Bartolomé, Lorena Couce-Montero, Ana Espino-Ruano,
David Jiménez-Alvarado, José J. Castro and Catalina Perales-Raya.

3.1. Introduction

The African cuttlefish *Sepia bertheloti* (Orbigny, 1839) is distributed in Eastern Atlantic from the Canary Islands and Western Sahara to Angola, occurring predominantly on sandy bottoms from 20 to 160 m (Jereb & Ropper, 2005; Guerra et al., 2014) and can reach sizes of 180 mm mantle length for males and 130 mm for females (Guerra et al., 2014). It is a species captured by trawling nets at depths between 70-140 m (Roper et al. 1984), with greater presence in the fisheries operating off the West Africa (FAO Fishing Area 34). It is one of the most productive world marine regions (Martos & Peralta, 1995; Doumbouya et al., 2017) due to its marked upwellings in the north (Western Sahara - Morocco), during spring, and in the central area (Senegal-Guinea-Bissau), during the winter (Berrit & Rebert, 1977).

There are no separate statistics for *S. bertheloti* as they are often traded together with *S. officinalis* in northern waters and with *S. hierredda* in southern waters or treated as commercial by-catch*. S. bertheloti* account for 11-35% of reported by-catch and they are marketed fresh or deep-frozen for export (Jereb & Roper, 2005). The target cephalopod species for the Saharan bank (northern distribution) are *Octopus vulgaris*, *Sepia officinalis* and *Loligo vulgaris* (Hernández-García & Castro, 1994), while for the southern fishing grounds (Guinea-Bissau) the target cephalopods are *O. vulgaris* and *Sepia hierreda* (FAO, 2021). Furthermore, probably due to the lower abundances and commercial value in comparison to the main target cuttlefishes, most of the biological and fishery knowledge about *S. bertheloti*, has been obtained from the analysis of the stomach content of its natural predators (Delgado de Molina et al., 1993; Monzón-Argüello et al., 2018), by exploratory fishing campaign to assess the state of the resources (Balguerías *et al*., 1993; Rocha *et al.,* 2017; García-Isarch et al., 2009; Perales-Raya *et al*., 2010), or for analysis of metal concentrations

(Ama-Abasi & Akpan, 2018). However, there is no information about age and growth pattern of *S. bertheloti* which are key aspects to estimate life-history parameters and to understand the population dynamics of the species in order to perform a correct biomass estimation available for fishing (Arreguín-Sanchez, 1996).

The use of Indirect methods such as length-frequency analysis is not useful for age estimation in cephalopods, since they are semelparous species and have a short life cycle and high variations among individuals, making their estimation imprecise (Jackson, 2004). Direct methods using hard structures, such as statoliths, beaks, lenses or gladius, based on the study of growth increments, have shown to be the most useful methodology for estimating the age and growth of cephalopods. Growth increments analysis in jaws has been shown to be an appropriate technique for age determination, which has been validated in other benthic cephalopods such as *O. vulgaris*: Hernández-López *et al*., 2001 for paralarvae; Oosthuizen (2003) preliminarily in a small sample of 5 individuals; Canali et al. (2011) covering until individuals of 650g of weight; Perales-Raya et al. (2014b) in the whole ontogenetic range; Armelloni et al. (2020) analysing the first increment in embryos and hatchlings. Other species as *O. maya* (Rodríguez-Domínguez et al., 2013; Bárcenas et al., 2014) and *S. officinalis* (Chapter 2 of this thesis), also showed that each growth increment represents 1 day of life.

Processing of cephalopod hard structures is a time-consuming process enabling age estimates with a high rate of precision and useful to identify seasonal cohorts, being an important component of cephalopod stock assessments. Nevertheless, the great variability of the growth rates (individuals of the same age with different lengths) makes age-based models impractical for real-time stock assessment (Arkhipkin et al., 2020). These authors propose a range of methodologies to assess cephalopod populations, although they stated that there is a high data requirement with a constant catch per unit effort report (CPUE). These data are not available for *S. bertheloti*, because its CPUEs data are included in other cuttlefish CPUE (Jereb & Roper, 2005), as *S. officinalis* for Northwest Africa or with *S. hierredda* for central-west Africa, so age analyses in hard structures are suitable alternatives for a future stock assessment.

Based on previous studies of other cuttlefish species, it is known that they have high growth rates (Perales-Raya et al. 1994; Perales-Raya 2001; Bettencourt & Guerra 2001; Guerra 2006) although differences of lengths and weights have been observed between the populations along the Canary Current large marine ecosystem (Hernández-García & Castro, 1994; Hernández-López, 2000; Almonacid-Rioseco, 2006; Jurado-Ruzafa et al., 2014).

This study contributes to: (i) age and life span estimations of *S. bertheloti* in wild populations using the beak microstructure, (ii) determine the hatching periods, (iii) test growth models to describe the one that best adapts to the population, and (iv) describe the growth rates by seasons, with the final purpose that these data can be used in future stock assessment models.

3.2. Material and methods

3.2.1. Sample collection

A total of 1124 individuals of the African cuttlefish *Sepia bertheloti* were collected from June 2018 to January 2020 in two areas of Northwest Africa (449 individuals from Morocco and 625 from Guinea Bissau) from commercial trawlers operating in each study area (Fig.1). Data sampling is summarised in Table I.

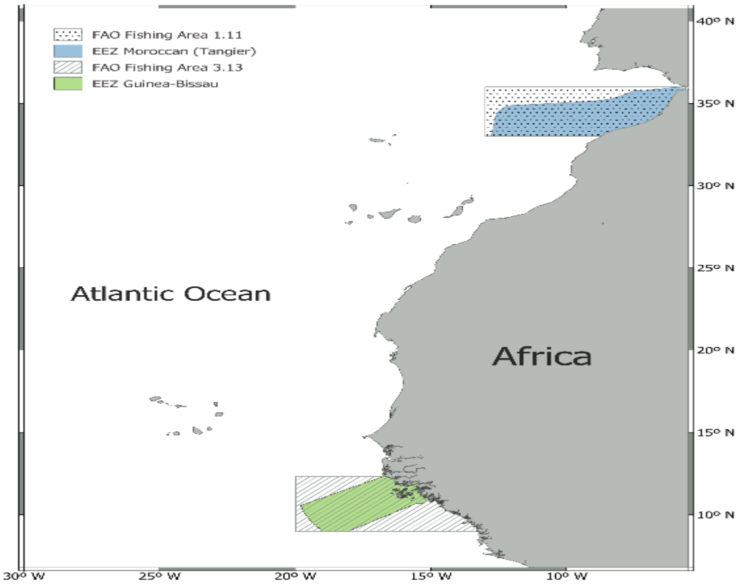


Figure 1. Sampling areas (FAO Fishing Area 34) where the commercial trawlers caught *Sepia bertheloti* in Morocco (Tangier zone) (FAO 34.1.11) and Guinea-Bissau (FAO 34.3.13). Exclusive Economic Zone (EZZ) for Morocco (Tangier zone) and Guinea-Bissau in the FAO Fishing Area 34 are shaded.

Table I. Number of individuals of *Sepia bertheloti* analysed in two areas of West Africa from July 2018 to January 2020

Date	Morocco	Guinea-Bissau
July 2018	234	
August 2018	43	
September 2018	44	
July 2019		42
August 2019		36
September 2019		97
October 2019		78
November 2019		157
December 2019		155
January 2020	178	60
Total	**499**	**625**

The cuttlefish were immediately frozen at -20ºC after fishing until they were processed in the laboratory. Dorsal mantle length (DML) and body weight (BW) were measured to the nearest 1 mm and 0.01 g respectively. Sex was recognized and maturity stages identified according to the macroscopically maturity scale proposed by ICES (2010) for *Sepia officinalis*, who defined 0 as undetermined, 1 as Immature, 2a as Developing, 2b as Maturing, 3a as Mature/Spawning and 3b as Spent. Beak extraction and measurements were taken according to Perales-Raya et al. (2010) and Hernández-García (2003), respectively. The individuals caught in both areas were categorized according to the capture season (spring, summer, autumn, and winter).

3.2.2. Length – weight relationship

The Length-weight relationship (LWR) was calculated using the equation $BW= aDML^b$ (power function), where a and b are the regression parameters estimated by linear regression of the data logarithmically transformed and adjusted by least squares method. Student's t-test was used to verify the 'b' values to determine if they have isometric ($b = 3$) or allometric (negative allometric $b < 3$, and positive allometric $b > 3$) growth.

2.3. Beak analysis

After dissection, the beaks were extracted, cleaned and stored in distilled water at a temperature of 4ºC, according to the procedure described by Perales-Raya et al. (2014a). A beak subsample of 78 individuals from Morocco and 128 from Guinea-Bissau were analysed. It was randomly performed categorizing the individuals by size range for both sexes in each 5 mm range of DML.

After the analysis of the different structures in the upper and lower jaws, the rostrum sagittal sections (RSS) of the lower beak were selected according to Perales-Raya et al. (2010; 2014a). Once the beaks were processed, they were analysed using a Nikon Microscope Multizoom AZ100 with and UV epi-illumination attachment (vertical reflected light) and different magnifications (100-400x) to observe de growth increments (Fig. 2).

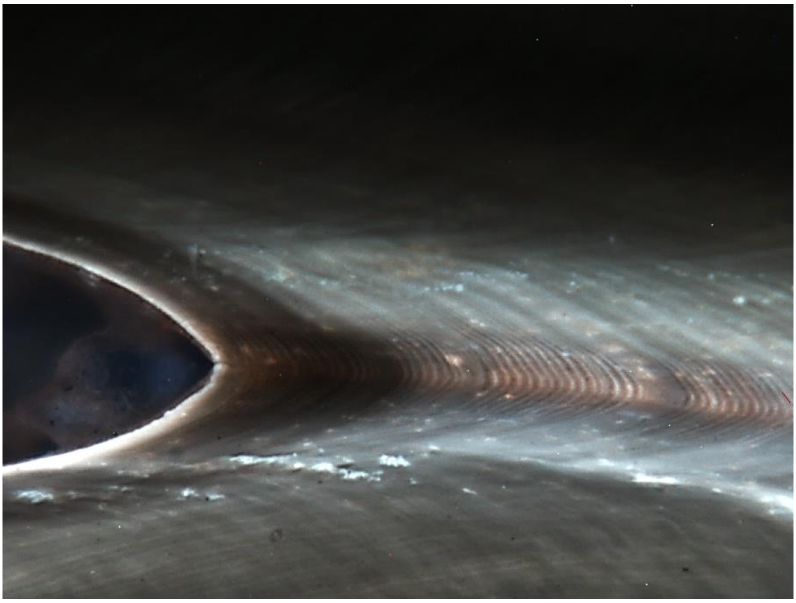


Figure 2. Appearance of growth increments in the rostrum sagittal section of lower beak of *Sepia bertheloti (*300x).

The increments observed were counted twice by the same trained reader. The Coefficient of variation (CV) was used to estimate the precision of the readings and the reproducibility of the method. The CV was calculated as the ratio of the standard deviation over the mean:

$$\mathrm{CV}(\%) = \frac{100\, x \sqrt{(R1 - R)^2 + (R2 - R)^2}}{R}$$

Where, R1, R2 were the number of increments from the first and the second reading, respectively. R was the average of the number of increments of the two readings. According to Campana *et al*. (2001), to avoid any bias, the mean of CV was averaged for each study area, and the CV<7.6% were taken as valid, rejecting reads with higher values of CV.

The relationship between rostral length of lower beak (LRL) and the number of increments (NI) was calculated to observe the growth of the reading area according to the estimated age. The analysis of covariance (ANCOVA) was carried out to analyze possible significant differences in LRL-DML and LRL-NI relationships according to sex and study areas. Relationships and all the different analysis were made using the second reading (R2) according to Perales-Raya *et al*. (2010), because the R2 is supposedly more reliable since the reader have a greater experience and practice.

3.2.4. Growth models and growth rate estimation

Length-at-age data of *Sepia bertheloti* were fitted into seven growth models (lineal, power, exponential, von Bertalanffy, Gompertz, logistic, and Schnute (a≠0 and b≠0) models). According to Bolser *et al.* (2018), model parameters for Von Bertalanffy, Gompertz, logistic and Schnute were estimated using non-linear least squares regression with the Levenberg Marquardt algorithm, and confidence limits were placed around parameter estimates in R studio (using the R packages Ogle, 2017; Elzhov et al., 2015 and Baty et al., 2015).

- von Bertalanffy growth model (Von Bertalanffy, 1938):

$$L(t) = L_{\infty}[1 - e^{-K(t-t_0)}]$$

- Gompertz growth model (Gompertz, 1825):

$$L(t) = L_{\infty} e^{\left(-\left(\frac{1}{K}\right) e^{-K(t-t_0)}\right)}$$

- Logistic growth model (Ricker, 1975):

$$L(t) = L_{\infty}\left[1 + \ e^{-K(t-t_0)}\right]^{-1}$$

- Schnute growth model (Schnute, 1981):

$$L(t) = [L_1^b + (L_2^b - L_1^b)\frac{1 - \ e^{-a(t-T_1)}}{1 - \ e^{-a(T_2-T_1)}}]^{1/b}$$

where L(t) is length (in mm DML) at age t, L_{∞} is the maximum average length (in mm DML), K is the growth rate coefficient (in year $^{-1}$), and t_0 is the theoretical age at which length is zero (in years). For the Schnute growth model, T1 is the first specified age, T2 is the second specified age, L1 is length at age T1; L2 is length at age T2, *a* is the constant relative rate of relative growth (in year $^{-1}$), and *b* is the incremental relative rate of relative growth (dimensionless). Since the Schnute model does not calculate the parameter L_{∞} directly, the following equation must be used (Schnute, 1981):

$$L_{\infty} = \left[\frac{e^{aT2}L2^b - e^{aT1}L1^b}{e^{aT2} - e^{aT1}}\right]^{1/b}$$

The parameters L1, L2, T1 and T2 are the same as used in the Schnute equation previously, while the parameters *a* and *b* are the resulting parameters of the growth model.

The best model for each sex and area was determined using the Akaike's information criterion (AIC) (Akaike, 1974), transformed to Akaike weight (AICw) (Burnham & Anderson, 2002) and the Bayesian Information Criterion (BIC) using the "AICcmodavg" package in R (Mazerolle, 2017). Akaike weights provide relative likelihood of each model from the tested set of models.

Estimated growth rates for length-at-age relationships were calculated for each 90-day age class according to the following equations (Forsythe & Van Heukelem, 1987; Gonzalez et al., 1996):

a. Instantaneous relative growth rate, G (% DML d^{-1})

$$G = \frac{\ln R_2 - \ln R_1}{t_2 - t_1} \; x \; 100$$

b. Absolute growth rate, AGR (mm d^{-1})

$$AGR = \frac{R_2 - R_1}{t_2 - t_1}$$

3.2.5. Hatching date estimation

To study the influence of the seasonality on growth, the hatching date of each cuttlefish was back-calculated according with de estimated age and the date of capture. According to hatch dates, four seasonal hatching groups were defined: Spring group (March-May), Summer group (June-August), Autumn group (September-November), and Winter group (December-February). Kruskal-Wallis test and the Post hoc Dunn test were used to describe possible differences between hatching seasons.

The normal distribution of the data was checked using the Shapiro-wilk test in each analysis. When the data showed a normal distribution, a two-group independent *t*-test was used to compare differences in age according to the area and differences in age by sex. ANCOVA was also used to analyse differences between areas and sexes. When a normal distribution was not achieved, a non-parametric Kruskal-Wallis test and Dunn post hoc test were used. All statistical analyses were carried out using R v-4.1.1 (R Core Team, 2022).

3.3. Results

3.3.1. Size-structure

Cuttlefish lengths from Morocco ranged from 60-120 mm DML in females (21.87-127.87 g BW) and from 50-138 mm DML in males (18.94-206.98 g BW) (Fig. 3). Regarding Guinea-Bissau, females were ranged from 32-168 mm DML (20.03-314.00 g BW) and from 60-176 mm DML in males (28.44-456.61 g BW) (Fig. 4). All cuttlefish analysed for Morocco were mature/spawning or spent, while for Guinea-Bissau we found all stages of maturity. Mature males from Morocco ranged from 50-130 mm DML, and from 60-110 mm DML for mature females. Guinea-Bissau mature males showed a range from 60-176 mm DML, and from 68-140 mm DML for mature females.

The regression parameters of the DML-BW relationship (power equation) for males and females from Morocco and Guinea-Bissau are shown in Table II.

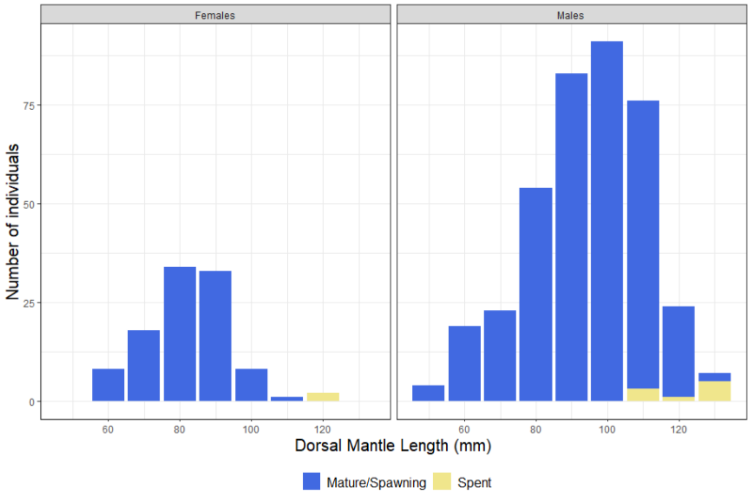


Figure 3.- Dorsal Mantle Length (DML) frequency distribution for the sample of *Sepia bertheloti* females and males caught off Morocco

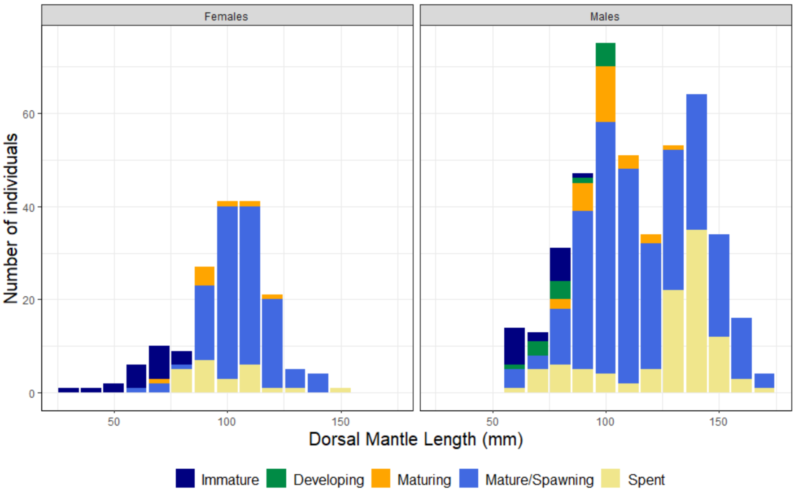


Figure 4.- Dorsal Mantle Length (DML) frequency distribution for the sample of *Sepia bertheloti* females and males caught off Guinea-Bissau

Table II. Statistical parameters of the Dorsal Mantle Length (DML) and Body Weight (BW) relationships for females, males and all individuals caught in Morocco and Guinea Bissau.

	DML-BW relationship	R^2	Confidence interval of b	Growth model*
Morocco				
Females	$BW = 0.4813DML^{2.3012}$	0.903	2.1701-2.4323	a-
Males	$BW = 0.414DML^{2.3576}$	0.934	2.2973-2.4179	a-
All	$BW = 0.4433DML^{2.3303}$	0.932	2.2774-2.3832	a-
Guinea-Bissau				
Females	$BW = 0.4619DML^{2.3183}$	0.922	2.2058-2.4308	a-
Males	$BW = 0.266DML^{2.5662}$	0.962	2.5147-2.6177	a-
All	$BW = 0.3296DML^{2.4757}$	0.952	2.4297-2.5216	a-

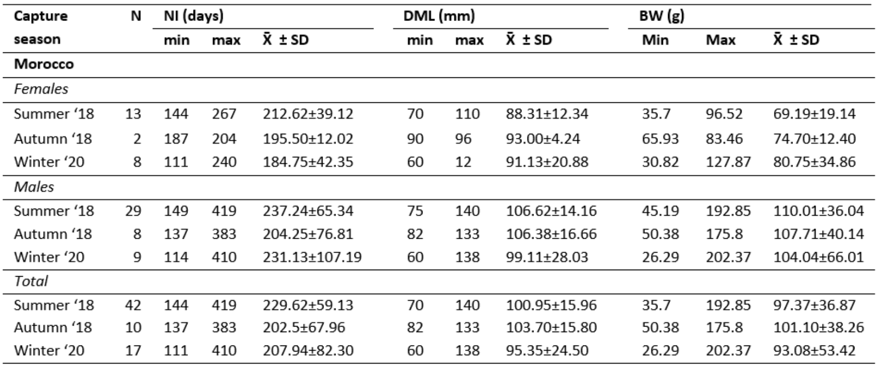
* a-: negative allometry

The ANCOVA test showed significant differences in DML-BW relationships between sex and areas (*$p<0.0001$*). Males of both areas were larger and heavier than the females, and the individuals from Morocco were smaller and lighter than Guinea-Bissau specimens. In terms of growth, the LWRs showed negative allometry (See Table I) for both sexes and areas.

3.3.2. Age analysis

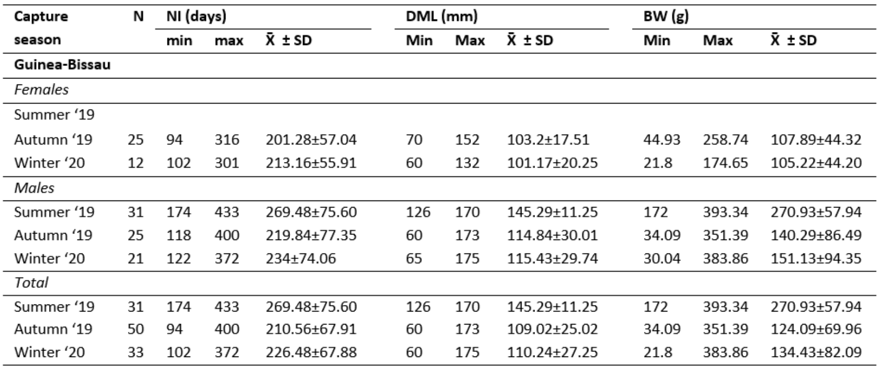
Of the 206 beaks analysed, 183 allowed a reliable reading. Twenty-three beaks (11.17%) were discarded because the structure had malformations (see image in Supplementary material), and a reliable reading was not allowed or they were severely damaged during grinding. Of the 183 beaks, 69 belonged to cuttlefish from Morocco (Table III), and 114 to Guinea-Bissau (Table IV).

Table III. Descriptive statistics for *Sepia bertheloti* females, males and total sample collected throughout different seasons off Morocco. NI: number of growth increments, DML: dorsal mantle length, BW: body weight, X̄: mean, SD: standard deviation.



Capture season	**N**	**NI (days)**			**DML (mm)**			**BW (g)**		
		min	**max**	**X̄ ± SD**	**min**	**max**	**X̄ ± SD**	**Min**	**Max**	**X̄ ± SD**
Morocco										
Females										
Summer '18	13	144	267	212.62±39.12	70	110	88.31±12.34	35.7	96.52	69.19±19.14
Autumn '18	2	187	204	195.50±12.02	90	96	93.00±4.24	65.93	83.46	74.70±12.40
Winter '20	8	111	240	184.75±42.35	60	12	91.13±20.88	30.82	127.87	80.75±34.86
Males										
Summer '18	29	149	419	237.24±65.34	75	140	106.62±14.16	45.19	192.85	110.01±36.04
Autumn '18	8	137	383	204.25±76.81	82	133	106.38±16.66	50.38	175.8	107.71±40.14
Winter '20	9	114	410	231.13±107.19	60	138	99.11±28.03	26.29	202.37	104.04±66.01
Total										
Summer '18	42	144	419	229.62±59.13	70	140	100.95±15.96	35.7	192.85	97.37±36.87
Autumn '18	10	137	383	202.5±67.96	82	133	103.70±15.80	50.38	175.8	101.10±38.26
Winter '20	17	111	410	207.94±82.30	60	138	95.35±24.50	26.29	202.37	93.08±53.42

Table IV. Descriptive statistics for *Sepia bertheloti* females, males and total sample collected throughout different seasons off Guinea-Bissau. NI: number of growth increments, DML: dorsal mantle length, BW: body weight, X̄: mean, SD: standard deviation.



Capture season	**N**	**NI (days)**			**DML (mm)**			**BW (g)**		
		min	**max**	**X̄ ± SD**	**Min**	**Max**	**X̄ ± SD**	**Min**	**Max**	**X̄ ± SD**
Guinea-Bissau										
Females										
Summer '19										
Autumn '19	25	94	316	201.28±57.04	70	152	103.2±17.51	44.93	258.74	107.89±44.32
Winter '20	12	102	301	213.16±55.91	60	132	101.17±20.25	21.8	174.65	105.22±44.20
Males										
Summer '19	31	174	433	269.48±75.60	126	170	145.29±11.25	172	393.34	270.93±57.94
Autumn '19	25	118	400	219.84±77.35	60	173	114.84±30.01	34.09	351.39	140.29±86.49
Winter '20	21	122	372	234±74.06	65	175	115.43±29.74	30.04	383.86	151.13±94.35
Total										
Summer '19	31	174	433	269.48±75.60	126	170	145.29±11.25	172	393.34	270.93±57.94
Autumn '19	50	94	400	210.56±67.91	60	173	109.02±25.02	34.09	351.39	124.09±69.96
Winter '20	33	102	372	226.48±67.88	60	175	110.24±27.25	21.8	383.86	134.43±82.09

For Morocco, the youngest specimen was a female (111 days old, 60 mm DML), and the oldest specimens was male (419 days, 140 mm DML). No significant difference in age was found between sexes (t-test: p=0.09034), with the median age of 186 ± 41 days in females and 220 ± 70 days in males. The oldest individual was caught in summer 2018, while the youngest individual was caught during the winter 2020 (see Table III). Mature females were found between 111-234 days while the mature males were found between 11-370 days (see Fig. 5)

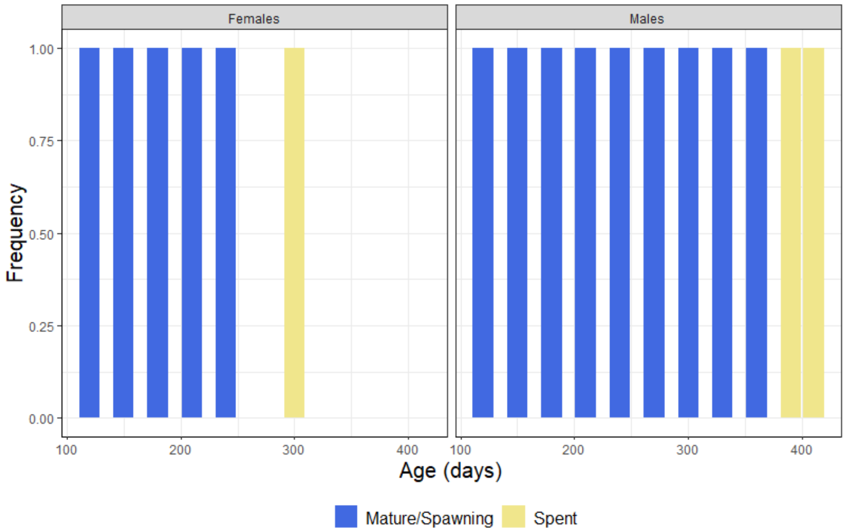


Figure 5.- Age frequency distribution for females and males of *Sepia bertheloti* caught off Morocco

For Guinea-Bissau, the youngest specimen was a 94 days old female (72 mm DML), and the oldest specimens was a 433 days old male (160 mm DML). Statistically significant difference in age was found between the sexes (t-test: *p*=0.0082), with the mean age of 198± 56 days in females and 235 ± 78 days in males. The oldest individual was caught in summer 2019, while the youngest individual was caught during the fall of the same year (see Table IV). Mature females were found between 126-289 days while the mature males were found between 118-400 days (see Fig. 6)

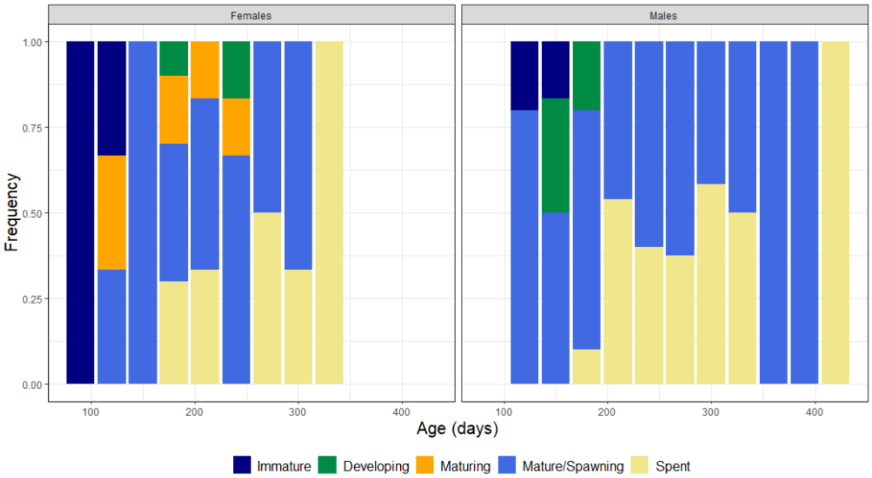


Figure 6.- Age frequency distribution for females and males of *Sepia bertheloti* caught off Guinea-Bissau

No significant difference in age was found between areas (t-test: *p*=0.3285) and sexes (t-test: *p*=0.784 for females and *p*=0.354 for males). Mean reading precision (CV) from the beaks readings was 2.72 ± 3.95% for individuals from Guinea-Bissau and 2.61 ± 3.54% for individuals from Morocco. Statistically significant positive correlation was found between LRL and DML ($r = 0.81$; $p < 0.001$), NI and LRL ($r = 0.66$; $p < 0.001$) and between NI and DML ($r = 0.84$; $p < 0.001$) for cuttlefishes from Guinea-Bissau. For both sexes, the relationship between LRL and DML was best described by linear model (Table V). In the case females, the best LRL and NI relationship was fitted by the linear model, while for males this relationship was best described by the power model (Table V). ANCOVA showed that there was statistically significant difference in the DML-LRL relationship of both sexes (p=0.001), but not in the LRL-NI (p=0.155) relationship. Greater variability of the DML-LRL and LRL-NI relationships was observed in males than in females, which resulted in lower R^2 values.

Table V. Statistical parameters of the Dorsal Mantle Length (DML) and Lower Rostral Length (LRL) according to the numbers of increments (NI) observed in males and females caught in Morocco and Guinea-Bissau.

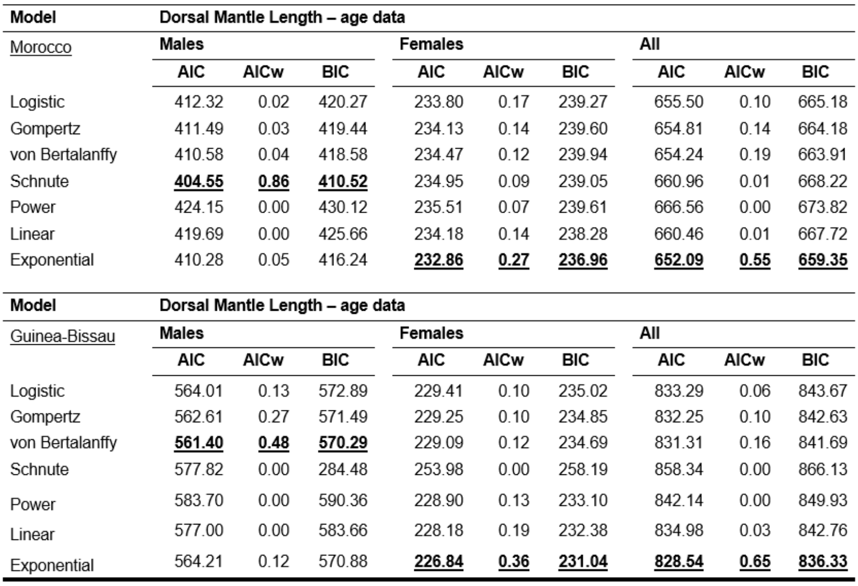
Area	Equations	R2
Guinea-Bissau		
Females	$DML = 32.499\,LRL + 8.9974$	0.600
	$LRL = 0.0059\,NI + 1.7166$	0.580
Males	$DML = 32.114\,LRL + 25.17$	0.630
	$LRL = 0.2698\,NI + 0.4569$	0.410
Morocco		
Females	$\mathrm{DML} = 36.36\,e^{0.4235\,LRL}$	0.563
	$\mathrm{LRL} = 1.414\,e^{0.0023\,NI}$	0.568
Males	$\mathrm{DML} = 34.297\,e^{0.483\,LRL}$	0.500
	$\mathrm{LRL} = 1.945\,e^{0.0008\,NI}$	0.430

Moreover, significant negative correlations were found between LRL and DML ($r = 0.45$; $p < 0.001$) and between NI and LRL (r = 0.48; $p < 0.001$) for individual from Morocco, while between NI and DML showed statistically significant positive correlation ($r = 0.77$; $p < 0.001$). For both sexes, the relationship between LRL and DML were best fitted by exponential model (Table V). Moreover, the exponential model was the best model to describe the relationship between LRL and NI (Table V). ANCOVA showed that there were statistically significant differences between the sexes with respect to DML-LRL relationship ($p = 0.022$), but not significant differences were found in LRL-NI relationship (p=0.587). Also, the greater variability of the LRL-NI relationship was observed in males than in females, which resulted in lower R^2 values, as observed in samples from Guinea-Bissau.

3.3.3. Growth models and growth rates

The estimated statistical parameters for the different growth models are shown in Table VI. According to the AIC parameters, the Schnute and exponential models were those that best described the growth pattern of males and females, respectively, in the Morocco population. Exponential model was the best one to describe the growth of the entire population (males and females together). In the case of Guinea-Bissau *Sepia bertheloti* population, the von Bertalanffy model was the best one that described the growth pattern of males and the exponential model for females, while for the entire population (males and females together) the exponential model showed the best fit. Figure 7 shows the best growth curves fitted for males and females of each study area.

Table VI. Statistical parameters of different growth model fitted to *Sepia bertheloti* Dorsal Mantle Length-age data from Morocco and Guinea-Bissau. AIC: Akaike's information criterion, AICw: Akaike weight, BIC: Bayesian Information Criterion. K: number of parameters in each model. Best growth model fit is given in bold underlined.



Model	**Dorsal Mantle Length – age data**								
Morocco	**Males**			**Females**			**All**		
	AIC	**AICw**	**BIC**	**AIC**	**AICw**	**BIC**	**AIC**	**AICw**	**BIC**
Logistic	412.32	0.02	420.27	233.80	0.17	239.27	655.50	0.10	665.18
Gompertz	411.49	0.03	419.44	234.13	0.14	239.60	654.81	0.14	664.18
von Bertalanffy	410.58	0.04	418.58	234.47	0.12	239.94	654.24	0.19	663.91
Schnute	**404.55**	**0.86**	**410.52**	234.95	0.09	239.05	660.96	0.01	668.22
Power	424.15	0.00	430.12	235.51	0.07	239.61	666.56	0.00	673.82
Linear	419.69	0.00	425.66	234.18	0.14	238.28	660.46	0.01	667.72
Exponential	410.28	0.05	416.24	**232.86**	**0.27**	**236.96**	**652.09**	**0.55**	**659.35**

Model	**Dorsal Mantle Length – age data**								
Guinea-Bissau	**Males**			**Females**			**All**		
	AIC	**AICw**	**BIC**	**AIC**	**AICw**	**BIC**	**AIC**	**AICw**	**BIC**
Logistic	564.01	0.13	572.89	229.41	0.10	235.02	833.29	0.06	843.67
Gompertz	562.61	0.27	571.49	229.25	0.10	234.85	832.25	0.10	842.63
von Bertalanffy	**561.40**	**0.48**	**570.29**	229.09	0.12	234.69	831.31	0.16	841.69
Schnute	577.82	0.00	284.48	253.98	0.00	258.19	858.34	0.00	866.13
Power	583.70	0.00	590.36	228.90	0.13	233.10	842.14	0.00	849.93
Linear	577.00	0.00	583.66	228.18	0.19	232.38	834.98	0.03	842.76
Exponential	564.21	0.12	570.88	**226.84**	**0.36**	**231.04**	**828.54**	**0.65**	**836.33**

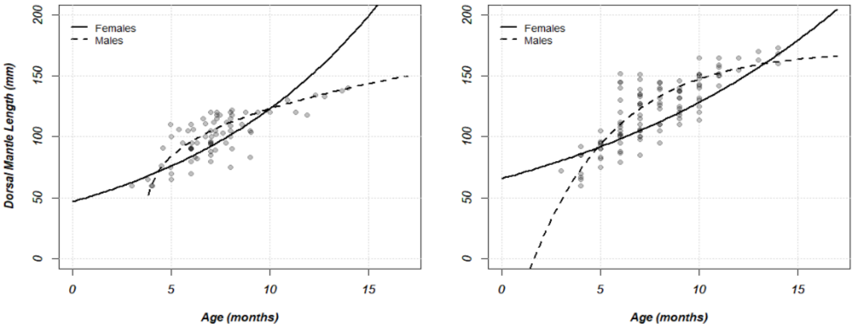
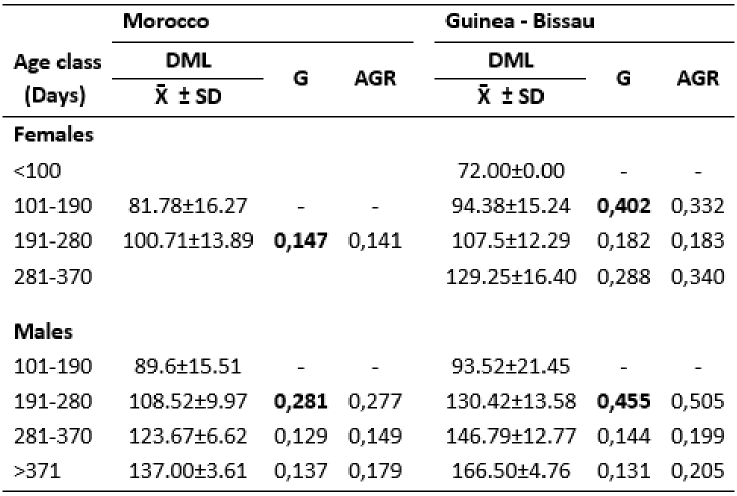


Figure 7. Best growth models fitted to Dorsal Mantle Length at age data for females, males and all individuals of *Sepia bertheloti* caught off Morocco (left) and Guinea Bissau (right).

The asymptotic length (L∞), according to the Von Bertalanffy model for males from Guinea-Bissau was 173 mm DML, while according to the Schnute model, the males from Morocco showed a L∞ of 140 mm DML.

The largest number of individuals were aged from 191 – 280 days (Table VII), for Morocco (51.47%) and Guinea-Bissau (41.22%), with the youngest age classes (<100 days old) being the least present (Morocco: 0.00 % and Guinea-Bissau: 0.88%). In the case of males, the lowest instantaneous relative growth rate (G) values were for the age classes of 281-370 and >371 days old for Morocco and Guinea-Bissau, respectively. In the case of females, the lowest G values were for the 191-280 days old age classes for Guinea-Bissau. The fastest growth patterns were found in the lower age classes of 191-280 for males from Morocco and Guinea-Bissau, while for females it was in the range of 101-190 days old for Guinea-Bissau. Females from Morocco have not been compared, since just being able to obtain a value of G could misinterpret their result. Even so, it is observed that for the age range available for Morocco females (191-280 days old), they have a lower G than individuals of the same age from Guinea-Bissau. This also occurs for males, where those from Guinea-Bissau show a higher G for all age classes, except for individuals >371 days old, where cuttlefishes from Morocco shows a value of 0.137% *DML* d^{-1} and those from Guinea-Bissau of 0.131% *DML* d^{-1}. In Table VII all G and AGR data are summarized.

Table VII. Dorsal mantle length growth-rates for each age-class of *Sepia bertheloti* females and males from Morocco and Guinea-Bissau. G: instantaneous relative growth rate (% DML d^{-1}); AGR: absolute growth rate (mm d^{-1}). X̄: average; SD: standard deviation.



Age class (Days)	Morocco DML X̄ ± SD	Morocco G	Morocco AGR	Guinea - Bissau DML X̄ ± SD	Guinea - Bissau G	Guinea - Bissau AGR
Females						
<100				72.00±0.00	-	-
101-190	81.78±16.27	-	-	94.38±15.24	**0,402**	0,332
191-280	100.71±13.89	**0,147**	0,141	107.5±12.29	0,182	0,183
281-370				129.25±16.40	0,288	0,340
Males						
101-190	89.6±15.51	-	-	93.52±21.45	-	-
191-280	108.52±9.97	**0,281**	0,277	130.42±13.58	**0,455**	0,505
281-370	123.67±6.62	0,129	0,149	146.79±12.77	0,144	0,199
>371	137.00±3.61	0,137	0,179	166.50±4.76	0,131	0,205

Significant differences in G and AGR growth rates between sexes (t-test, $p < 0.0001$) and areas (t-test, $p<0.0001$) were found. The individuals from Guinea-Bissau showed a higher G value than the individuals from Morocco, showing faster growth at the same age (See Table VII). On the other hand, within each area, males had a higher growth rate than females. This is reflected in the fact that males showed larger sizes than females in both areas for the same age. The differences in G and AGR between areas are observed: individuals from Guinea-Bissau showed larger sizes than individuals from Morocco at the same age ranges.

3.3.4. Hatching season

The back-calculation method indicated that the cuttlefish hatched between June 2017 and September 2019 for Morocco, and between May 2018 and October 2019 for Guinea-Bissau. It was observed that cuttlefish hatched throughout the year in Morocco (Fig. 8) and Guinea-Bissau (Fig. 9), although 45.59% of the total sample hatched in winter for Morocco, while for Guinea Bissau the hatchings had two marked peaks, one in summer with 30.70% and another in winter with 35.08% of the hatchings. Kruskal-Wallis test (W=4.0462, *p*=0.2565) did not show significant differences in length ranges according to season of hatching for individuals from Morocco. Nevertheless, individuals from Guinea-Bissau showed significant differences in the length ranges (Kruskal-Wallis test; W=36.439, *p*<0.0001). The post hoc Dunn test (*p*<0.001) showed that these differences were due to the fact that individuals born during warm seasons (spring and summer) were smaller than those born in the autumn-winter. Individuals hatched in winter showed larger sizes.

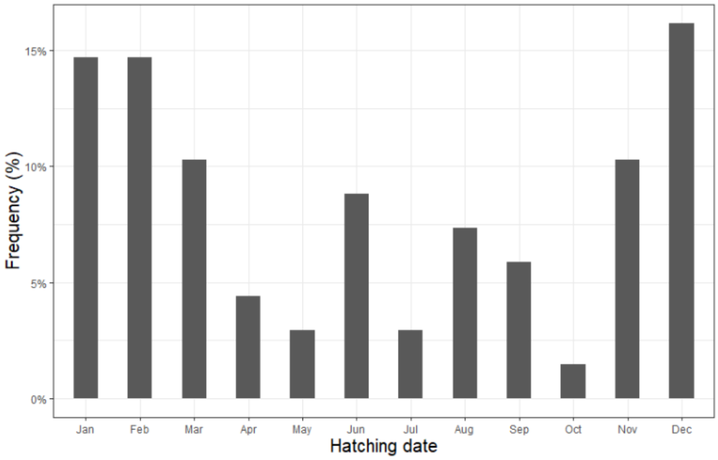


Figure 8.- Frequency distribution of back calculated hatching months for *Sepia bertheloti* from Morocco.

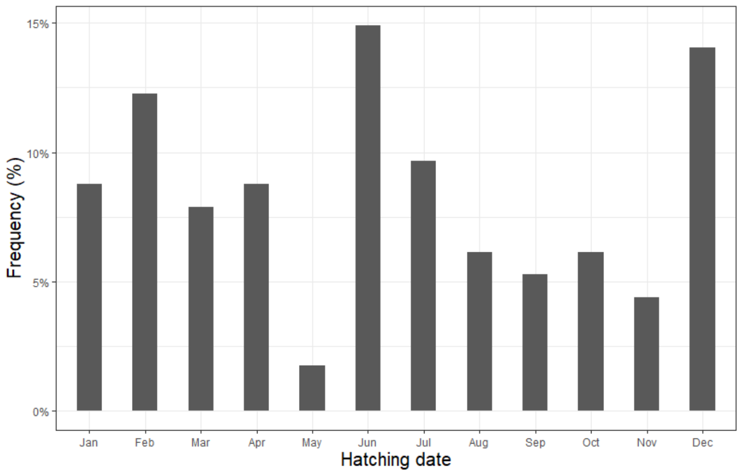
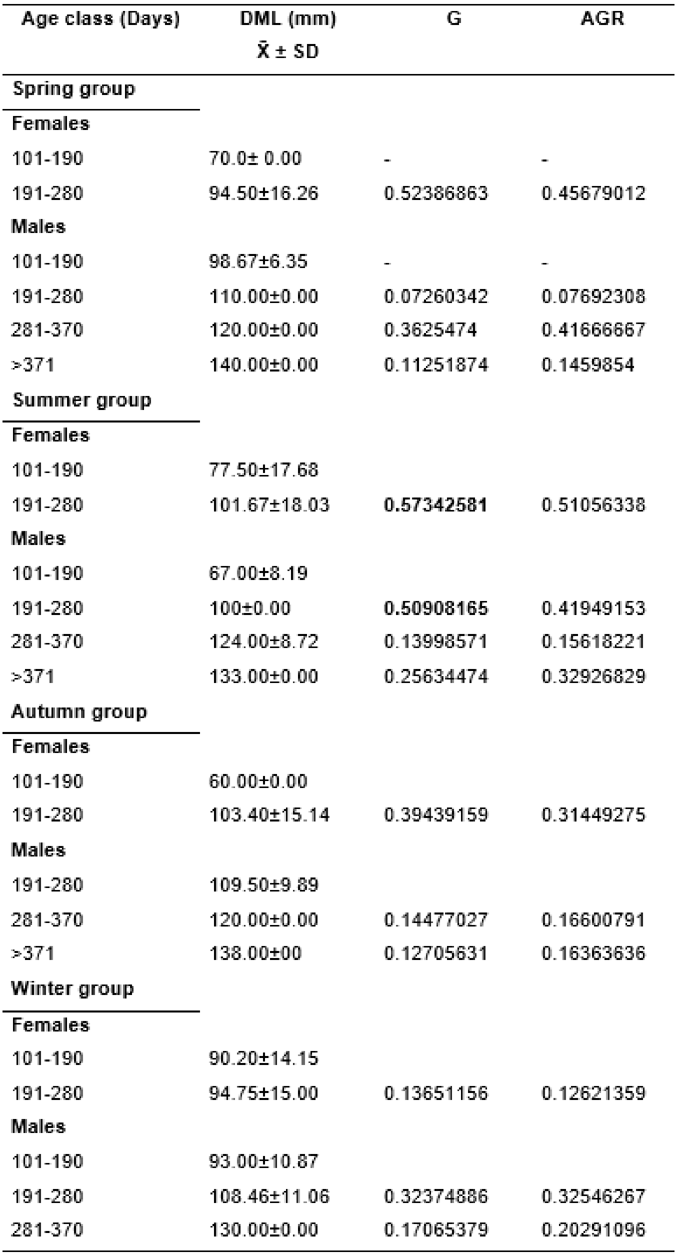


Figure 9.- Frequency distribution of back calculated hatching months for *Sepia bertheloti* from Guinea-Bissau.

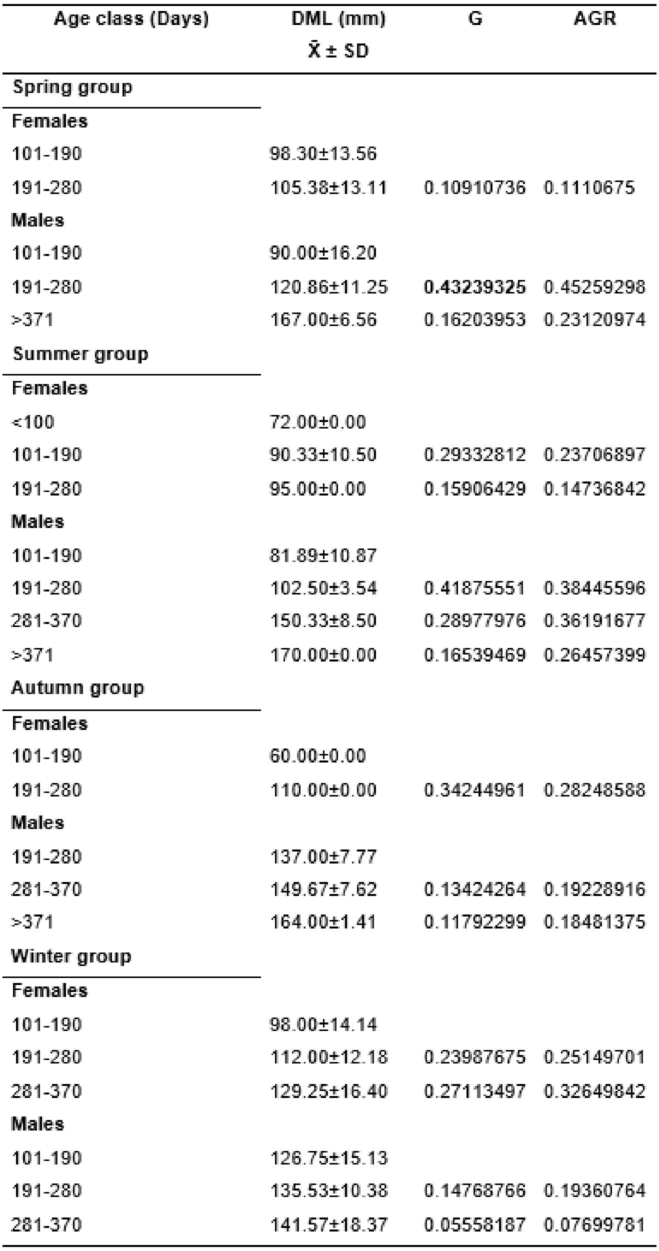
Growth rates for each hatching season group were analysed for females and males separately (See supplementary material). In Morocco, the highest values of G for males and females were found for individuals born in summer, while for Guinea-Bissau the highest values of G in spring (Table VIII and IX). In both areas and sexes, a decreasing trend in the growth rhythm with age was observed.

Table VIII. Dorsal mantle length (DML) growth rates for each hatching groups (spring, summer, autumn and winter) of *Sepia bertheloti* males and females in Morocco. G: instantaneous relative growth rate (% DML d^{-1}); AGR: absolute growth rate (mm d^{-1}). $\bar{X}$: average; SD: standard deviation.



Age class (Days)	DML (mm) $\bar{X}$ ± SD	G	AGR
Spring group			
Females			
101-190	70.0± 0.00	-	-
191-280	94.50±16.26	0.52386863	0.45679012
Males			
101-190	98.67±6.35	-	-
191-280	110.00±0.00	0.07260342	0.07692308
281-370	120.00±0.00	0.3625474	0.41666667
>371	140.00±0.00	0.11251874	0.1459854
Summer group			
Females			
101-190	77.50±17.68		
191-280	101.67±18.03	**0.57342581**	0.51056338
Males			
101-190	67.00±8.19		
191-280	100±0.00	**0.50908165**	0.41949153
281-370	124.00±8.72	0.13998571	0.15618221
>371	133.00±0.00	0.25634474	0.32926829
Autumn group			
Females			
101-190	60.00±0.00		
191-280	103.40±15.14	0.39439159	0.31449275
Males			
191-280	109.50±9.89		
281-370	120.00±0.00	0.14477027	0.16600791
>371	138.00±00	0.12705631	0.16363636
Winter group			
Females			
101-190	90.20±14.15		
191-280	94.75±15.00	0.13651156	0.12621359
Males			
101-190	93.00±10.87		
191-280	108.46±11.06	0.32374886	0.32546267
281-370	130.00±0.00	0.17065379	0.20291096

Table IX. Dorsal mantle length (DML) growth rates for each hatching groups (spring, summer, autumn and winter) of *Sepia bertheloti* males and females in Guinea-Bissau. G: instantaneous relative growth rate (% DML d^{-1}); AGR: absolute growth rate (mm d^{-1}). X̄: average; SD: standard deviation.



Age class (Days)	DML (mm) X̄ ± SD	G	AGR
Spring group			
Females			
101-190	98.30±13.56		
191-280	105.38±13.11	0.10910736	0.1110675
Males			
101-190	90.00±16.20		
191-280	120.86±11.25	**0.43239325**	0.45259298
>371	167.00±6.56	0.16203953	0.23120974
Summer group			
Females			
<100	72.00±0.00		
101-190	90.33±10.50	0.29332812	0.23706897
191-280	95.00±0.00	0.15906429	0.14736842
Males			
101-190	81.89±10.87		
191-280	102.50±3.54	0.41875551	0.38445596
281-370	150.33±8.50	0.28977976	0.36191677
>371	170.00±0.00	0.16539469	0.26457399
Autumn group			
Females			
101-190	60.00±0.00		
191-280	110.00±0.00	0.34244961	0.28248588
Males			
191-280	137.00±7.77		
281-370	149.67±7.62	0.13424264	0.19228916
>371	164.00±1.41	0.11792299	0.18481375
Winter group			
Females			
101-190	98.00±14.14		
191-280	112.00±12.18	0.23987675	0.25149701
281-370	129.25±16.40	0.27113497	0.32649842
Males			
101-190	126.75±15.13		
191-280	135.53±10.38	0.14768766	0.19360764
281-370	141.57±18.37	0.05558187	0.07699781

3.4. Discussion

In this study, the length ranges obtained from commercial fisheries did not allow to separate the catches into different ontogenetic groups (juveniles and adults), due to the inability to characterize the juvenile phase. Sweeney *et al*. (1992) described the category of "juveniles" to that stage of development between hatching and the subadult stage, defining the category of subadult stage as that stage in which the morphological characteristics of cephalopod are completely developed to determine the species and ending when it reaches the sexual maturity. Bellanger *et al*. (2005) defined the juvenile category for *Sepia officinalis* as individuals up to 3 months old.

Significant differences in mean length between sexes have already been described for other cuttlefish such as *Sepia latimanus*, *S. koilados, S. rhoda* or *S. subplana* (Bettencourt & Guerra, 2001; Dan *et al*., 2012), where males were larger than the females. However, this is not a characteristic that can be extrapolated to the whole Sepiidae family, since most species have a different growth pattern, where females are larger than males (i.e., *S. orbignyana or S. elegans* among others; Jereb & Roper, 2005).

Differences in growth conditioned by environmental factors (i.e. latitude, temperature, food, etc.) have been described in cephalopods (e.g. Arkhipkin et al., 1998; Semmens et al., 2004; Guerra, A., 2006; Batista et al. 2021). In the case of *S. bertheloti* it was observed that individuals from Guinea-Bissau (Central Africa) showed larger sizes than individuals captured in Morocco (North Africa) at the same age. The oceanographic differences of both zones, due to the influence of high productivity from Western Sahara upwelling (Aristegui et al. 2009) and the different thermal ranges between the areas due to the seasonality of upwellings and wings (Aristegui et al., 2009; Pelegrí et al., 2017) may be the indicators in the different length frequency distributions. In relation to growth, males and females showed negative allometric pattern, growing faster in dorsal mantle length than in total weight, which is comparable to other species of cuttlefish such as *S*. *officinalis* (Vasconcelos et al., 2018).

In this study, the analysis of beak microstructure for *Sepia bertheloti* used rostrum sagittal sections to determine age. In controversy with other benthic cephalopods such as *Octopus vulgaris* (e.g. Perales-Raya et al., 2010; 2014a, b Canali et al. 2011; Cuccu et al. 2012), or *O. insularis* (Batista et al. 2021), or O. maya (Rodríguez-Domínguez et al. 2013) where the lateral wall surfaces (LWS) of upper beaks were successfully used for age estimation, in the case of *S. bertheloti*, and after exploring RSS and LWS in the upper and lower jaws, the RSS of the lower beak showed the most clear pattern of growth increments. On the contrary, in the LWS of the upper beaks no clear sequence of growth increments were observed for age estimation of *S. bertheloti*.

Although differences were observed in the length distributions for the same age class between both studied areas, the maximum age recorded did not differ between areas (14 months). Nevertheless, males showed a higher life span than females in both areas. The males showed a maximum estimated age of 14 months, while in females the maximum estimated age was 9-10 months. Using age data from statoliths, Perales-Raya (2001) obtained a maximum age of 223 days for both sexes for *S. hierredda* from Western Sahara, reaching males larger sizes. Bettencourt & Guerra (2001) showed that the maximum age of *S. officinalis* under culture conditions was 420 days (14 months), although the number of increments in the statoliths could have been underestimated due to the large number of narrow increments close to the nucleus, which was very dark, and the increases were not very visible. Challier *et al*. (2005) described an approximate life expectancy of 2 years for *S. officinalis* for the English Channel. Similarly, Nabhitabhata & Nilaphat (1999) described the *S. pharaonis* life expectancy of 1 year or over 2 years depending on the time of birth. This characteristic of life expectancy was also described by Hernandez-López (2000), that observed that depending on the time of birth, the life expectancy of *Octopus vulgaris* could increase. Therefore, the results indicate a life span duration of *S. bertheloti* in both fishing areas of around 1 year. It should be emphasized that this is not the maximum estimated age for the species, but rather the age range of the individuals caught by the commercial fishing fleets. In addition, a deeper study of both populations would be necessary in order to observe possible differences in life expectancy and sexual maturity, as reported in other cephalopods species. In the Western Sahara, where the upwelling system is more intense than in the regions of the present study, the maximum age estimated from statoliths in *S. hierredda* was around 8 months using also fishery-caught individuals (Perales-Raya, 2001).

The use of asymptotic models for the growth of cephalopods is something that has been under discussion for years, where Jackson et al. (2000) described the inefficiency of the Von Bertalanffy model for cephalopods. On the other hand, authors such as Uozumi & Shiba (1993) or Brodziak & Macy (1996) recommended the use of the Gompertz and Schnute asymptotic models (Petric et al., 2021). Arkhipkin & Roa-Ureta (2005) and Arkhipkin et al. (2021) recommended using the Schnute model to describe growth since the use of Von Bertalanffy parameters for assessment models is inappropriate for cephalopods and their semelparous life history needs to be accounted. In this study, seven growth models were analysed, including 4 with asymptotic growth (Logistic, Von Bertalanffy, Gompertz, and Schnute models). The absence of individuals of smaller and larger lengths means that our growth models are adapted to the fished part of the population. Forsythe & Van Heukelem (1987) indicated that cephalopods grow differently in each life stage, so the absence of extreme length ranges determines which model fit better. According to our length frequency distributions, the exponential model was the one that best described the growth of *S. bertheloti* population of Morocco and Guinea-Bissau, which has also been described as adequate for other cephalopods species during the first part of their life cycles (Forsythe & Van Heukelem, 1987). However, the exponential model was not the best model adapted to each sex separately. The females, with a shorter maximum age, showed an exponential growth pattern, but for males the asymptotic models (Schnute's for males from Morocco and Von Bertalanffy's for males from Guinea-Guinea) showed a better fitting. This variation in growth between males and females may be due to life expectancy factors, since males have a longer life span than females. Furthermore, an asymptotic model in the final phase of its life would be expected since its growth rate slows down.

The instantaneous growth rates generally showed high values in the early stages of life and are expected to decrease with age. Many authors have already described this growth pattern in cephalopods (Richard, 1971; Dominguez et al., 2006 or Petric et al., 2021 among others). Cuttlefish from Guinea-Bissau showed higher growth rates than individuals from Morocco at the same age class. By sexes, males from both areas showed a longer life span than females. These differences between sexes and geographic areas have also been observed in other cephalopods as *Illex coindetti* (Arkhipkin, 1996) which females grow faster than males, and individuals from Central Africa (Sierra Leone) grow faster than the individuals from Western Sahara.

Regarding growth differences by hatching season, it was observed that individuals from Guinea-Bissau born during the warm seasons (spring and summer) had smaller lengths at a given age than individuals born during the autumn-winter period. Conversely, in the cuttlefish *S. hierredda* from Western Sahara the individuals worn in spring showed larger sizes at a given age than those born in autumn (Perales-Raya, 2001), although the author also found inter annual differences. The back-calculation analysis showed that *Sepia bertheloti* from Morocco and Guinea-Bissau hatches continuously throughout the year. A peak of hatching was observed for Morocco in winter, whereas off Guinea-Bissau two marked peaks are shown, one in summer and other in winter. Continuous spawning has been observed for many benthic cephalopods as *Octopus vulgaris, S. officinalis and S. hierredda* standing out in West Africa, although they usually had two marked reproductive periods (Hatanaka, 1979; Jurado-Ruzafa, 2014). For both areas, it was observed that the highest G values coincide with the periods of greatest intensity of the upwellings (Ingham, 1970; Aristegui et al., 2009), where the availability of nutrients at the time of hatching makes them grow faster.

In conclusion, the results obtained from this research suggest that the life span of *S. bertheloti* is around 9-10 months for females and around 14 months for males, with differences between the growth rates for each sex probably due to genetic, environmental and geographical factors, as has been shown for other cephalopods species (Guerra, 2006). In order to have a greater comprehension of the life cycles of *S. bertheloti*, future efforts should be focused on accessing a wider range of lengths, ages and maturity stages in order to analyse upwelling influences and the hypothesis that individuals from colder waters (Morocco, Pelegrí et al., 2017) areas have a greater life span with slower growth rate and late reproduction (Hernández-García & Castro, 1998) than individuals of warmer waters (Guinea-Bissau, Pelegrí et al., 2017), but also to provide more useful biological information for fisheries management of this species in the Eastern Atlantic.

CAPÍTULO 4

Fotografía portada Capítulo 4: Threatening Broadclub Cuttlefish Displaying Tentacles on Black Background.
Edward Rowland/Alamy Stock Photo

Capítulo 4

MORFOMETRÍA DEL SEPIÓN

Cuttlebone morphometrics and sex identification of *Sepia bertheloti* (d'Orbigny,1835) from the central-east Atlantic[1].

Airam Guerra-Marrero, David Jiménez-Alvarado, Vicente Hernández-García, Leticia Curbelo-Muñoz and José J. Castro.

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SHORT COMMUNICATION **Open Access**

Cuttlebone morphometrics and sex identification of *Sepia bertheloti* (d'Orbigny, 1835) from the central-east Atlantic

Airam Guerra-Marrero*, David Jiménez-Alvarado, Vicente Hernández-García, Leticia Curbelo-Muñoz and José Juan Castro-Hernández

Abstract

Analysis of 322 cuttlebones of *Sepia bertheloti* caught in the waters of the Northwest Africa showed significant differences in growth between males and females. Morphometric analysis revealed a relatively different cuttlebone growth pattern between sexes, with males presenting faster growth in length to reach larger sizes and females displaying greater growth in width. This difference in cuttlebone growth is related to female gonadal development and the subsequent increase of the paleal cavity, providing more support and space to accommodate a higher number of oocytes.

Keywords: African cuttlefish, *Sepia bertheloti*, Cuttlebone, Fragmocone

Introduction

The use of morphometric analysis to define basic characters of growth or development of some structures in cephalopods has been applied from the first contributions of Hoyle [1]. These morphometric analyses, called "Traditional morphometry" [2], compare the linear dimensions of different parts of an organism to define statistical relationships with objectives, such as the taxonomic differentiation of species or intra-specific morphometric differences between sexes. These characteristics have been used for the Sepiidae family, mainly for taxonomic differentiation [3], as well as to analyse morphometric differences within the same species [4].

Within the cephalopods context, the Sepiidae family represents a special interest for studies of hard structures due to the presence of the cuttlebone [5]. The cuttlebone is a complex structure composed of calcium carbonate in its aragonite polymorph mixed with a small amount of organic matter and a complex of β-chitin and protein [6, 7] that provides internal skeletal support and buoyancy to the individual [8]. The cuttlebone shows a structure finely laminated (lamellas). According to Bettencourt and Guerra [9] and Chung and Wang [10], the periodicity of lamellar deposition depends on a combination of physiological and environmental factors (i.e., water temperature).

Sepia bertheloti and *Sepia hierredda* are by-catch species in the bottom trawl fishery targeting *Sepia officinalis* along the coast of the western Sahara [11]; There are no separate statistics of catches/landings for both species because they are caught and marketed together, but *S. bertheloti* represents between 11 and 35% of catches reported for both by-catch species [12]. In addition, probably due to the low commercial interest for *S. bertheloti*, most knowledge on this species has been obtained from the analysis of stomach contents of their natural predators [13, 14] by exploratory fishing to assess the status of the resources [15, 16] or for analyses of metal concentrations [17].

In this context, any contribution to the biology and ecology of *S. bertheloti* would contribute to its conservation and fishery management. The morphologic study of the cuttlebone could provide useful information for the assessment and estimation of mortality, particularly when the individuals are broken and only the cuttlebone

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*Correspondence: airamgmarrero@gmail.com
Instituto Universitario EcoAqua, University of Las Palmas de Gran Canaria, Edf. Ciencias Básicas, Campus de Tafira, Las Palmas de Gran Canaria, 35017 Las Palmas, Spain

5.1. Introducción

The use of morphometric analysis to define basic characters of growth or development of some structures in cephalopods has been applied from the first contributions of Hoyle (1886). These morphometric analyses, called "Traditional morphometry" (Neige, 2006), compare the linear dimensions of different parts of an organism to define statistical relationships with objectives, such as the taxonomic differentiation of species or intra-specific morphometric differences between sexes. These characteristics have been used for the Sepiidae family, mainly for taxonomic differentiation (Guerra et al. 2001), as well as to analyse morphometric differences within the same species (Almonacid-RIoseco et al., 2009). Within the cephalopod's context, the Sepiidae family represents a special interest for studies of hard structures due to the presence of the cuttlebone (Guerra, 1992). The cuttlebone is a complex structure composed of calcium carbonate in its aragonite polymorph mixed with a small amount of organic matter and a complex of β-chitin and protein (Hare & Abelson, 1965; Checa et al., 2015) that provides internal skeletal support and buoyancy to the individual (Richard, 1969). The cuttlebone shows a structure finely laminated (lamellas). According to Bettencourt & Guerra (2001) and Chung & Wang (2013), the periodicity of lamellar deposition depends on a combination of physiological and environmental factors (i.e., water temperature). *Sepia bertheloti* and *Sepia hierredda* are by-catch species in the bottom trawl fishery targeting *Sepia officinalis* along the coast of the western Sahara (Jouffre & Inejih, 2005); There are no separate statistics of catches/landings for both species because they are caught and marketed together, but *S. bertheloti* represents between 11 and 35% of catches reported for both by-catch species (Jereb & Roper, 2005). In addition, probably due to the low commercial interest for *S. bertheloti*, most knowledge on this species has been obtained from the analysis of stomach contents of their natural predators (Delgado de Molina-Acevedo et al., 1993; Monzón-Argüello et al.,

2018) by exploratory fishing to assess the status of the resources (Balguerias-Guerra et al., 1993; Rocha et al., 2017) or for analyses of metal concentrations (Ama-Abasi & Akpan, 2008). In this context, any contribution to the biology and ecology of *S. bertheloti* would contribute to its conservation and fishery management. The morphologic study of the cuttlebone could provide useful information for the assessment and estimation of mortality, particularly when the individuals are broken and only the cuttlebone appear in the captures (Almonacid-Rioseco et al., 2009). Almonacid-Rioseco (2006) indicated that in the small-scale trap fishery of the Canary Islands, approximately 50% of *S. officinalis* caught were represented only by cuttlebones and obviously not reported in the landings. This characteristic makes it necessary to study these hard structures to estimate not only the actual catches by the different fishing gears but also the productivity of the area where the diverse fishing sectors operate. In this context, the objective of this study was to describe the morphometric relationships of the cuttlebone of *S. bertheloti* and detect eventual differences between males and females caught in the northwest African waters.

5.2. Material and Methods

A total of 322 individuals (247 males and 74 females) of *S. bertheloti* were obtained from commercial catches landed in the port of Tanger (Morocco) and by the bottom trawl fishery in the central-east Atlantic (CECAF area 34.1.11) from July to September 2018. All samples were immediately frozen after being caught. The specimens of *S. bertheloti* were identified following the key proposed by Nesis (1987). After defrosting, the Dorsal Mantle Length (DML), Total wet Weight (TW) and Gonad Weight (GW) were recorded for each specimen. Moreover, each cuttlebone was removed, weighted and measured according to parameters described by

Roper & Voss (1983): Cuttlebone Length (CL), Total Cuttlebone Length (CL1), Cuttlebone Height (CH), Cuttlebone Width (CW), Fragmocone Length (FL), Fragmocone Width (FW), Internal Cuttlebone Width (ICW), and External Cuttlebone Width (ECW) (Fig. 1).

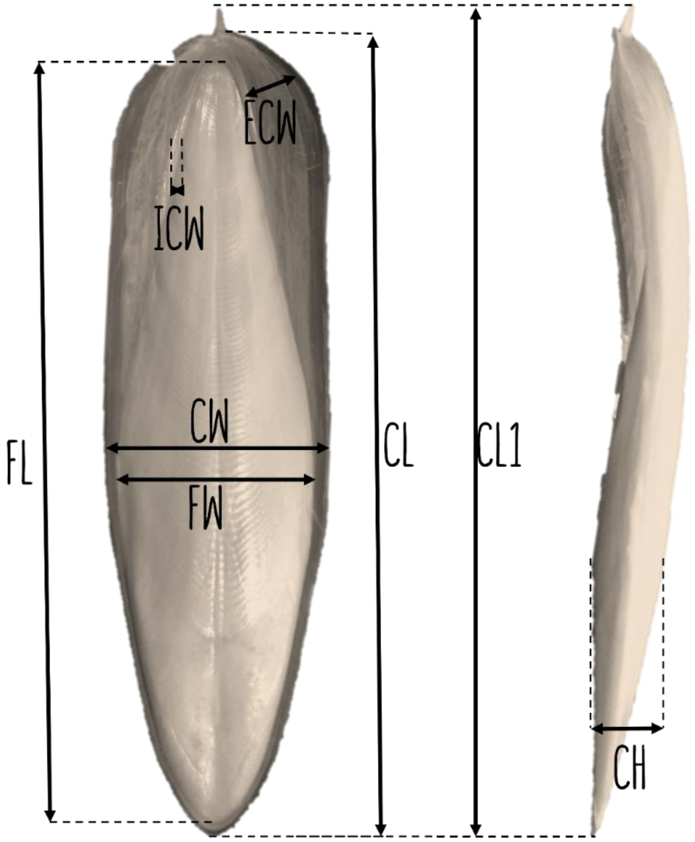

Figure 1.- Morphometric measurements taken of the cuttlebone of *Sepia bertheloti:* Cuttlebone Length (CL), Total Cuttlebone Length (CL1), Cuttlebone Height (CH), Cuttlebone Width (CW), Fragmocone Length (FL), Fragmocone Width (FW), Internal Cuttlebone Width (ICW) and the External Cuttlebone Width (ECW).

All length measurements were taken to the nearest millimetre (0.001), and the weights were taken to the nearest centigram (0.01). For each specimen, sex was determined macroscopically, and the maturity stage was assigned based on the scale described by Nigmatullin (1989). Total cuttlebone length (CL1) was not taken in individuals with totally or partially fractured spines due to damages during trawling or handling on board. To observe differences between the parts of the cuttlebone and the DML, a regression analysis was performed using the linear regression model (Table I). These functions were performed individually for males (247 individuals) and females (74 individuals). Analysis of covariance (ANCOVA) was performed to detect significant differences between male and female cuttlebones. The first test determined whether the regression slopes for each size class are statistically homogeneous. If the slopes are homogeneous, the second test was performed to verify whether there were differences between sexes in each size class. The mean values of the dependent variables (cuttlebone measurements) for each size class predict differences between sexes. Moreover, the gonadosomatic index (GSI=GW/TW×100) of the individuals was calculated and plotted against cuttlebone measures to determine eventual differences between sexes. All statistical analyses were performed using R (v 3.4.2) IBM-SPSS Statistics© package.

Table I. Parameters of the morphometric relationships established between the dorsal mantle length (DML) and cuttlebone measurements in male and female *Sepia bertheloti*.

Variable	Sex	a	a standard error	b	b standard error	R	F
FL	F	0.139	0.020	0.933	0.033	0.968	1778.5
	M	0.255	0.050	0,796	0.045	0.939	1315.1
FW	F	0.476	0.059	0.939	0.040	0.954	2538.1
	M	3.321	0.186	0.799	0.024	0.931	1063.3
CW	F	0.211	0.036	1.147	0.054	0.946	2452.1
	M	3.814	0.179	0.794	0.020	0.949	1500.2
ECW	F	0.941	0.126	1.094	0.067	0.913	1266.4
	M	0.402	0.280	1.182	0.030	0.951	1543.1
CL	F	0.915	0.028	0.148	0.018	0.977	1056.9
	M	0.192	0.036	0.856	0.043	0.951	3398.6
CL1	F	0.957	0.082	0.119	0.043	0.880	436.9
	M	0.181	0.061	0.863	0.075	0.888	530.9
CH	F	0.212	0.044	1.614	0.098	0.914	2272.1
	M	0.305	0.025	1.378	0.036	0.949	1472.8
TW	F	0.591	0.094	2.001	0.075	0.972	1716.8
	M	0.326	0.049	2.327	0.176	0.939	4191.5

5.3. Results

DML ranged between 63-133 mm in males and 67-110 mm in females, whereas TW was 35.5-192.9 g in males and 37.3-103.5 g in females. The morphometric relationships established through regression analyses between DML and cuttlebone measurements in males and females (Fig. 1) are compiled in Table I. The relationship DML-CL1 displayed the lowest Pearson correlation coefficient (r) for both sexes, which could be due to the low number of specimens without broken spines.

Figure 2. Dorsal and ventral views of the cuttlebone of a mature female (DML=96.0 mm) and male (DML=95.3 mm).

ANCOVA revealed that FW (F=124.417, *p*<0.0001), CW (F=449.185, *p*<0.0001), and ECW (F= 148.228, *p*<0.0001) were the morphometric measurements with statistically significant differences between sexes. These differences indicated that cuttlebone width, fragmocone width and external width are proportionally larger in females compared with males for a given length class (Figs. 2 and 3a, b, c). Female cuttlebones also presented greater weights than male cuttlebones for the same length class (Fig. 3d).

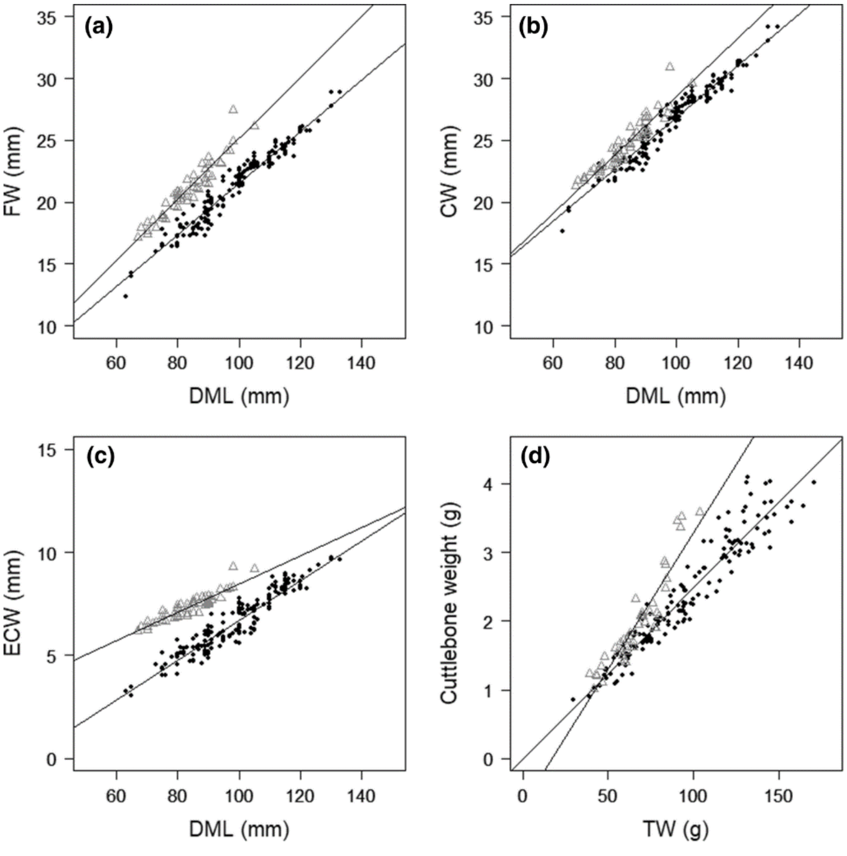

Figure 3 Morphometric relationships between Dorsal Mantle Length (DML) and **a** Fragmocone Width (FW), **b** Cuttlebone Width (CW), **c** External Cuttlebone Width (ECW) and between **d** Total wet Weight (TW) and Cuttlebone weight (CW) for males (black dots) and females (empty triangles) of *Sepia bertheloti.*

All individuals were mature and showed a high development of the gonads, being ready to spawn. Significant differences were recorded between the GSI of males and females in relation to FW, CW and ECW (Figs. 4a-d).

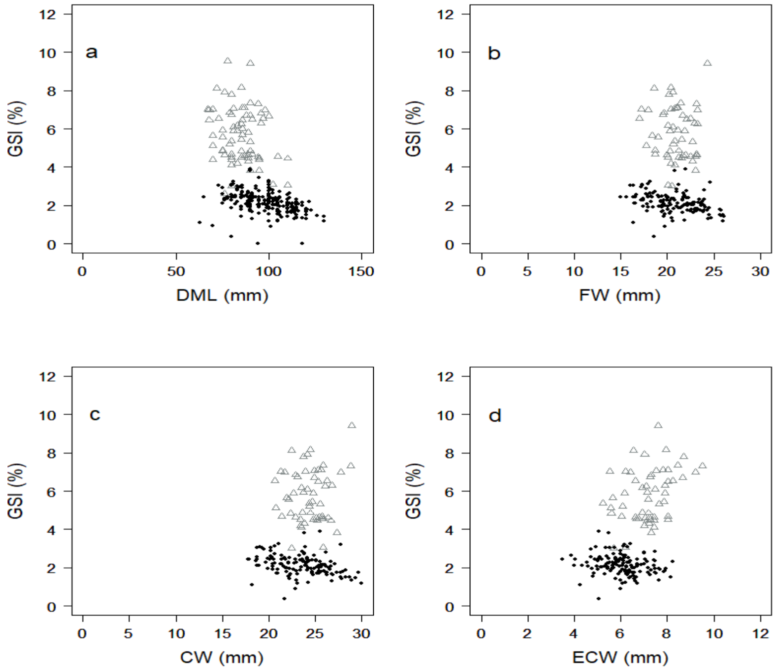

Figure 4. Relationships between Gonadosomatic Index (GSI) and **a** Dorsal Mantle Length (DML), **b** Cuttlebone width (CW), **c** Fragmocone width (FW) and **d** External Cuttlebone Width (ECW) for males (black dots) and females (empty triangles) of *Sepia bertheloti.*

5.4. Discussion

External sexual dimorphism of *Sepia bertheloti* was mainly based on the fact that males present median arm suckers with greater diameter than marginal suckers and hectocotylus in the left ventral arm. Apart from sexual structures, females internally show the buccal membrane extending ventrally with two spermathecae (Jereb & Roper, 2005). However, minimal attention has been paid to cuttlebone as a potential element to differentiate males from females. This study showed that female cuttlebones are significantly wider probably due to the need for a bigger volume of the paleal cavity to increase the capacity to accommodate the gonads. Jereb & Roper (2005) remarked that the mantle is relatively wider in females than in males.

S. bertheloti males are larger than females (Jereb & Roper, 2005), which is also noted in *S. latimanus* (Dan et al., 2012) *koilados*, *S. rhoda*, and *S. subplana*. However, in most cuttlefish species (i.e., *S. acuminata*, *S. australis*, *S. bidhaia, S. braggi, S. elegans, S. filibranchia, S. grahami, S. hedley, S. latimanus, S. limata, S. mestus, S. orbignyana, S. plana, S. senta, S. smithi, S. sulcata, Sepiella inermis,* and *S. weberi*) females growth larger than males (Jereb & Roper, 2005). Regarding *S. latimanus*, Dan et al. (2012) observed that there were no morphometric differences in the growth pattern of both sexes during the initial life stages, but males become larger than females after one year of age. Males and females of *S. bertheloti* caught more northwards than the distributional range given by Jereb & Roper (2005) presented a maximum size of 133 and 100 mm DML, respectively, which is clearly smaller than the maximum sizes reported by Jereb & Roper (2005) for the Eastern Atlantic (175 and 134 mm DML, respectively). However, females were usually wider, and this aspect could be associated with the wider morphometric structure of their cuttlebone for a given mantle length.

This differentiation of the cuttlebone between sexes with females with a broader cuttlebone has also been described in other cuttlefish species, such as S. officinalis (Almonacid-Rioseco et al., 2009), *S. prabahari, S. weberi* and *Sepiella ornata* (Jereb & Roper, 2005). Therefore, although *S. bertheloti* males and females cannot be differentiated macroscopically (except for the presence of a hectocotylus), they show sexual differences in the morphometric structure of the cuttlebone.

The present results are comparable to those obtained by Almonacid-Rioseco et al. (2009) for *S. officinalis*, which also showed a differentiation between sexes for the same measurements of the cuttlebone (FW, CW, ECW). These results reveal that sexes have a relatively different growth pattern. Specifically, males exhibit faster growth in length to reach larger sizes, while females exhibit greater growth in the cuttlebone width in preparation for reproduction (Fig. 3a, b, c). Vasconcelos et al. (2018) also describe this sexual dimorphism for *S. officinalis* in the Algarve coast (southern Portugal). On the other hand, the gonadosomatic index allowed comparison of gonadal development with the cuttlebone measurements that presented differences between sexes, revealing that the faster growth in width of female cuttlebone is related to an increase in gonadal mass. Accordingly, this relationship can be interpreted as an adaptation of the female body to the gonadal development, which always exhibits increased occupation compared with the male gonad. In this sense, Akyol et al. (2011) reported that the total number of oocytes produced by *S. officinalis* varied from 49 to 828 with an average of 261±27 per female, whereas Laptikhovsky et al. (2003) reported a range of large yolk oocytes between 130 and 839. This body adaptation hypothesis was previously proposed by Hewitt & Stait (1988) and Sainz (1990), who mentioned that these changes in *S. officinalis* were due to phylogenetic features where females adapted to their reproductive stage by developing a wider cuttlebone than males. The volume of oocytes could justify a larger capacity of the female paleal cavity and therefore the adaptation of female cuttlebone to provide the required support and space.

Due to the lack of immature individuals, we are not able to determine whether the differentiation between sexes based on cuttlebone morphometrics is only possible when analysing ripe individuals prior to spawning (i.e., when the cuttlebone morphology adapts to lodge the voluminous gonad), which would decrease the usefulness of this "tool" for gender identification in juvenile’s stages.

CAPÍTULO 5

Fotografía portada Capítulo 5: *Sepia officinalis,* Richard vía Flickr [CC BY-ND 2.0]

Capítulo 5

DIETA Y ESTRATEGIA ALIMENTARIA

Feeding ecology of the African cuttlefish *Sepia bertheloti* (Cephalopoda: Sepiidae) in western Africa.

Airam Guerra-Marrero, Ana Espino-Ruano, Lorena Couce-Montero, David Jiménez-Alvarado
and José J. Castro.

5.1. Introduction

The Atlantic coast of North and West–Central Africa hosts one of the world’s most productive areas, the Canary Current Large Marine Ecosystem (CCLME). Due to encompassing several upwelling systems in Morocco, West Sahara, Mauritania, and Senegal that support a high diversity and abundance of marine species, the CCLME is critical for fisheries, particularly for pelagic species (Bas et al., 1995; Valdés & Déniz-González, 2015; Rocha & Cheikh-Abdellahi, 2015; Failler, 2020; Luna et al., 2021). Fishing in the area indeed represents an important economic activity from Morocco to the Gulf of Guinea, whether performed with artisanal boats or large industrial fleets. Valdes & Déniz-Gonzalez (2015) have highlighted the importance of such fishing grounds in the CCLME, given its annual estimated production of 2–3 million tons and the most important cephalopod fishery in the Atlantic Ocean. However, according to Gascuel et al. (2007), overfishing in an important part of the area has reduced biological productivity. In the case of Mauritania’s continental shelf, for example, the demersal biomass has shrunk by 75% in the past 25 years, and the trophic structure has been significantly altered.

In 2019, a total of 158,494 t of cephalopods were recorded to have been caught in Area 34 of the Food and Agriculture Organization of the United Nations (FAO, 2021)—56.08% was octopi, 16.87% was squids, and 27.05% was cuttlefish—although the actual catches were likely far higher due to unreported catches and illegal fishing activities described in the area (Belhabib et al., 2012). Those underestimated official catches, the lack of transparency in extractive activities, and the lack of biological information about the exploited species make Africa’s Atlantic coast an endangered system, one where overexploitation has been reported for years (Balguerias et al., 2000; Alder & Sumaila, 2004; Gascuel et al., 2007).

Although statistics indicate a decrease in cephalopod catches since 1980 (Balguerias et al., 2000, Gascuel et al., 2007), the oceanographic conditions in West Africa show high productivity thanks to the combination of upwelling systems (Bas et al., 1995; Aristegui et al., 2009; Pelegrí et al., 2017). According to Bas et al. (1995), such upwelling productivity systems are rather heterogeneous along the Atlantic coast of North and West–Central Africa, where the greatest upwelling activity, given its intensity and permanence, occurs in the area around Mauritania. By contrast, the northern zone (i.e. from the Gulf of Cádiz to Mauritania) and the southern zone (i.e. from Mauritania to Guinea-Bissau) are characterised by weaker seasonal upwellings (Bas et al., 1995; Aristegui et al., 2009; Pelegrí et al., 2017). Many studies have shown that those primary characteristics of production generate large exploitable stocks (Cury et al., 2000; Rocha & Cheikh-Abdellahi, 2015), particularly of small pelagic species (Bas et al., 1995; Gascuel et al., 2007). Even so, understanding the ecology of exploited species is a less studied subject, one that typically focuses on target species with high economic yield. The productivity and variability of those systems amid uncontrolled extractive activity induces changes in the population dynamics of such species, not only in their growth and reproduction but also in the system's ecological role (Gascuel et al., 2007). All of that productivity makes the trophic connectivity of ecosystems more complex than in other less productive or oligotrophic systems, where an increase or reduction of species in each area can significantly impact potential prey communities and alter trophic relationships (Gascuel et al., 2007; Butler et al., 2010). Concerning the marine trophic structure of Mauritanian waters in particular, Gascuel et al. (2007) have reported its significant modification and a declining mean trophic level (TL) of catchable biomass, from more than 3.7 to less than 3.5 since 1980.

Demonstrating opportunistic predatory behaviour, cephalopods feed primarily on crustaceans, fish, and other cephalopods (Rocha et al., 1994; Rodhouse & Nigmatullin, 1996). In studies on cephalopods' dietary changes (Castro & Guerra, 1990; Markaida & Sosa-Nishizaki, 2003), juveniles have been found to feed on crustaceans but to modify their diet to fish and other cephalopods as they grow (Guerra-Marrero et al., 2020). In West Africa, however, studies on cephalopods' feeding behaviours have been scarce (Hernández-García, 1992, 2003; Villanueva, 1993; Piatkowski et al., 1998; Smith, 2003; Idrissi et al., 2016, among others) and usually focused on octopus and squid. Regarding *Sepia* species, by contrast, only a few publications describe the feeding of *Sepia officinalis* and *Sepia australis*, the two most commercial species in the genus (Mqoqi et al., 2007; Mzaki et al., 2017; Oluboba & Lawal-Are, 2022).

In response, in our study we focused on gathering information about the feeding ecology of the African cuttlefish, *Sepia bertheloti*. Despite being distributed from northern Morocco to Guinea-Bissau, the species has no separate statistics regarding catches and landings because it is marketed with other cuttlefish such as *Sepia hierredda* (Jouffre & Inejih, 2005) and *Sepia* spp. (42.514 t for 2019; FAO, 2021). Per Jereb & Roper's (2005) estimate, *S. bertheloti* represent between 11 and 35% of the catches of both species.

5.2. Material and Methods

Biological samples of *Sepia bertheloti* were collected from commercial captures landed in Morocco and Guinea-Bissau (i.e. North and West–Central Africa) and caught with bottom trawl nets between July 2018 and January 2020. Samples were not available every month, sometimes due to the seasonality of the fishery or the biological stoppages of the fleet. Above and beyond that, because its capture is obtained as a by-catch of *Sepia officinalis* and because it is not always separated well in commercial captures, *S. bertheloti* is quite difficult to obtain. Data sampling is summarised in Table I.

After being caught, all samples were immediately frozen for further analysis. The cuttlefish were sorted, and *S. bertheloti* individuals were identified taxonomically from the key developed by Nesis (1987). In the laboratory, the sex of the samples was determined, and the dorsal mantle length (DML) and Total wet weight were recorded to the nearest 1 mm and 0.01 g, respectively. Next, digestive tracts were extracted and fixed in 70% ethyl alcohol for laboratory analysis. In all analyses, the normality and homoscedasticity of the data were analysed; to that end, differences in the distribution of length according to areas studied were compared using an analysis of variance (ANOVA).

Table I. Number of stomachs analysed as well as empty stomachs of *Sepia bertheloti* in two areas of West Africa from July 2018 to January 2020.

Date	**Morocco**		**Guinea-Bissau**	
	Stomachs	**Empty**	**Stomachs**	**Empty**
July 2018	234	83		
August 2018	43	24		
September 2018	44	9		
July 2019			42	17
August 2019			36	18
September 2019			97	43
October 2019			78	35
November 2019			157	86
December 2019			155	72
January 2020	168	90	60	16
Total	**489**	**206**	**625**	**287**

To establish the number of stomachs suitable for diet characterisation, we created a randomised cumulative prey curve using the vegan package (Oksanen et al., 2010) based on identified preys. The vegan package allowed calculating the cumulative curve (±2 *SD*) by plotting 500 random permutations of the data. The number of stomachs needed to describe the diet was determined when the last four points approached the asymptote (Hurtubia, 1973), and the trend line did not differ significantly (Bizarro et al., 2007).

All stomach contents were weighed to the nearest 0.0001 g. Each item in the stomach contents was analysed with an Olympus SZ-40 stereoscopic microscope, and prey items were identified to the lowest taxonomic level possible. Prey items were identified using species identification guides by Estrada & Genicio (1970), Newell & Newell (1970), Manning & Holthuis (1981), Zariquiey-Alvarez (1986), and Burukovskii (1992) to identify Decapoda crustaceans; guides by Härkönen (1986), Campana (2004), Tuset et al. (2008), and Lombarte et al. (2006) to identify sagittal otoliths in fish; Clarke's (1986) guide to identify cephalopod beaks; and Hernández et al. (2011) guide to classify gastropods, bivalves, and other molluscs.

For each prey taxa, the frequency of occurrence (%FO), numerical frequency (%N), and weight percentage (%W) of the prey items were calculated by following Hyslop's (1980) approach. To pinpoint significant differences, we compared the frequency at which the prey categories occurred between sexes using the distribution of χ^2 (observed vs. expected).

Prey abundance, Brillouin's richness and diversity indices, and Berger–Parker dominance indices were also calculated using the vegan package (Oksanen et al., 2010), and an ANOVA was performed to identify differences between the areas under study (i.e. Morocco and Guinea-Bissau).

To characterise the feeding strategy of *S. bertheloti* in the two areas, we used the SPAA package (Zhang, 2016) to calculate the standardised Levin's index (B_{sta}):

$$Bsta = (B - 1)/(n - 1)$$

in which *B* is Levin's index and *n* the number of prey species. B_{sta} values ranged from 0 (minimum niche breadth and maximum selectivity: specialist predator) and 1 (maximum niche breadth and minimum selectivity: generalist predator). To complement that analysis, the diagram described by Amundsen et al. (1996) was made, which proposes a modification of Costello's graph (1990) to provide information on the importance of each prey species after evaluating a two-dimensional plot of prey-specific abundance (%Pi) against %FO. %Pi was calculated with the following formula:

$$\%P_i = \frac{\sum S_i}{\sum St_i} \, x \, 100$$

in which S_i is the weight of prey *i* and St_i the weight of all prey in the stomachs containing prey *i*.

The results of the stomach content analysis were grouped into six categories of prey—crustaceans, cephalopods, fish, bivalves, gastropods, and echinoderms—to calculate the TL of *S. bertheloti* in each area under study. The analysis was performed only with data obtained in our study, namely because no other diet studies have previously been performed for the species.

To calculate the TL, we needed to know the proportion of each category of prey (P_j) in the diet (Cortés, 1999), calculated as:

$$P_j = \frac{\sum_{i=1}^{n} P_{ij} N_i}{\sum_{j=1}^{6} \left(\sum_{i=1}^{n} P_{ij} N_i \right)}$$

in which P_{ij} is the proportion of category of prey *j* in study *i*, N_i is the number of stomachs with food used to calculate P_{ij} in study *i*, *n* is the number of studies, *j* is the number of categories of prey (6), and $\Sigma P_j = 1$. In our study, P_{ij} values were calculated using %FO.

Meanwhile, TL was calculated by following Cortés's (1999) formula:

$$TL = 1 + \left(\sum_{j=1}^{5} P_j \ x \ TL_j \right)$$

in which TL_j is the TL of each category of prey *j*. According to Cortés (1999), the TL of each category of prey was obtained from the literature, especially from Pauly & Christensen (1995), Pauly et al. (1998), and Hobson & Welch (1192). The standard values for TL used are shown in Table II.

Table II. Standardised trophic level (TL) by category of prey (modified from Cortés, 1999).

Code	Category of prey	TL
FISH	Teleost fishes	3.24
CEPH	Cephalopods (e.g. squids and octopi)	3.20
MOL	Molluscs, excluding cephalopods	2.10
CR	Decapod crustaceans (e.g. shrimp, crabs, prawns, and lobsters)	2.52
INV	Other invertebrates (i.e. all invertebrates except molluscs, crustaceans, and zooplankton)	2.50

All statistical analyses were performed in R software (version 4.2.1, R Development Core Team, 2022), and the results were considered significant if $p < .05$, very significant if $p < .01$ and highly significant if $p < .001$, as described by Markaida & Sosa-Nishizaki (2003) for the stomach contents of jumbo squid.

5.3. Results

A total of 1114 individuals of *Sepia bertheloti* were analysed: 549 from Morocco and 565 from Guinea-Bissau (Table I). Males in both areas were more abundant with a sex ratio of 1:0.27 and 1:0.45 for Morocco (DML range = 6.0–13.8 cm) and Guinea-Bissau (DML range = 6.0–17.6 cm), respectively. DML showed significant differences between the sexes and areas (ANOVA, $p < .001$), including that males were larger than females in both areas, and individuals from Guinea-Bissau were larger than those from Morocco (Fig. 1). Although all stomachs were considered in the analysis, only 57.87% and 54.08% of African cuttlefish from Morocco and Guinea-Bissau, respectively, had stomach contents (Table I). The absence of juveniles in the catches (i.e. DML<60 mm) did not allow assessing ontogenetic changes of the species or diet according to length, which could have helped to prevent erroneous conclusions due to the sample size.

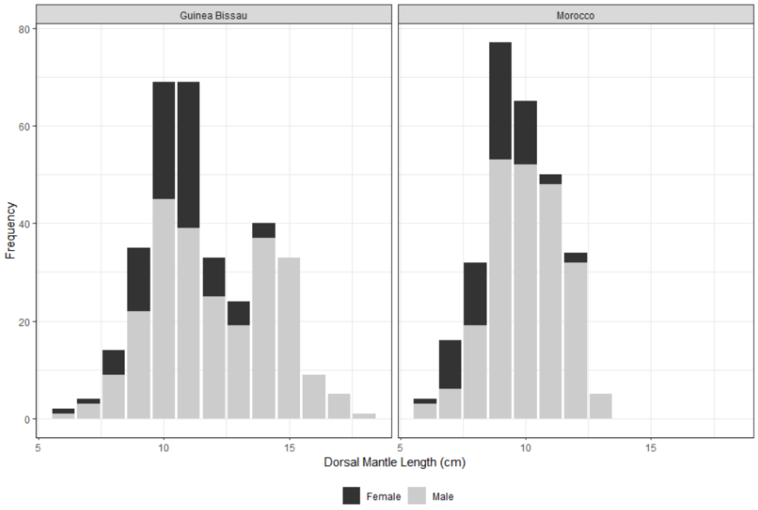

Figure 1. Size–frequency distribution of female and male *Sepia bertheloti* in each studied area.

The cumulative prey curves revealed that the number of individuals subjected to stomach content analysis was adequate for characterising the African cuttlefish diet for the accumulation prey curve representing Morocco (*n* = 283, *p* = .31) and the curve representing Guinea-Bissau (*n* = 338, *p* = .22), as shown in Fig. 2.

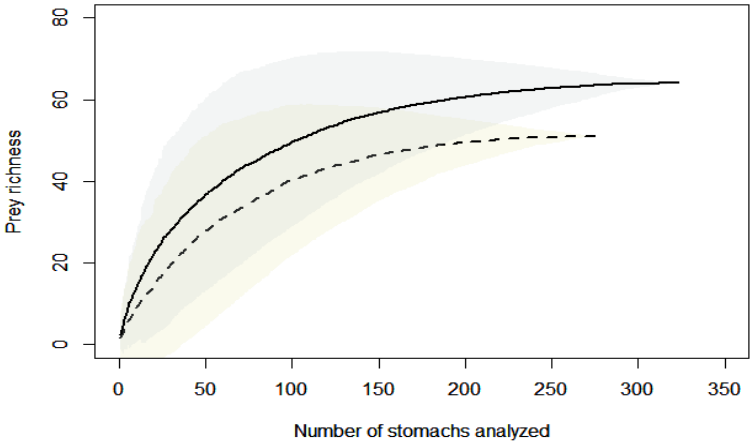

Figure 2. Cumulative prey curve of the *Sepia bertheloti* stomachs analysed from Guinea-Bissau (dashed line) and Morocco (continuous line).

Shown in Table III, 76 prey items were recorded from the stomach content analysis for both areas: 65 from Morocco and 49 from Guinea-Bissau. The prey species identified were categorised as bivalves, cephalopods, echinoderms, gastropods, crustaceans, or fish. No significant differences surfaced between the areas studied concerning bivalves (χ^2 = 1.41, *p* = .23), cephalopods (χ^2 = 3.43, *p* = .06), echinoderms (χ^2 = 0.35, *p* = .55), and gastropods (χ^2 = 3.09, *p* = .07), whereas crustaceans (χ^2 = 5.96, *p* = .01) and fish (χ^2 = 4.97, *p* = .026) did show significant differences. They were also more representative in the diet of individuals from Morocco.

Table III. Diet composition of the African cuttlefish *Sepia bertheloti* from Morocco and Guinea-Bissau. %FO = frequency of occurrence in percentage, %N = numerical frequency in percentage, %W = weight percentage.

Prey categories	**Morocco**			**Guinea-Bissau**		
	%FO	**%N**	**%W**	**%FO**	**%N**	**%W**
BIVALVIA	**7,07**	**1,48**	**1,57**	**3,25**	**1,61**	**0,49**
Cardiidae	0,35	0,06	0,02			
Donax sp.	0,71	0,11	0,07			
Moerella sp.	2,83	0,51	0,53	0,29	0,12	0,02
Unidentified bivalvia	3,53	0,63	0,67	2,96	1,36	0,39
Venerupis sp.	1,06	0,17	0,27	0,30	0,12	0,07
CEPHALOPODA	**13,78**	**4,34**	**5,41**	**5,62**	**2,85**	**1,28**
Octopus vulgaris	1,77	0,29	0,24			
Sepia bertheloti	8,13	1,31	1,35	1,18	0,50	0,35
Sepia sp.	2,82	0,46	0,30	0,59	0,25	0,05
Unidentified cephalopods	13,22	2,28	3,52	5,03	2,11	0,88
CRUSTACEA	**96,81**	**78,82**	**63,31**	**65,68**	**82,90**	**70,71**
Amphipoda						
Orchestia sp.	8,12	13,47	3,40			
Rhachotropis sp.	1,06	0,17	0,12			
Gammarus spp.	30,87	38,64	7,89	6,50	32,96	2,46
Isopoda	6,36	1,83	0,57	2,37	3,59	0,89
Decapoda						
Bathynectes maravigna	2,12	0,34	0,97			
Cryptosoma cristatum	1,06	0,17	0,45	0,30	0,12	0,12
Unidentified decapods	21,55	4,05	6,54	5,03	2,97	3,51
Euchirograpsus liguricus	0,35	0,06	0,02			
Inachus nanus	2,47	0,40	0,36			
Maja sp.	0,71	0,17	0,27			
Munida sp.				0,89	0,37	0,86
Oplophoridae				0,30	0,12	0,02
Paguridae	0,35	0,06	0,15	1,18	0,50	0,28
Palinuridae	1,77	0,57	0,26	0,30	0,12	0,64
Pandalidae	0,35	0,06	0,89	1,48	0,62	2,79
Penaeidae	0,71	0,11	0,25	0,89	0,62	0,17
Polycheles typhlops	3,53	0,57	1,01	0,30	0,12	0,08

Continued.						
Porcellanidae	0,71	0,11	0,23	1,18	0,50	1,87
Portunidae	4,24	0,68	1,24			
Thranita sp.	6,00	1,03	2,12	0,30	0,12	0,77
Richardina spinicincta	0,71	0,11	0,47			
Scyllaridae	0,35	0,06	0,09	0,59	0,25	0,17
Upogebia pusilla	2,47	0,40	0,18			
Unidentified decapods	21,55	4,05	6,54	5,03	2,97	3,51
Unidentified crustacea	57,95	11,70	29,29	51,18	36,93	52,57
ECHINODERMATA	**0,35**	**0,11**	**0,13**	**0,00**	**0,00**	**0,00**
Ophiura sp.	0,35	0,06	0,07			
Unidentified Echinodermata	0,35	0,06	0,07			
GASTROPODA	**9,54**	**2,68**	**1,50**	**3,25**	**1,86**	**0,35**
Nayticidae	0,71	0,11	0,17			
Tona sp.	6,36	1,03	0,87	0,59	0,25	0,08
Unidentified Gastropoda	6,71	1,54	0,46	2,96	1,61	0,27
FISHES	**44,81**	**16,61**	**33,49**	**26,04**	**13,75**	**28,01**
Argyropelecus hemigymnus				0,30	0,12	0,10
Arnoglossus imperialis				0,30	0,12	0,55
Arnoglossus sp.	0,71	0,11	1,80	1,48	0,62	1,41
Bathysolea profundicola	1,06	0,17	0,13	0,30	0,12	0,07
Bothus podas	1,77	0,29	0,78	1,48	0,62	2,14
Derichthys serpentinus	0,35	0,11	0,03			
Dicoglossa cuneata	2,12	0,63	0,48	0,30	0,12	0,85
Dicologlosa hexopthalma				0,59	0,25	0,19
Gobius cruentatus	0,35	0,06	0,02			
Gobius sp.	0,35	0,06	0,37	0,89	0,37	0,91
Gymnothorax maderensis					0,25	0,61
Halobatrachus sp.	0,71	0,11	2,06	0,30	0,12	0,02
Hippocampus hippocampus	0,35	0,06	0,71			
Lepidorhombus boscii	0,35	0,17	0,08	0,59	0,25	1,15
Lesueurigobius sanzi	0,71	0,11	0,04			
Lesueurigobius sp.	0,35	0,06	0,08			
Melanostigma atlanticum	3,89	0,80	0,91	0,59	0,25	0,31
Microchirus azevia				0,59	0,25	0,22

Continued.						
Microchirus boscanion	4,59	1,48	1,88	0,89	0,50	0,57
Microchirus ocellatus	6,71	1,14	0,96	0,89	0,37	0,13
Monochirus hispidus	1,41	0,23	0,72			
Myctophum sp.	1,07	0,17	0,39	1,18	0,50	0,74
Parapistipoma octolineatum	0,35	0,06	0,71			
Pegusa sp.	0,35	0,06	0,52	0,89	0,37	1,29
Scorpaena sp.	0,70	0,11	1,30	0,30	0,12	0,36
Serranus cabrilla	1,77	0,29	2,14	1,18	0,50	0,98
Serranus sp.	4,59	0,74	0,74	1,48	0,62	0,97
Solea solea	0,35	0,06	0,05	0,30	0,12	0,22
Stomias boa				0,30	0,12	0,15
Sygnathus sp.	1,77	0,29	0,10			
Sygnathus typhle	0,71	0,11	0,04			
Symphurus lugulatus				0,30	0,12	0,58
Symphurus nigrescens	1,06	0,63	0,10			
Synodus saurus	0,35	0,06	0,46			
Trachurus sp.				0,30	0,12	0,29
Trisopterus sp.	0,35	0,06	0,52	0,89	0,37	1,29
Unidentified fishes	38,86	8,39	15,37	14,79	6,44	11,90
Unidentified organic matter			**1,13**			**2,67**

Although no significant differences emerged in %FO of all categories of prey and sexes (i.e. chi-square observed vs. expected, $p > .09$), abundance of prey showed significant differences between areas (ANOVA: $F = 21.46$, $p < .001$). The mean number of prey species per stomach was 3.19 for individuals from Morocco and 1.43 for ones from Guinea-Bissau (Table IV). Along similar lines, richness (ANOVA: $F = 79.3$, $p < .001$) and diversity (ANOVA: $F = 86.99$, $p < .001$) differed between the areas, although no differences emerged in dominant categories of prey (ANOVA: $F = 0.15$, $p = .69$), as shown in Table IV.

Table IV. Prey abundance, richness, diversity, and dominance of prey taxa in the stomach contents of *Sepia bertheloti* in each area studied.

	Morocco		Guinea-Bissau	
	Mean	**SD**	**Mean**	**SD**
Abundance	3.19	6.48	1.43	3.89
Richness	2.46	1.63	1.44	0.88
Diversity	0.38	0.37	0.13	0.23
Dominance	0.31	0.55	0.23	0.39
Bsta	0.51		0.54	
TL	3.63		3.60	

In the stomach contents of African cuttlefish from Morocco, having one (58.88%) or two (16.27%) prey species dominated, whereas in those from Guinea-Bissau the proportion of individuals with only one prey species was slightly less (33.92%), even though other stomachs from that area far more frequently contained two (19.08%) or three (12.72%) prey items. More than 3 prey items were present in 34.28% and 18.34% of the stomachs from Morocco and Guinea-Bissau, respectively, normally in larger individuals. Fish was the category of prey with the greatest diversity of species—29 from Morocco and 25 from Guinea-Bissau—followed by crustaceans, with 22 and 15 species present in the stomachs of individuals from Morocco and Guinea-Bissau, respectively. Even so, crustaceans were the most abundant category of prey in both areas in terms of weight, followed by fish and cephalopods, whereas bivalves, echinoderms, and gastropods were far less represented. *Sepia* spp. from Morocco fed more on amphipods, which were the most significant kind of prey in terms of weight (%W = 7.89), whereas those from Guinea-Bissau fed more on pandalids (%W = 2.79). Nevertheless, amphipods were the more frequent and numerous types of prey identified in both areas. Species of amphipods could not be established due to their degree of digestion but given their morphological characteristics were primarily classified as *Gammarus* spp., except for *Orchestia* sp. (Tralitridae) and *Rachotropsis* sp. (Eusiridae). At the same time, it should be highlighted that the presence of body parts of conspecifics indicates the cannibalistic behaviour of *S. bertheloti*.

The niche breadth was very wide, and, as shown in Table IV, B_{sta} values of approximately 0.50 confirmed a heterogeneous diet among African cuttlefish in both areas, without any clearly specialist or generalist feeding behaviour. However, reflecting Amundsen et al.'s (1996) results, prey-specific abundance diagrams (Fig. 3) of *S. bertheloti* from Morocco and Guinea-Bissau show a heterogeneous diet with a generalist feeding pattern, with a varying degree of specialisation in relation to different prey species. Those diagrams suggest that although *S. bertheloti* have no dominant prey, crustacean decapods and fish are more dominant than all other categories of prey. In both areas, we observed a lot of occasional prey species predated by a few individuals (Fig. 3, upper-left panel), including *Euchirograpsus liguricus* and *Polycheles typhlops* (Fig. 3a) as well as penaids (Fig. 3b), which indicates a high degree of specialisation. At the same time, we also observed unimportant prey species (Fig. 3, bottom-left panel) with low specific abundance and occurrence in the stomachs of individuals from both areas.

Although a greater diversity and richness of species was observed among cuttlefish from Morocco, TL analysis showed that *S. bertheloti* from both Morocco and Guinea-Bissau are secondary consumers ($TL_k < 4$, Table IV) with great similarity in the %FO of prey items, among which crustaceans and fish dominated in the stomach contents.

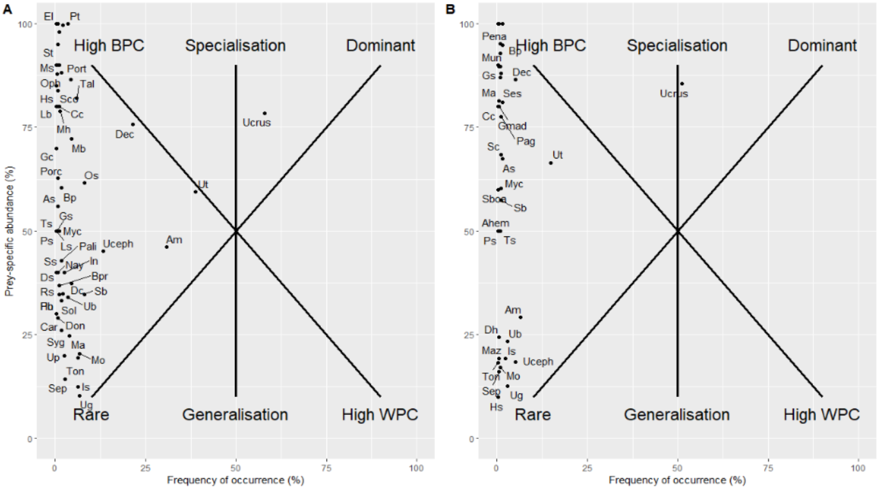

Figure 3. Prey-specific abundance plotted against the frequency of occurrence in the stomachs of individuals analysed in (**A**) Morocco and (**B**) Guinea-Bissau.

5.4. DISCUSSION

Despite many studies conducted to understand the biology and ecology of cephalopods (e.g. Clarke, 1966; Boyle & Rodhouse, 2008; Piatkowski et al., 2003), particularly their trophic spectrum as a means to know their function within the trophic web (e.g. Summers, 1983; Castro & Guerra, 1990; Rosero et al., 1996; Pinczon du Sel et al., 2000; Markaida & Sosa-Nishizaki, 2003; Coll et al., 2013; Hernández-Urcera et al., 2014; Hoving & Robinson, 2016; Villanueva et al., 2017), the Sepiidae family has rarely been studied and, in those rare cases, typically with a focus on *Sepia officinalis (*Mzaki et al., 2017; Oluboba & Lawal-Are, 2022). Our study was the first to seek to elucidate the feeding ecology of *Sepia bertheloti*, which, despite being a species of potential fishing interest, has rarely been examined in terms of its biology and ecology.

Males of the African cuttlefish predominated in the catches that we assessed and had a higher DML than females. That characteristic of sexual dimorphism has also been observed for other species such as *Sepia latimanus* (Dan et al., 2012), *S. koilados, S. rhoda*, and *S. subplana.* Even so, it is not particular of the Sepiidae family, within which Jereb & Roper (2005) have described the condition for most cuttlefish species (i.e. *S. acuminata*, *S. australis*, *S. bidhaia*, *S. braggi*, *S. elegans*, *S. filibranchia*, *S. grahami*, *S. hedley*, *S. latimanus*, *S. limata*, *S. mestus*, *S. orbignyana*, *S. plana*, *S. senta*, *S. smithi*, *S. sulcata*, *Sepiella inermis*, and *S. weberi*). However, in all of those cases, females were larger than males.

Sepia bertheloti from the Atlantic coast of North and West–Central Africa showed a similar diet based on six categories of prey categories: fish, cephalopods, bivalves, gastropods, echinoderms, and crustaceans, particularly decapods. The high relative importance of crustacean decapods in the diet of *S. bertheloti* has been observed in other species of the Sepiidae family (Castro & Guerra, 1990; Pinczon du Sel et al., 2000; Mzaki et al., 2017), for which fish and cephalopods also have dietary importance. Nevertheless, the analysis of stomach contents revealed that amphipods were the most common prey, one that represented more than 30 %N of the diet of the cuttlefish on Africa’s Atlantic coast. Pinczon du Sel et al. (2000) have also highlighted the importance of amphipods in the diet of *S. officinalis*, considering that they represented 30% of the prey items found in its stomach contents. However, amphipods become less important as cuttlefish increase in size and eventually become substituted for crustacean decapods and fish (Pinczon du Sel et al., 2000).

The marked presence of amphipods in the diet of Sepiidae spp. may be due to the strictly benthic habit of the Sepiidae family. In addition, the nutritional requirement of gammarids is greater than other amphipods, which could be caprellids. That nutritional effect was described by Baeza-Rojano et al. (2010) for the diet of *S. officinalis* in captivity, in which the specimens fed with gammarids showed greater growth in weight than individuals fed with caprellids.

Cannibalism is a common behaviour among cephalopods that has been reported on many occasions (Markaida & Sosa-Nishizaki, 2003; Hernández-Urcera et al., 2014; Hoving & Robinson, 2016). Such behaviour is associated with environmental variations, population density, the availability of food, and body size, among other factors (Villanueva et al., 2017). In our study, we documented such cannibalistic behaviour among *S. bertheloti*; however, as Markaida & Sosa-Nishizaki (2003) have indicated, we cannot rule out that the cannibalism observed was motivated and produced once in the fishing gear (i.e. bottom trawl), because the *Sepia* spp. Preyed upon were fresh and in a very low degree of digestion.

Differences in the abundance, richness, and diversity of species between the areas studied were expected due to different oceanographic conditions, such that Morocco is influenced by continuous upwelling (i.e. weak from winter to spring and more intense between summer and autumn, Aristegui et al, 2009), while Guinea-Bissau plays host to seasonal upwelling between winter and spring (Arístegui et al., 2009). High productivity in Guinea-Bissau also needs to be taken into account, which is additionally conditioned by the contribution of organic matter from rivers and lagoons (Fransen, 2014).

The African cuttlefish is an euryphagic feeder (standardised Levin's index, B_{sta} ~0.5), and although Amundsen's graph makes relevant the heterogeneity of its diet, even showing prey species that could define them as specialists, the high diversity of species and the abundance of sporadic prey species (with low %FO) characterise it as opportunistic species, with a wide and varied feeding strategy. That feeding strategy is similar to the one reported by Neves et al. (2009) for *S. officinalis*, with juveniles that have a less generalist feeding strategy than adults, which are more opportunistic and feed primarily on brachyurans and fish. Most likely, the change from a less generalist to a clearly opportunistic feeding strategy as the cuttlefish grows is simply a matter of improved hunting or predation skills; better motor skills make it possible to access other prey and/or habitats, while experience increases efficiency in capturing them.

According to Stergiou & Karpouzi's (2002) classification of Mediterranean fishes, *S. bertheloti* is an omnivorous feeder with a preference for animal (TL = 2.9–3.7) and feeds on a variety of prey, including fish, crustaceans, and cephalopods. However, according to our results, the African cuttlefish can be classified as an entirely carnivorous species and the possibility of its herbivory discarded, given the great predominance of amphipods in their diet, with very low TLs that would include it in the category of omnivores. Moreover, *S. bertheloti* individuals from the Atlantic coast North and West–Central Africa showed a TL slightly higher than that reported by Cortés (1999) for cuttlefish, thereby characterising them as secondary consumers.

CAPÍTULO 6

Fotografía portada Capítulo 6: Cuttlefish *Sepia officinalis,* Tenerife, Marine invertebrates of te Canary Islands. BIOSPHOTO/ Alamy Stock Photo.

Capítulo 6

CONCLUSIONES GENERALES

1.Tanto en Marruecos como en Guinea-Bissau los machos de *Sepia bertheloti* (sepia africana) predominaron frente a las hembras, con una proporción de sexos de 1:0,27 y 1:0,45, respectivamente. Las hembras mostraron un cuerpo más ancho, mientras que los machos fueron más largos.

2. El presente trabajo valida por primera vez la deposición diaria de incrementos de crecimiento en pico (o mandíbula) de *Sepia officinalis*, utilizando la zona del rostro del pico inferior, en individuos cultivados a 18 y 21ºC hasta los 31 días de vida.

3. La longevidad obtenida para *Sepia bertheloti*, a través de la estimación de edades en el pico, alcanzó los 14 meses (419 días para los individuos procedentes de Marruecos y 433 días para los de Guinea-Bissau).

4. Los machos presentaron una longevidad mayor que las hembras, que mostraron esperanza de vida menor, entre los 9 y 11 meses. La hembra más longeva de Marruecos alcanzó los 267 días, mientras que la más longeva de Guinea-Bissau llegó a 316 días de edad.

5. El crecimiento de S. *bertheloti* fue alométrico negativo, siguiendo un modelo exponencial. Este modelo fue el que mejor describió el crecimiento de las hembras en ambas áreas. En el caso de los machos el modelo de Schnute se adaptó mejor a la tendencia de crecimiento en los machos de Marruecos y el de Von Bertalanffy a la de los machos de Guinea-Bissau.

6. Las ratios de crecimiento también fueron diferentes entre áreas y sexos. En ambas zonas los machos mostraron un patrón de crecimiento instantáneo relativo mayor que las hembras. La población de Guinea-Bissau presentó una mayor ratio de crecimiento instantáneo relativo que la de Marruecos.

7. Se observó que en Guinea-Bissau los individuos nacidos en primavera y verano eran más pequeños que los nacidos en el periodo de otoño a invierno. En Marruecos no se observaron diferencias de talla en relación con la época de nacimiento.

8. Las hembras mostraron un sepión más ancho mientras que el de los machos fue más largo. Estas diferencias parecen relacionadas con adaptaciones para soportar gónadas más grandes en el caso de las hembras, mientras que los machos crecen más rápido a lo largo.

9. El sepión mostró ser una estructura útil para estimar biomasas, permitiendo conocer la Longitud Dorsal del Manto a partir de relaciones morfométricas y, consecuentemente, también el peso del animal.

10. La curva acumulativa de presas demostró que los estómagos analizados fueron suficientes para definir la dieta de la sepia africana en ambas áreas de estudio, con un total de 76 taxones de presas determinados para ambas áreas (65 para Marruecos y 49 para Guinea-Bissau).

11. Las categorías de presas identificadas fueron clasificadas en bivalvos, cefalópodos, equinodermos, gasterópodos, crustáceos y peces. Solo se encontraron diferencias significativas entre áreas con los crustáceos y los peces, ya que fueron mas representativos en la dieta de los ejemplares procedentes de Marruecos.

12. Aunque en términos de frecuencia de ocurrencia de las presas no se encontraron diferencias asociadas al sexo, la abundancia de las presas por estómagos si mostró diferencias entre ambos sexos. El número medio de presas en los estómagos de ejemplares de Marruecos fue de 3,19 mientras que en Guinea-Bissau este fue de 1,43.

13. La riqueza y diversidad de especies de presas en los contenidos estomacales también fue diferente entre áreas, presentando los individuos procedentes de Marruecos valores más altos. En cambio, la dominancia de las categorías de presas fue similar en ambas áreas de estudio.

14. La población de *Sepia bertheloti* capturada en Marruecos se alimenta principalmente de anfípodos, que fue la presa más importante en peso, mientras que en Guinea-Bissau fueron los pandálidos. Aun así, los anfípodos gammaridos fueron los que se encontraron con mayor frecuencia de ocurrencia y número de las presas identificadas en los estómagos de ambas áreas de estudio.

15. El espectro del nicho trófico confirmó que *Sepia bertheloti* tiene una dieta heterogénea en ambas áreas, sin que exista una clara estrategia generalista o especialista por parte de la especie.

16. Aunque se observó una gran diversidad y riqueza de presas en los contenidos estomacales, *Sepia bertheloti* es una especie omnívora, caracterizada como consumidor segundario, con un nivel trófico estimado de 3.6.

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CONTRIBUCIONES CIENTÍFICAS DURANTE LA TESIS DOCTORAL

Fotografía portada Contribuciones científicas durante la tesis doctoral: Cuttlefish Sepia officinalis swims away at night in defensive movement. Ustica Island, Italy. Jeff Rotman/ Alamy Stock Photo.

La investigación presentada se ha centrado en la ecología de *Sepia bertheloti,* aunque durante el desarrollo de la tesis doctoral se han realizado otras contribuciones relacionadas con las pesquerías del Atlántico centro oriental. Aunque no se relacionan (a excepción del artículo 1, que corresponde con el Capítulo 4 de esta tesis) con el tema principal de la tesis, su desarrollo se ha producido dentro del periodo de desarrollo de ésta, aportando información útil y necesaria para una mejor gestión pesquera de los ecosistemas marinos. Los artículos desarrollados durante el periodo de desarrollo de la tesis doctoral son los 7 que se citan a continuación:

Artículo 1. **Guerra-Marrero, A.**, Jiménez-Alvarado, D., Hernández-García, V., Curbelo-Muñoz, L., & Castro-Hernández, J. J. (2019). Cuttlebone morphometrics and sex identification of *Sepia bertheloti* (d'Orbigny, 1835) from the central-east Atlantic. *Helgoland Marine Research*, *73*(1), 1-7.

Artículo 2. **Guerra-Marrero, A.**, Alvarado, D. J., & Hernández, J. J. C. (2019). First Record of Exotic Fish *Canthidermis maculata* (Bloch, 1786)(Pisces: Balistidae) in the Canary Islands (Central-East Atlantic). *Thalassas: An International Journal of Marine Sciences*, *35*(2), 675-678.

Artículo 3. Jiménez-Alvarado, D., Sarmiento-Lezcano, A., **Guerra-Marrero, A**., Tuya, F., Santana Del Pino, Á., Sealey, M. J., & Castro, J. J. (2019). Historical photographs of captures of recreational fishers indicate overexploitation of nearshore resources at an oceanic island. *Journal of Fish Biology*, *94*(6), 857-864.

Artículo 4. Guerra-Marrero, A., Hernández-García, V., Sarmiento-Lezcano, A., Jiménez-Alvarado, D., Santana del Pino, A., & Castro, J. J. (2020). Migratory patterns, vertical distributions and diets of

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Artículo 5. Jiménez-Alvarado, D., **Guerra-Marrero, A**., Sarmiento-Lezcano, A., Meyers, E. K., & Castro, J. J. (2020). First assessment of the spearfishing impact in the Canary Islands. *Regional Studies in Marine Science*, *38*, 101385.

Artículo 6. Guerra-Marrero, A., Couce-Montero, L., Jiménez-Alvarado, D., Espino-Ruano, A., Núñez-González, R., Sarmiento-Lezcano, A., Santana del Pino, A. & Castro, J. J. (2021). Preliminary assessment of the impact of Covid-19 Pandemic in the small-scale and recreational fisheries of the Canary Islands. *Marine Policy*, *133*, 104712.

Artículo 7. Xavier, J.C., Golikov, A.V., Queirós, J., Perales-Raya, C., Rosas-Luis, R., Abreu, J., Bello, G., Bustamante, P., Capaz, J.C., Dimkovikj, V.H., Gonzalez, A.F., Guímaro, G., **Guerra-Marrero, A.**, Gomes-Pereira, J.N., Kubodera, T., Laptikhovsky, V., Lefkaditou, E., Lishchenko, F., Luna, A., Liu, B., Pierce, G.J., Pissarra, V., Reveillac, E., Romanov, E., Rosa, R., Roscian, M., Rose-Mann, L., Rouget, I., Sanchez, P., Sanchez-Marquez, A., Seixas, S., Souquet, L., Varela, J., Vidal, E.A. & Cherel, Y. The significance of cephalopod beak as a research tool: an update, *Frontiers in physiology, in press.*

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Helgoland Marine Research

SHORT COMMUNICATION

Open Access

Cuttlebone morphometrics and sex identification of *Sepia bertheloti* (d'Orbigny, 1835) from the central-east Atlantic

Airam Guerra-Marrero*, David Jiménez-Alvarado, Vicente Hernández-García, Leticia Curbelo-Muñoz and José Juan Castro-Hernández

Abstract

Analysis of 322 cuttlebones of *Sepia bertheloti* caught in the waters of the Northwest Africa showed significant differences in growth between males and females. Morphometric analysis revealed a relatively different cuttlebone growth pattern between sexes, with males presenting faster growth in length to reach larger sizes and females displaying greater growth in width. This difference in cuttlebone growth is related to female gonadal development and the subsequent increase of the paleal cavity, providing more support and space to accommodate a higher number of oocytes.

Keywords: African cuttlefish, *Sepia bertheloti*, Cuttlebone, Fragmocone

Introduction

The use of morphometric analysis to define basic characters of growth or development of some structures in cephalopods has been applied from the first contributions of Hoyle [1]. These morphometric analyses, called "Traditional morphometry" [2], compare the linear dimensions of different parts of an organism to define statistical relationships with objectives, such as the taxonomic differentiation of species or intra-specific morphometric differences between sexes. These characteristics have been used for the Sepiidae family, mainly for taxonomic differentiation [3], as well as to analyse morphometric differences within the same species [4].

Within the cephalopods context, the Sepiidae family represents a special interest for studies of hard structures due to the presence of the cuttlebone [5]. The cuttlebone is a complex structure composed of calcium carbonate in its aragonite polymorph mixed with a small amount of organic matter and a complex of β-chitin and protein [6, 7] that provides internal skeletal support and buoyancy to the individual [8]. The cuttlebone shows a structure finely laminated (lamellas). According to Bettencourt and Guerra [9] and Chung and Wang [10], the periodicity of lamellar deposition depends on a combination of physiological and environmental factors (i.e., water temperature).

Sepia bertheloti and *Sepia hierredda* are by-catch species in the bottom trawl fishery targeting *Sepia officinalis* along the coast of the western Sahara [11]; There are no separate statistics of catches/landings for both species because they are caught and marketed together, but *S. bertheloti* represents between 11 and 35% of catches reported for both by-catch species [12]. In addition, probably due to the low commercial interest for *S. bertheloti*, most knowledge on this species has been obtained from the analysis of stomach contents of their natural predators [13, 14] by exploratory fishing to assess the status of the resources [15, 16] or for analyses of metal concentrations [17].

In this context, any contribution to the biology and ecology of *S. bertheloti* would contribute to its conservation and fishery management. The morphologic study of the cuttlebone could provide useful information for the assessment and estimation of mortality, particularly when the individuals are broken and only the cuttlebone

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*Correspondence: airamgmarrero@gmail.com
Instituto Universitario EcoAqua, University of Las Palmas de Gran Canaria, Edf. Ciencias Básicas, Campus de Tafira, Las Palmas de Gran Canaria, 35017 Las Palmas, Spain

appear in the captures [4]. Almonacid-Rioseco [18] indicated that in the small-scale trap fishery off the Canary Islands, approximately 50% of *S. officinalis* caught were represented only by cuttlebones and obviously not reported in the landings. This characteristic makes it necessary to study these hard structures to estimate not only the actual catches by the different fishing gears but also the productivity of the area where the diverse fishing sectors operate.

In this context, the objective of this study was to describe the morphometric relationships of the cuttlebone of *S. bertheloti* and detect eventual differences between males and females caught in the northwest African waters.

Material and methods

A total of 322 individuals (247 males and 74 females) of *S. bertheloti* were obtained from commercial catches landed in the port of Tanger (Morocco) and by the bottom trawl fishery in the central-east Atlantic (CECAF area 34.1.11) from July to September 2018. All samples were immediately frozen after being caught. The specimens of *S. bertheloti* were identified following the key proposed by Nesis [19].

After defrosting, the Dorsal Mantle Length (DML), Total wet Weight (TW) and Gonad Weight (GW) were recorded for each specimen. Moreover, each cuttlebone was removed, weighted and measured according

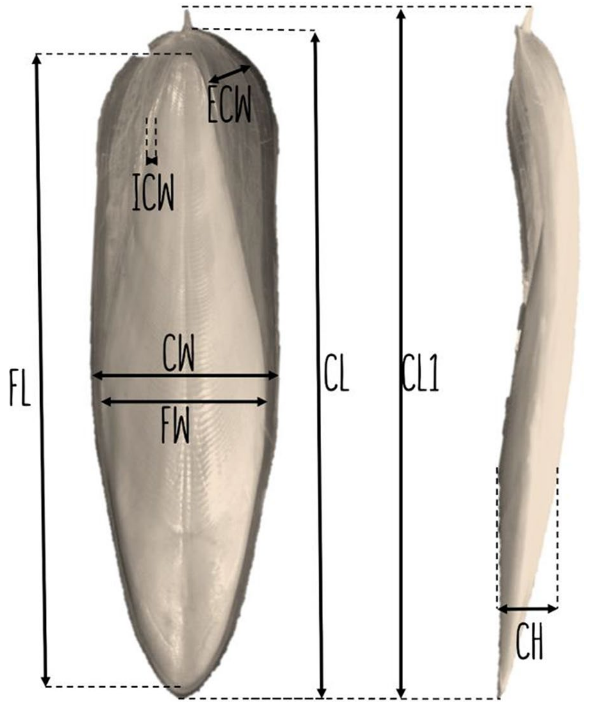

Fig. 1 Morphometric measurements of the cuttlebone of *Sepia bertheloti:* Cuttlebone Length (CL), total Cuttlebone Length (CL1), Cuttlebone Height (CH), Cuttlebone Width (CW), Fragmocone Length (FL), Fragmocone Width (FW), Internal Cuttlebone Width (ICW) and External Cuttlebone Width (ECW)

Table 1 Parameters of the morphometric relationships established between the dorsal mantle length (DML) and cuttlebone measurements in male and female *Sepia bertheloti*

Variable	Sex	a	a standard error	b	b standard error	R	F
FL	F	0.139	0.020	0.933	0.033	0.968	1778.5
	M	0.255	0.050	0.796	0.045	0.939	1315.1
FW	F	0.476	0.059	0.939	0.040	0.954	2538.1
	M	3.321	0.186	0.799	0.024	0.931	1063.3
CW	F	0.211	0.036	1.147	0.054	0.946	2452.1
	M	3.814	0.179	0.794	0.020	0.949	1500.2
ECW	F	0.941	0.126	1.094	0.067	0.913	1266.4
	M	0.402	0.280	1.182	0.030	0.951	1543.1
CL	F	0.915	0.028	0.148	0.018	0.977	1056.9
	M	0.192	0.036	0.856	0.043	0.951	3398.6
CL1	F	0.957	0.082	0.119	0.043	0.880	436.9
	M	0.181	0.061	0.863	0.075	0.888	530.9
CH	F	0.212	0.044	1.614	0.098	0.914	2272.1
	M	0.305	0.025	1.378	0.036	0.949	1472.8
TW	F	0.591	0.094	2.001	0.075	0.972	1716.8
	M	0.326	0.049	2.327	0.176	0.939	4191.5

Parameters of the potential equations between morphometric variables of the cuttlebone and the dorsal mantle Length (DML) of *Sepia bertheloti* females parameters described by Roper and Voss [20]: Cuttlebone Length (CL), Total Cuttlebone Length (CL1), Cuttlebone Height (CH), Cuttlebone Width (CW), Fragmocone Length (FL), Fragmocone Width (FW), Internal Cuttlebone Width (ICW), and External Cuttlebone Width (ECW) (Fig. 1). All length measurements were taken to the nearest millimetre (0.001), and the weights were taken to the nearest centigram (0.01). For each specimen, sex was determined macroscopically, and the maturity stage was assigned based on the scale described by Nigmatullin [21]. Total cuttlebone length (CL1) was not taken in individuals with totally or partially fractured spines due to damages during trawling or handling on board.

To observe differences between the parts of the cuttlebone and the DML, a regression analysis was performed using the linear regression model (Table 1). These functions were performed individually for males (247 individuals) and females (74 individuals). Analysis of covariance (ANCOVA) was performed to detect significant differences between male and female cuttlebones. The first test determined whether the regression slopes for each size class are statistically homogeneous. If the slopes are homogeneous, the second test was performed to verify whether there were differences between sexes in each size class. The mean values of the dependent variables (cuttlebone measurements) for each size class predict differences between sexes. Moreover, the gonadosomatic index ($GSI = GW/TW \times 100$) of the individuals was calculated and plotted against cuttlebone measures to determine eventual differences between sexes. All statistical analyses were performed using R (v 3.4.2) IBM-SPSS Statistics© package.

Results

DML ranged between 63 and 133 mm in males and 67–110 mm in females, whereas TW was 35.5–192.9 g in males and 37.3–103.5 g in females. The morphometric relationships established through regression analyses between DML and cuttlebone measurements in males and females are compiled in Table I. The relationship DML-CL1 displayed the lowest Pearson correlation coefficient (r) for both sexes, which could due to the low number of specimens without broken spines.

ANCOVA revealed that FW ($F = 124.417$, $p < 0.0001$), CW ($F = 449.185$, $p < 0.0001$), and ECW ($F = 148.228$, $p < 0.0001$) were the morphometric measurements with statistically significant differences between sexes. These differences indicated that cuttlebone width, fragmocone width and external width are proportionally larger in females compared with males for a given length class (Figs. 2, 3a–c). Female cuttlebones also presented greater weights than male cuttlebones for the same length class (Fig. 3d).

Fig. 2 Dorsal and ventral views of the cuttlebone of a mature female (DML = 96.0 mm) and male (DML = 95.3 mm)

All individuals were mature and showed a high development of the gonads, being ready to spawn. Significant differences were recorded between the GSI of males and females in relation to FW, CW and ECW (Fig. 4b–d).

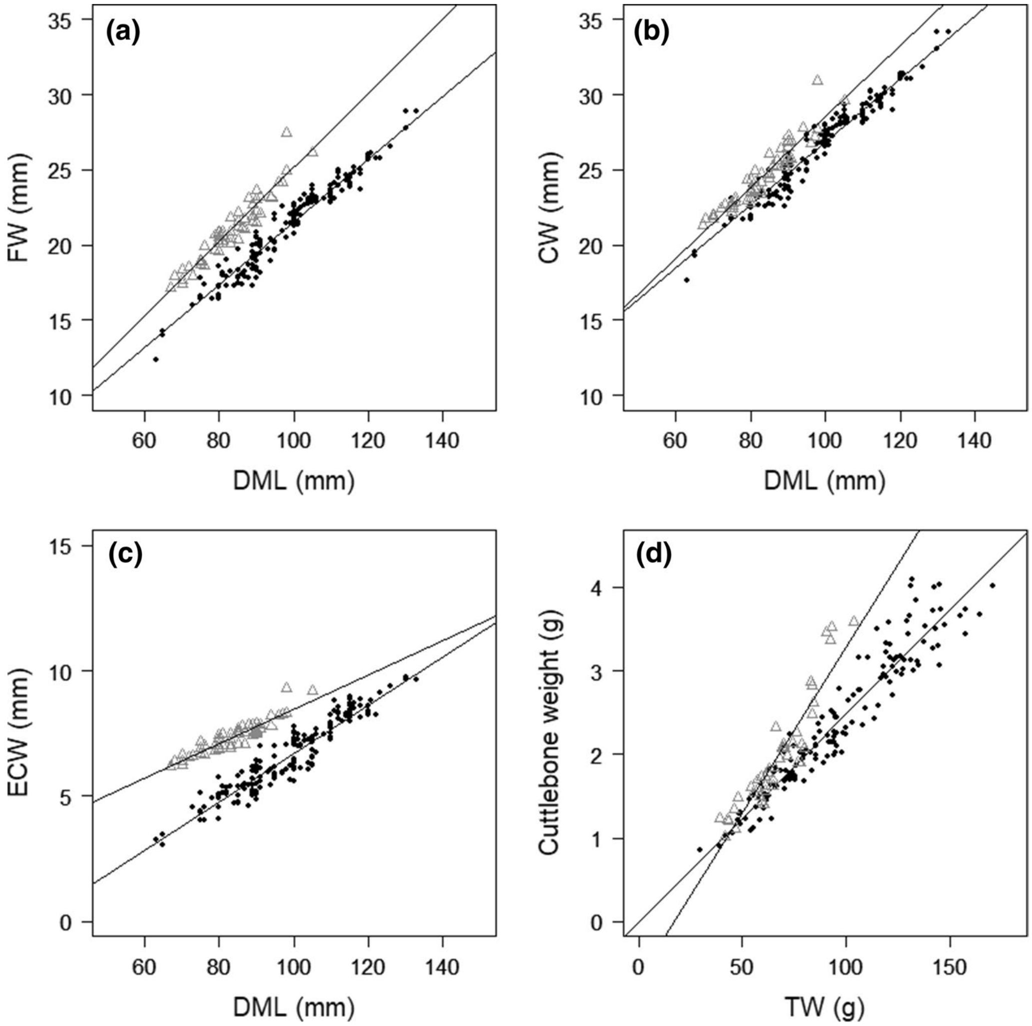

Fig. 3 Morphometric relationships between Dorsal Mantle Length (DML) and **a** Fragmocone Width (FW), **b** Cuttlebone Width (CW), **c** External Cuttlebone Width (ECW) and between **d** Total wet Weight (TW) and Cuttlebone weight (CW) for males (black dots) and females (empty triangles) of *Sepia bertheloti*

Discussion

External sexual dimorphism of *Sepia bertheloti* was mainly based on the fact that males present median arm suckers with greater diameter than marginal suckers and hectocotylus in the left ventral arm. Apart from sexual structures, females internally show the buccal membrane extending ventrally with two spermathecae [12]. However, minimal attention has been paid to cuttlebone as a potential element to differentiate males from females. This study showed that female cuttlebones are significantly wider probably due to the need for a bigger volume of the paleal cavity to increase the capacity to accommodate the gonads. Jereb and Roper [12] remarked that the mantle is relatively wider in females than in males.

Sepia bertheloti males are larger than females [12], which is also noted in *S. latimanus* [9, 22], *S. koilados*, *S. rhoda*, and *S. subplana*. However, in most cuttlefish species (i.e., *S. acuminata*, *S. australis*, *S. bidhaia*, *S. braggi*, *S. elegans*, *S. filibranchia*, *S. grahami*, *S. hedley*, *S. latimanus*, *S. limata*, *S. mestus*, *S. orbignyana*, *S. plana*, *S. senta*, *S. smithi*, *S. sulcata*, *Sepiella inermis*, and *S. weberi*) females growth larger than males [12]. Regarding *S. latimanus*, Dan et al. [22] observed that there were no morphometric differences in the growth pattern of both sexes during the initial life stages, but males become larger than females after 1 year of age. Males and females of *S. bertheloti* caught more northwards than the distributional range given by Jereb and Roper [12] presented a maximum size of 133 and 100 mm DML, respectively,

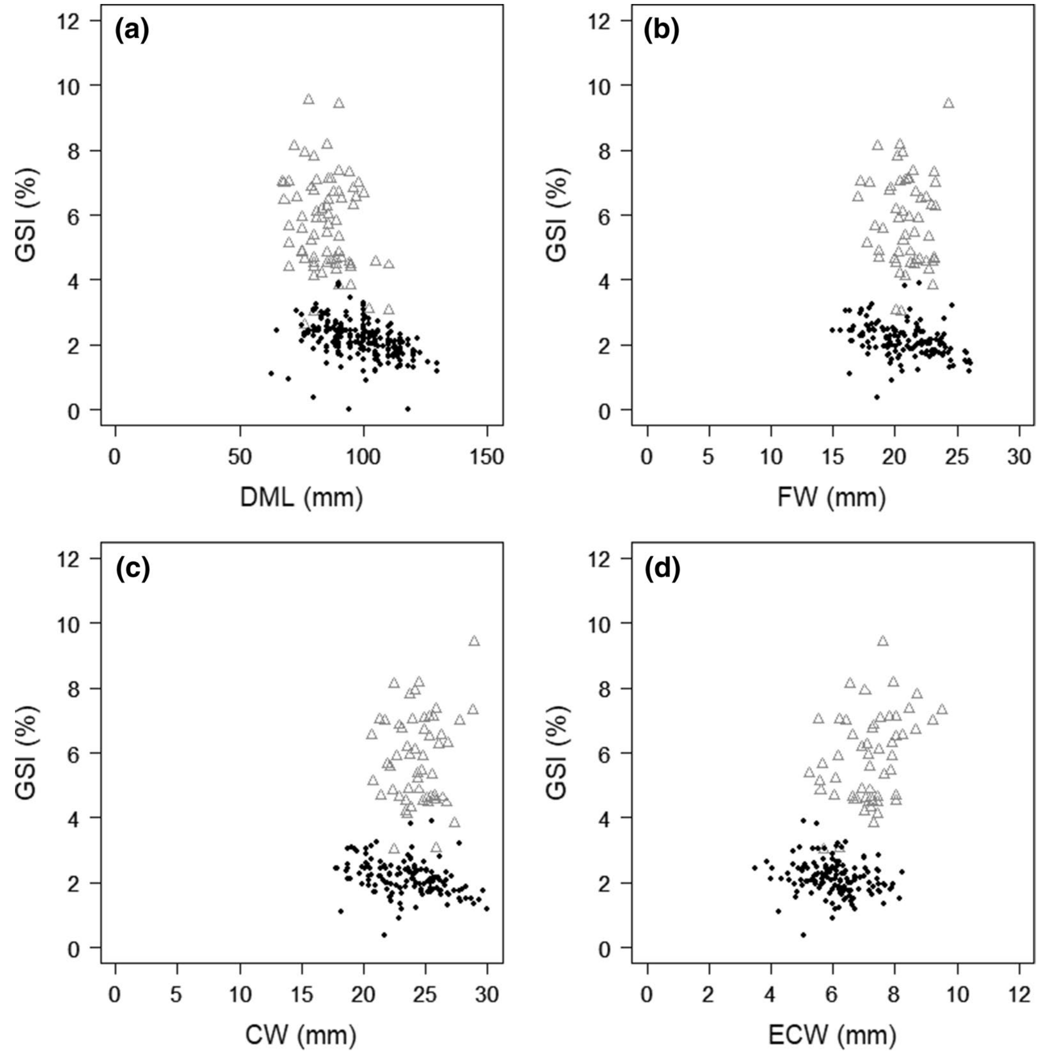

Fig. 4 Relationships between Gonadosomatic Index (GSI) and **a** Dorsal Mantle Length (DML), **b** Cuttlebone width (CW), **c** Fragmocone width (FW) and **d** External Cuttlebone Width (ECW) for males (black dots) and females (empty triangles) of *Sepia bertheloti*

which is clearly smaller than the maximum sizes reported by Jereb and Roper [12] for the Eastern Atlantic (175 and 134 mm DML, respectively). However, females were usually wider, and this aspect could be associated with the wider morphometric structure of their cuttlebone for a given mantle length.

This differentiation of the cuttlebone between sexes with females with a broader cuttlebone has also been described in other cuttlefish species, such as *S. officinalis* [4], *S. prabahari*, *S. weberi* and *Sepiella ornata* [12]. Therefore, although *S. bertheloti* males and females cannot be differentiated macroscopically (except for the presence of a hectocotylus), they show sexual differences in the morphometric structure of the cuttlebone.

The present results are comparable to those obtained by Almonacid-Rioseco et al. [4] for *S. officinalis*, which also showed a differentiation between sexes for the same measurements of the cuttlebone (FW, CW, ECW). These results reveal that sexes have a relatively different growth pattern. Specifically, males exhibit faster growth in length to reach larger sizes, while females exhibit greater growth in the cuttlebone width in preparation for reproduction (Fig. 3a–c). Vasconcelos et al. [23] also describe this sexual dimorphism for *S. officinalis* in the Algarve coast (southern Portugal). On the other hand, the gonadosomatic index allowed comparison of gonadal development with the cuttlebone measurements that presented differences between sexes, revealing that the faster growth in width of female cuttlebone is related to an increase in gonadal mass. Accordingly, this relationship can be interpreted as an adaptation of the female body to the gonadal development, which always exhibits increased occupation compared with the male gonad. In this sense, Akyol et al. [24] reported that the total number of oocytes produced by *S. officinalis* varied from 49 to 828 with an average of 261 ± 27 per female, whereas Laptikhovsky et al. [25] reported a range of large yolk oocytes between 130 and 839. This body adaptation hypothesis was previously proposed by Hewitt and Stait [26] and Sainz [27], who mentioned that these changes in *S. officinalis* were due to phylogenetic features where females adapted to their reproductive stage by developing a wider cuttlebone than males. The volume of oocytes could justify a larger capacity of the female paleal cavity and therefore the adaptation of female cuttlebone to provide the required support and space.

Due to the lack of immature individuals, we are not able to determine whether the differentiation between sexes based on cuttlebone morphometrics is only possible when analysing ripe individuals prior to spawning (i.e., when the cuttlebone morphology adapts to lodge the voluminous gonad), which would decrease the usefulness of this "tool" for gender identification in juveniles stages.

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Authors' contributions
AG-M performed data collection and analysis and interpretation of the results. LC-M performed data collection and analysis. DJ-A performed data collection and interpretation of results. JJC-H performed data analysis and interpretation of the results. The manuscript was written and substantially revised by all the authors, who also approved the version submitted to the journal. All authors read and approved the final manuscript.

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The datasets generated and analysed during the current study are not publicly available because data are being used for another research, but are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
The scientific study was conducted with animals from commercial fishing without any treatment of live animals.

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First Record of Exotic Fish *Canthidermis maculata* (Bloch, 1786) (Pisces: Balistidae) in the Canary Islands (Central-East Atlantic)

Airam Guerra Marrero[1] · **David Jiménez Alvarado**[1] · **José Juan Castro Hernández**[1]

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Abstract
The distribution of the Rough triggerfish, *Canthidermis maculata*, has been established in the East Atlantic for the west coast of subtropical central Africa, from Cape Verde Islands to Gabon, but with some records also toward Angola. The capture of a single specimen (TL: 289.6 mm) by tuna vessels in the Canary Islands, expand the distribution range of this species northward.

Keywords Rough triggerfish · *Canthidermis maculata* · Canary Islands · East Atlantic · Exotic fish · Drifting floating objects

Introduction

Rough triggerfish, *Canthidermis maculata* (Bloch, 1786), has a circumglobal distribution, and like other Balistidae species it is distributed among the first 100 m of depth (Lieske and Myers 1994). Triggerfishes normally have benthic habits, although some species such of the genus *Canthidermis* also present pelagic habits (Matsuura 2001). Juveniles and adults of *C. maculata* are found in coastal and oceanic waters, usually associated with drifting floating objects (Taquet et al. 2007) and generally in groups or schools (Castro et al. 2002).

The 9th of December 2018 an unsexed individual of *Canthidermis maculata* was caught by live-bait tuna boat off La Palma Island, in the western Canary Islands (Central-east Atlantic). This fish was aggregated under a floating plastic box. The individual was identified according to the taxonomic key described by the FAO (Matsuura 2001). The morphometric measurements were taken using an ictiometer and a caliper (0.01 mm) being preserved in 70% ethyl alcohol later, and deposited in the biological collection of the University of Las Palmas de Gran Canaria under *CANTH12/2018* code.

There are not previous reports of the presence of this species in the Canary Islands area, although it has been cited by Borges et al. (2010) as a member of the ichthyofauna of Azores Islands, over 1000 km northward. However, it is frequent in waters southward Cape Verde Archipelago, about 1300 Km in distance, and frequently caught as by-catch of the tune purse-seine fishery with FADs (Fish Aggregating Devices) (Lezama-Ochoa et al. 2016).

Description of the Specimen

The rough triggerfish caught (*CANTH12/2018)* was 289.6 mm of total length (TL) and 648.9 g of wet weight (Table 1). The body was robust and compressed, black color with gray tones in the ventral area. It has intense white spots on the body, while the fins were more blurred (Fig. 1). It has a small mouth in terminal position with a series of 8 teeth arranged in each jaw. The caudal fin had a recurve bow border. The first dorsal fin had 3 hard spines in descending order of size, while the second dorsal fin had 24 soft rays (Tables 1 and 2). The anal fin presented 22 soft rays and peduncle at the end of the hard-touch pelvis (circumscribed flake pattern) (Fig. 1).

Distribution

Canthidermis maculata has been reported from Cape Verde and the Central-East Coast of Africa to Angola (Harmelin-Vivien and Quéro 1990) in the Eastern Atlantic, and is absent in the Mediterranean. However, it has been also cited far beyond subtropical waters, with reports in South Africa (Smith and Heemstra 1986), Azores Islands (Borges

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✉ Airam Guerra Marrero
airamgmarrero@gmail.com

[1] Instituto Universitario EcoAqua, University of Las Palmas de Gran Canaria, Edf. Ciencias Básicas, Campus de Tafira, Las Palmas de Gran Canaria, 35017 Las Palmas, Spain

Table 1 Morphometric and meristic data of the specimen of *Canthidermis maculata* (*CANTH12/*2018) caught in La Palma Island

	in mm	Number of times in *SL*	Number of times in *HL*
Total Length	289.6		
Standard Length (*SL*)	267.2		
Head length (*HL*)	81.6	3.27	
Eye diameter	11.2	23.86	7.29
Predorsal length of the first dorsal fin	86.4	3.09	0.94
Predorsal length of the second dorsal fin	158.4	1.69	0.52
Base length between two dorsal fin	59.2	4.51	1.54
Preanal distance	196.8	1.36	0.41
First dorsal fin Length	19.2	13.92	4.25
Second dorsal fin Length	76	3.52	1.07
Pectoral fin length	36.8	7.26	2.22
Anal fin length	78.4	3.41	1.04
Caudal fin Length	32	8.35	2.55
Body depth	102.4	2.61	0.80
Head height	99.2	2.69	0.82
	Meristic features		
Dorsal spines	III		
Dorsal soft rays	24		
Anal soft rays	22		
Total weight (in grams)	648.9		
Sex	Undertermined		

et al. 2010), and now in the Canary Islands where it has not been cited previously.

Discussion

The appearance of subtropical species in the Canary Islands may be related to the water warming (Brito et al. 2005), maritime shipping (Triay-Portella et al. 2015), drifting floating objects (Castro et al., 1999; Kiessling et al. 2015). Lezama-Ochoa et al. (2016), using by-catch data from purse seine tuna fishery establish a model to predict the potential suitable habitat for *C. maculata*, establishing a new range of future distribution. They do not include the Canary Islands or Azores in the future scenarios of occupation, because were considered far from their native habitat range, but the arrival of an adult specimen associated to floating object indicates that its range of distribution could be wider than previously thought and could change with time depending on oceanographic conditions.

The morphometric measurements obtained from the fish caught in La Palma island were within the ranges reported for *Canthidermis maculata* in other areas (Table 2). Nevertheless, this individual, although was within the length range of those reported in other areas (Lindberg et al. 1997; Tuponogov 2015), showed relatively larger eyes than others (Table 2). According to Tuponogov (2015) this phenotypic difference may be due to factors of expression of individuals,

Fig. 1 *Canthidermis maculata* specimen of 289.6 mm of total length, caught by live-bait tuna vessel in La Palma Island (Canary Islands, Spain)

Table 2 Comparison of morphometric relationships of the rough triggerfish *Canthidermis maculata*. In **bold** the different values from the averages of previous studies. D1: First Dorsal fin, D2: Second Dorsal fin, A: Anal fin

	Afonso et al. 2013	Lindberg et al. 1997	Tuponogov 2015	Present study, 2018
Location	Azores	Hawaiian Islands	Southern Kuril Islands	Canary Islands
Measurements				
SL (mm)	220–280	197–257	88	267.2
	Number of times in *SL*			
Head length (*HL*)		2.86–3.33	2.88	3.27
Body height		1.94–2.62	1.90	2.61
Predorsal distance to D1		2.53–2.94	2.50	**3.09**
Predorsal distance to D2		1.41–2.26	1.50	1.69
Preanal distance		1.31–1.51	1.39	1.36
	Number of times in *HL*			
Eye diameter		4.34–5.9	4.42	**7.29**
Distance between D1 and D2		1.14–1.51	1.51	**1.54**
Caudal fin length		1.64–2.48	1.94	**2.55**
	Meristic features			
D1		III	III	III
D2		23–24	24	24
A		21	22	22

age or geographic variation. However, the individual analyzed in this study was larger than the specimens described from Hawaii and Kurile waters (Lindberg et al. 1997; Tuponogov 2015), but within the length range reported by Afonso et al. (2013) for the rough triggerfish caught off Azores.

On the other hand, it has become more frequent the report of new tropical and exotic fish species in the Canary Islands area (Brito et al. 2005; Triay-Portella et al. 2015, between others), increasing the worry about the real possibilities of colonization process and displacement of less competitive native species (Riera et al. 2014), or for its effects on the fisheries economy and public health. In this line, from 2017 on, it has been reported the regular and massive presence of *Lagocephalus lagocephalus* in the warm season (Graiño and Lozano 2017). In this sense, *Canthidermis maculata* is defined as "r" strategist with a high reproductive rate (Clark et al. 2015), and it is frequent to observe hundreds to thousands of individual aggregated under floating objects (Taquet et al. 2007). In the case here reported, a single individual was observed, contrary to what is reported elsewhere (Castro et al. 2002), and it's possible that only be an anecdotal record as other previously reported in the north-eastern Atlantic (Borges et al. 2010; Afonso et al. 2013). However, it is becoming more frequent in the region, and probably associated to the oceanic warming process in the Canary Islands area (Valdés and Déniz-González 2015).

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Data Availability All data generated or analyzed during this study are included in this published article.

Compliance with Ethical Standards

Ethical Approval and Consent to Participate The scientific study was conducted with animals from commercial fishing without any treatment of animals in their live stage.

Consent for Publication Not applicable.

Competing Interests The authors declare that they have no competing interests.

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Historical photographs of captures of recreational fishers indicate overexploitation of nearshore resources at an oceanic island

David Jiménez-Alvarado | Airam Sarmiento-Lezcano | Airam Guerra-Marrero | Fernando Tuya | Ángelo Santana Del Pino | Michael J. Sealey | José J. Castro

Grupo en Biodiversidad y Conservación, IU-ECOAQUA, Universidad de Las Palmas de Gran Canaria, Las Palmas, Spain

Correspondence
David Jiménez-Alvarado, Grupo en Biodiversidad y Conservación, IU-ECOAQUA, Universidad de Las Palmas de Gran Canaria, 35017 Las Palmas de G.C., Islas Canarias, Spain.
Email: david.jimenezalvarado@gmail.com

In this study, we used a historical collection of photographs taken by recreational fishers from 1940 to 2014, at the island of Gran Canaria, to show both a significant decrease in the mean total length of *Epinephelus marginatus* and a concurrent change in the composition of captures. Before 1980, the mean total length of fish caught and photographed was *c.* 100 cm, while after 2009 this was typically < 40 cm. Before 1980, the predominant captured species was *E. marginatus* (an apex predator), but currently the majority of catches are of omnivorous species, in particular the parrotfish, *Sparisoma cretense* and seabreams *Diplodus* spp. Overall, integration of these results indicates a qualitative and quantitative variation in captures of recreational fishers, probably as a sign of change in ecological balances and the overfished status of many target species.

KEYWORDS

Atlantic Ocean, grouper, overexploitation, recreational fisheries, spearfishing, target species

1 | INTRODUCTION

Over the past century, nearshore ecosystems have experienced a significant degradation, with direct implications on biodiversity and ecosystem functioning (McClenachan, 2009; Myers & Worm, 2003; Pauly, 2009). For example, overexploitation of coastal resources has decreased abundances and sizes of species of commercial relevance, principally those occupying the top of food webs (McCauley *et al.*, 2015), even causing the disappearance of some species as a result of excessive fishing pressure and concurrent degradation of habitats (Zeller *et al.*, 2009).

Empirical demonstration of the disappearance or deterioration of species is not always easy, due to the difficulty in obtaining information, particularly where there are no historical records from fisheries, including both commercial and recreational. The majority of fisheries around the world are, in turn, classified as deficient in data (Costello *et al.*, 2012; Hyder *et al.*, 2017; Kurien & Willmann, 2009). Recently, scientists and managers have developed alternative ways to assess the status of fisheries with scarcity of historical data, also known as data-poor fisheries (Dowling *et al.*, 2015; Honey *et al.*, 2010; Pazhayamadom *et al.*, 2015). Data from recreational fishers may be a valuable tool to assess temporal tendencies in the status of nearshore fisheries. For example, captures from spearfishing competitions through long-term series have pointed towards extirpation of certain fish species from the Mediterranean Sea and an overall deterioration of resources; *i.e.*, lower abundances and sizes through time (Lloret *et al.*, 2008). Nevertheless, the relative high capacity of selection by spearfishers has been directed towards a few species (Frisch *et al.*, 2012; Giglio *et al.*, 2017), either due to the remarkable value of their physical characteristics (size, colour, *etc.*), or in order to show as a fishing trophy, this makes the information of the effects of this fishing on the subjected communities to be very distorted and limited. However, this competitive value of the captures has also favoured a tendency to take photos of the caught fish, particularly those of big size. Therefore, historical series of photographs taken by recreational fishers might be a useful tool to provide qualitative and quantitative evidence of changes in the status of exploited stocks through, for example, variation in the mean size of captured specimens and in the composition of captures as well (McClenachan, 2009).

In the Canary Islands it has been found that recreational fishermen have a high preference for species such as the dusky grouper *Epinephelus marginatus* (Lowe 1834) and island grouper *Mycteroperca fusca* (Lowe 1838), both currently scarce in the catches reported by the small-scale commercial fishery. Also, large specimens of parrotfish *Sparisoma cretense* (L. 1758) and seabreams (*Diplodus* spp.), some of them currently classified as overfished (González, 2008), in which sexual reversal processes occur in large-sized specimens (Pajuelo et al., 2003; Pajuelo & Lorenzo, 1995, 1996; Pajuelo, Lorenzo, et al., 2006; Pajuelo, Socorro, *et al*., 2006). There are several examples in the scientific literature that highlight the effect of spearfishing on fish populations in this regard (ASFB, 2004; Birkeland & Dayton, 2005; Dayton, 1998; Frisch *et al*., 2012; Gordoa, 2009; Johannes, 1978; Pita & Freire, 2014; Pogonoski *et al*., 2002).

Temporal trends in the size structure of fish populations is a direct proxy of the degree of overexploitation (Dulvy *et al*., 2004; Shin *et al*., 2005). Photographs taken by recreational fishers, showing their catches as trophies, provide visual evidence of the size of fishes, usually the biggest captures. Large-sized fishes, mainly those occupying top trophic levels in marine ecosystems (*e.g*., groupers) are the priority target of recreational fishers, which are typically slow-growing and face low resilience under intense fishing pressure (Jennings, 2005; Reynolds *et al*., 2005). Selective removal of large-sized individuals of whatever species results in a decrease of the size at first maturity of the species and displayed substantial declines in fecundity, *etc*. (Alós *et al*., 2014; Audzijonyte *et al*., 2013; Froese, 2004; Pauly, 1983; Walsh *et al*., 2006). However, these genetically based changes also generally reduce the capacity for population recovery (Walsh *et al*., 2006).

In this study, we hypothesised that a reduction in the length and abundance of target species (*e.g*., groupers) would be reflected in historical time series of photographs taken by recreational fishers. This provides a proxy to examine ecological changes experienced by these species in the last decades.

2 | METHODS

We compiled a photographic dataset of captures of shallow-water (≤ 30 m depth) fish species from 1940 to 2014 at the island of Gran Canaria (Canary Islands, eastern Atlantic Ocean). Photos were supplied mainly by spearfishers and shore-line anglers (78.4%), as well as by some fishing clubs and tackle shops. In total, we collected 473 photographs. The number of photographs in the more recent period is far greater than before year 2000 (Table 1).

For each photograph, we annotated the year, place of collection and the fishing method. All the photos used were supplied by different fishers in different places and dates, so can be considered as independent samples. From each photo we recorded the species caught and the approximate sizes of fishes using available scales in each photograph (Figure 1), by means of the image analysis software Oprika-Proview vx64 (www.optikamicroscopes.com). The level of error in fish length estimations was 18.9 ± 12.7%. If no scale was available, the photo was discarded for fish length estimation. In total, we analysed 373 photographs (Table 1). Photographs were categorized according to the type of recreational fishing: shore angling with rods, shore fishing with spearguns (spearfishing), boat angling with rods and lines and boat fishing with spearguns.

We assume that limitations of taking pictures previously to year 2000 could be an important source of bias, due to the possibility that only exceptional catches were recorded. However, the development of digital cameras and smartphones and its subsequent democratization, has made possible that since 2000 almost all fishing events may be photographed, particularly in spearfishing tournaments. However, we also assume that in both periods the fondness to record exceptional catches has not changed.

The data obtained (length, number of species and number of specimens in each capture) was arranged temporally separately and analysed. Relationships between time (years) and mean length, number of specimens or species caught, were initially explored using generalized additive mixed models (GAM; with identity link function). The effective degrees of freedom (edf) parameter of the model was found to be equal to 1 in all cases, thus penalizing the smooth term to a simple linear relationship. We therefore refitted simple linear regression models to the data. We firstly tested for significant changes in the total length (L_T) of all fish caught and photographed through time using linear regression. As *E. marginatus* was the most frequent species for the entire dataset, we also tested for changes in the L_T of this species through the years using linear regression. For the other species recorded in the photos (Table 2), only a few were normally available along the time series; hence we were not able to perform any robust analysis on long-term change for these species. However, we tested for changes in the catch composition by fitting a linear regression to the number of species of captures through time. In addition, a comparison of the species composition of captures was made performing a non-parametric statistical analysis to check if there were significant differences between them. All statistical analyses, as well as any data processing, have been carried out in R (www.r-project.org).

3 | RESULTS

During the period 1940–2014, there was a progressive and significant decrease in the mean L_T of fish caught and photographed by recreational fishers (linear regression: decrease of -1.17 ± 0.14 cm year^{-1}, $R^2 = 0.81$, $P < 0.001$; Figure 2). Between 1940 and 1960, the mean L_T of fish caught and photographed was 108 ± 22 cm (mean ± SD), while between 2000 and 2008, most fish caught and photographed ranged between 50 and 60 cm L_T (52.1 ± 28.9 cm). From 2009 to 2014, fish caught were typically smaller than 40 cm L_T (30.9 ± 17.5 cm; Figure 2). In this sense, the total length of *E. marginatus* showed a significant decrease over time (linear regression: decrease of -1.22 ± 0.19 cm year^{-1}, $R^2 = 0.56$, $P < 0.001$; Figure 3).

FIGURE 1 Examples of photographs where the lengths of captured fishes were obtained relative to an object of known size: (a) a water bottle, (b) a lighter, (c) a watch (fisherman with the black shirt) and (d) buttonholes in the shirt of a fisherman

TABLE 1 Temporal distribution of photographs provided by recreational fishermen

	1940–1949	1950–1959	1960–1969	1970–1979	1980–1989	1990–1999	2000–2009	2010–2014	All years
All photos	4	4	12	32	5	4	92	320	473
Photos used to estimate fish length	1	0	3	22	0	0	69	278	373

Epinephelus marginatus captured and photographed before 1980 were often > 80–90 cm L_T, while after 2010, sizes were often < 60 cm L_T.

There was a significant increase in the number of target species caught and photographed through time (linear model, increase of 0.505 species year^{-1}, $R^2 = 0.20$, < 0.05; Figure 4). During the decades from 1940 to 1970, fish caught and photographed almost always belonged to one species only, *E. marginatus*. Through time, however, the composition of catches showed a greater diversity of species, where medium and small-sized species dominated, such as *S. cretense*), *Diplodus* spp., bogue *Boops boops* (L. 1758) and European seabass *Dicentrarchus labrax* (L. 1758) (Table 2).

After 2004 (the first year where photos of line anglers' captures were available), spearfishers caught fishes of larger sizes (38.8 ± 20.2 cm L_T, $n = 129$) than those captured by hook and line anglers (31.1 ± 20.7 cm L_T, $n = 209$; Mann–Whitney *U*-test, $Z = 5.14$; $P < 0.001$).

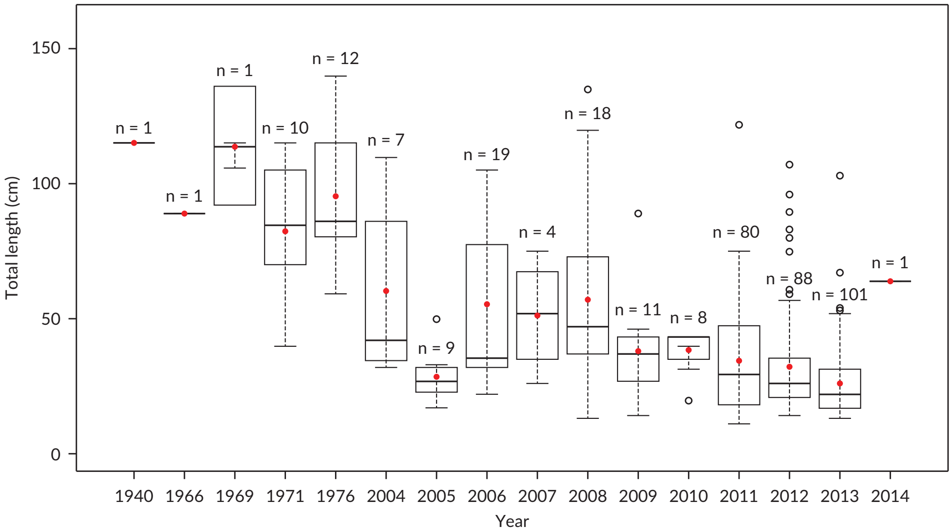
4 | DISCUSSION

Recreational and commercial fisheries have so many differences in so many aspects, beyond mere economic value of the catch. Thus, while

TABLE 2 Total species dataset obtained from historical photographs. For each species, the mean (± SD) total length (L_T, cm), by time-period, and number of photographs (n) are indicated

	1940s		1960s		1970s		2000s	
Taxonomic group and species	L_T	n	L_T	n	L_T	n	L_T	n
Fishes								
Anguilliformes								
Conger conger							136	1
Enchelycore anatina							83	1
Muraena spp.	115	1					70.5 ± 17.7	6
Aulopiformes								
Synodus saurus							25.5 ± 0.7	2
Cyprinodontiformes								
Belone belone gracilis							70.1 ± 40.9	6
Perciformes								
Acanthocybium solandri							122	1
Bodianus scrofa							42.8 ± 11.1	7
Boops boops							17.6 ± 3.6	43
Coryphaena hippurus							85.9 ± 18.7	6
Dicentrarchus labrax							41.7 ± 14.3	30
Diplodus sargus cadenati							21.9 ± 5.3	50
Diplodus vulgaris							32.7 ± 3.8	3
Epinephelus marginatus			105.7 ± 26.3	4	94 ± 20.8	21	49.4 ± 15.4	27
Heteropriacanthus cruentatus							21	1
Liza aurata							34.8 ± 11.2	9
Mullus surmuletus							21	2
Mycteroperca fusca							75	1
Oblada melanura							32.3 ± 0.7	3
Pagellus erythrinus							23.2 ± 10.7	5
Pagrus auriga							53.9 ± 14.4	8
Pomadasys incisus							37	1
Pseudocaranx dentex							53.4 ± 11.6	8
Salpa salpa							19.4 ± 7.7	5
Sarda sarda							64.3 ± 31.8	5
Seriola dumerili							53.7 ± 14.5	8
Serranus cabrilla							21.6 ± 10.6	11
Sparisoma cretense							28.3 ± 7.9	77
Sparus aurata							27.2 ± 3.1	6
Sphyraena barracuda					85	1	78 ± 29.9	4
Spondyliosoma cantharus							36.5 ± 10.8	4
Trachinotus ovatus							18.5 ± 9.2	2
Umbrina cirrosa							26.5 ± 9.2	2
Tetraodontiformes								
Balistes capriscus							30.5 ± 4.3	10
Cephalopods								
Sepia officinalis							42.5	1
Octopus vulgaris							78 ± 45.2	2

FIGURE 2 Box plots (——, median; □, 25th–75 percentiles; ¦, 95%range; ○, outliers) of total length of fishes captured by recreational fishermen from 1940 to 2014



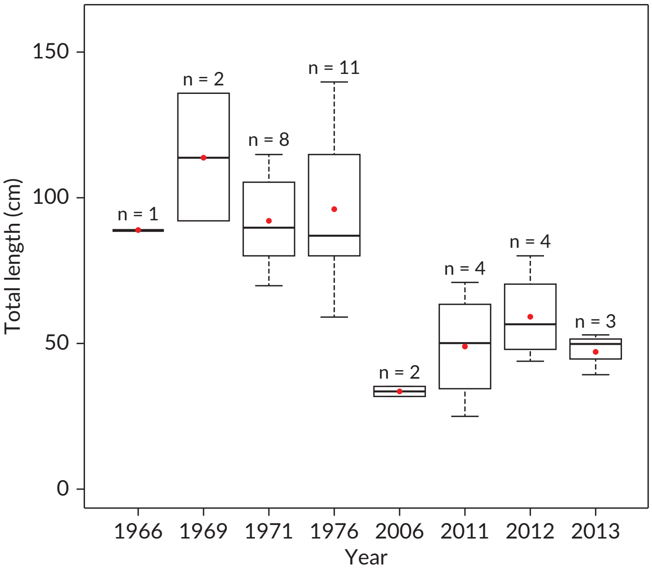


FIGURE 3 Box plots (——, median; □, 25th–75 percentiles; ¦, 95% range; ○, outliers) changes in the total length of *Epinephelus marginatus* in the catches of recreational fishermen from 1970 to 2010

the professional fishers, whether industrial or artisanal, show a tendency to procure heavy catches of those species that have a high economic value, recreational fishers argued many reasons to fish (catch, relaxation, time with family and friends, personal challenge, contact with nature, *etc.*), but normally declare their tendency to catch large individuals, just as a conservative rule, or merely for catching the more combative fish, that have greater resistance to the capture (Castro *et al.*, 2018; Santana-Ojeda, 2014). There is a growing interest has emerged in knowing the reasons which motivate fishermen to fish, in particular those of recreational fishers (Arlinghaus, 2006; Calvert, 2002; Farr *et al.*, 2014; Jiménez-Alvarado *et al.*, 2019; Morales-Nin *et al.*, 2015; Young *et al.*, 2016) and obviously there is not a general pattern. However, many recreational fishers (but also commercial fishermen) have the tendency to flaunt their captures and show the fish caught as a trophy, as proof of the feat achieved (McClenachan, 2009).

The lack of information in data-poor fisheries about the state of the stocks of fish can be, in part, supplemented through indirect evaluation methods, also applied to fisheries trade data (Costello *et al.*, 2012; Kurien & Willmann, 2009). In this way, the analysis of the historical evolution of captures and target species recorded in the pictures taken by recreational fishers could provide valuable information about the changes suffered by the fishery, the status of target species and the existence of possible unbalanced ecological processes behind the succession of species along time (Tuya *et al.*, 2004, 2006) Nevertheless, the greater number of photographs in the more recent period could cause important bias if used to assess the status of stocks. But obviously the information recorded in old photos can be an indicator of gross changes when compared with recent ones. For example, changes in the mean length of target species, particularly when large individuals are absent in more recent pictures, can be used as an index of variation in the status of these species.

In the specific case of the island of Gran Canaria and in the same way that showed McClenachan (2009) in the Florida Keys, over the past 70 years have produced very significant changes, in the health of target species for recreational and artisanal fishing and in their fishing strategy (Castro *et al.*, 2015; Couce-Montero *et al.*, 2015). Historical photographs indicate that species such as *E. marginatus* have suffered a significant reduction in the mean length of capture. There are previous papers that demonstrate that many fish stocks in the Canary Islands waters are overfished (Couce-Montero *et al.*, 2015; García-Cabrera, 1970; González, 2008) and the historical photos are also reflecting one of the negative effects of overfishing, reducing the mean length of some key species (Alós *et al.*, 2014; Froese, 2004). These data confirm the chronic process of overexploitation that many fish stocks are suffering in the Canary Islands (Bas *et al.*, 1995; Castro *et al.*, 2015; García-Cabrera, 1970; Riera *et al.*, 2014), which is more evident in species of the highest trophic levels of the bentho-demersal ecosystems.

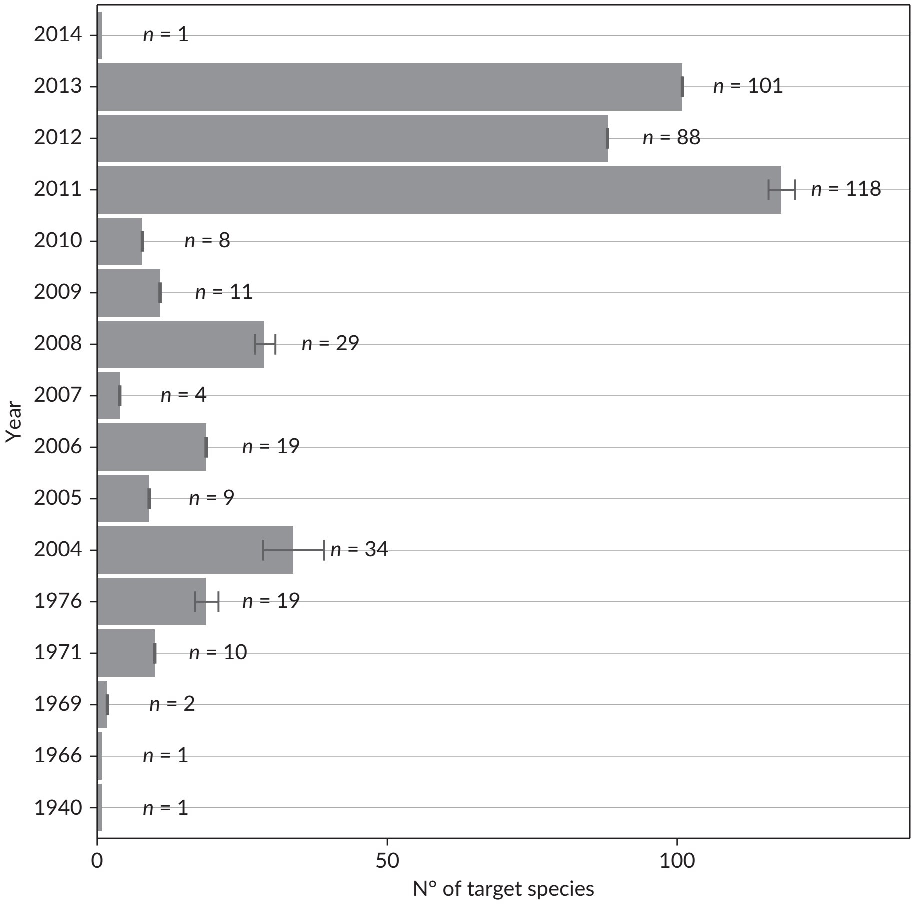


FIGURE 4 Changes through time 1940–2015 in the mean (± SD) number of species in the catches of recreational fishermen. *n*, Numer of species recorded

This overexploitation process not only has resulted in the rarefied of certain species in the island ecosystems, such as the barred hogfish *Bodianus scrofa* (Valenciennes 1839), spotfin burrfish *Chilomycterus reticulatus* (L. 1758) or *E. marginatus*, *M. fusca* (Aguilera-Klink *et al*., 1993; Riera *et al*., 2014; Zeller *et al*., 2009), but that also may have been the basis for deeper changes in these ecosystems, facilitating the succession of species and the population explosion of other opportunistic ones (Ortega *et al*., 2009). Although the reason is still unclear, the selective fishing process may have resulted in the target species to have experienced genetic overfishing, as has been suggested by (Walsh *et al*., 2006). In a similar way, Coll *et al*. (2004) indicated that *E. marginatus* caught by spearfishers in the Balearic Islands (west-central Mediterranean Sea) has suffered a drastic reduction in weight after 1987. But they also indicated that the species recorded as largest specimens clearly changed since this date, showing a serial depletion process, suggesting that both recreational and competition spearfishing have had an important effect on rocky bottom resources between 0 and 40 m depth.

The selective fishing process could generate a deterioration of fish populations, because the active selection of greater individuals causes a significant loss of the reproductive potential of target species (Barneche *et al*., 2018), the genetic load associated with these individuals of great size (Pandolfi, 2009; Swain *et al*., 2007; Walsh *et al*., 2006) and also an increase in vulnerability and predation mortality (Alós *et al*., 2014; Audzijonyte *et al*., 2013). This effect also produces a greater presence of genes associated with individuals that are played at smaller, causing a significant reduction at the first maturity size (de Roos *et al*., 2006; Olsen *et al*., 2004). And this is the reason why fishery management should never be oriented to reduce the legal size of first capture, because this decrease in the mean size of first reproduction, would only further aggravate the problem of overexploitation.

On the other hand, the depletion in target species into the fishing area also has as an immediate consequence-where the fishing effort is reoriented to other species as potential targets (Klaer, 2001; Lear, 1998; Salas & Gaertner, 2004; Smith, 1968). In the case of Gran Canaria, this change in fishing strategy has caused two very clear consequences: (a) a succession on target species from groupers to seabreams and parrotfish, that is also seen in the small-scale fishery, which sequentially change the target species to run out the depletion in main species in the fishing areas (*e.g*., *Bodianus scrofa*, *Umbrina ronchus* Valenciennes 1843, *Sciaena umbra* L. 1758, *Polyprion americanus* (Bloch & Schneider 1801), *M. fusca*, among many others; Aguilera-Klink *et al*., 1993; Espino *et al*., 2006; Riera *et al*., 2014), even with the help of boats and accessing more remote coastal waters; (b) the mean sizes of the fish caught in recent years are smaller, in general, as is possible to see in pre-1980's photographs.

Although coastal fish communities are negatively affected by many factors (pollution, habitat fragmentation and climate change; Poulard & Blanchard, 2005; Lawrence & Hemingway, 2007; Yeager *et al.*, 2016), historical photographs provide valuable information about the effects of over-exploitation, through the decrease in the mean size of target species and the reduction of the abundance of bentho-demersal top predators, like groupers, but also can document the process of succession of species (Tuya *et al.*, 2004).

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Migratory patterns, vertical distributions and diets of *Abralia veranyi* and *Abraliopsis morisii* (Cephalopoda: Enoploteuthidae) in the eastern North Atlantic

Airam Guerra-Marrero[1], Vicente Hernández-García[1], Airam Sarmiento-Lezcano[1],
David Jiménez-Alvarado[1], Angelo Santana-del Pino[2] and José J. Castro[1]

[1] *Instituto Universitario EcoAqua, Universidad de Las Palmas de Gran Canaria, 35017 Campus Universitario de Tafira, Canary Islands, Spain; and*
[2] *Departamento de Matemáticas, Universidad de Las Palmas de Gran Canaria, 35017 Campus Universitario de Tafira, Canary Islands, Spain*

Correspondence: A. Guerra-Marrero; e-mail: airamgmarrero@gmail.com

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ABSTRACT

Abralia veranyi and *Abraliopsis morisii* were the most abundant cephalopods caught during epipelagic and mesopelagic surveys off the Canary Islands and accounted for 26% and 35% of the cephalopod catch, respectively. Diel vertical migration patterns were observed in both species. At night, *A. veranyi* was recorded at depths as shallow as 38–90 m, whereas *Abraliopsis morisii* occurred at depths of 98–219 m. As individuals grow in mantle length, their diet changes substantially. *Abraliopsis morisii* showed ontogenetic shifts at 22.9 mm and 35.3 mm dorsal mantle length (DML), while *A. veranyi* showed ontogenetic shifts at 20.5 mm and 30.9 mm DML. Prior to the first ontogenic shift, both species fed mainly on copepods and mysids. After this shift they fed on larger prey, such as decapods and fish; the diets of larger individuals also contained cephalopods.

INTRODUCTION

Cephalopods are common inhabitants of the mesopelagic zones of the ocean and occupy key roles in many marine ecosystems, both as predators and prey (Clarke, 1996; Piatkowski, Pierce & Morais da Cunha, 2001; Boyle & Rodhouse, 2005). Although mesopelagic cephalopods are globally widespread, they live in inaccessible environments, so little is known about their behaviour. According to Xavier *et al*. (2015), knowledge about noncommercially exploited oceanic cephalopods is scarce, with most of this knowledge having been obtained from the analysis of the stomach contents of predators (e.g. Hernández-García, 1995; Clarke, 1996). As has also been reported for fish and planktonic crustaceans (Torres *et al*., 2018), many mesopelagic cephalopod species migrate vertically over hundreds of meters to feed near the surface during the night, returning to deep water at dawn (Clarke & Lu, 1974; Roper & Young, 1975). This behaviour facilitates the transfer of energy and organic matter from productive shallow waters to the deep ocean (Ariza, 2015).

While the importance of mesopelagic cephalopods in oceanic ecosystems has been described by several authors (Clarke, 1969; Clarke & Lu, 1974; Vecchione & Roper, 1991; Shea *et al*., 2017), their role in the trophic relationships of open-ocean ecosystems is poorly understood (Clarke, 1962; Rocha & Cheikh, 2015). The enoploteuthids are likely to be ecologically particularly important. They constitute a large biomass at depths between 200 and 400 m (Laptikhovsky, 1999) and are an important and abundant prey source for many predators (Anastasopoulou *et al*., 2013; Kousteni *et al*., 2018).

The enoploteuthids *Abralia veranyi* (Rüppel, 1844) and *Abraliopsis morisii* (Vérany, 1839) are important components of the mesopelagic fauna of the warm waters of the Atlantic Ocean, including the Mediterranean Sea and the Gulf of Mexico (Nesis, 1987). Despite this, the feeding behaviour of these two species, particularly in the eastern North Atlantic, is still poorly known. Using data gathered in the Canary Current region of the eastern North Atlantic, we describe the diets of *A. veranyi* and *Abraliopsis morisii* and detail the daily migratory patterns and distribution of these species in the water column.

MATERIAL AND METHODS

Sampling

Cephalopods were collected off the Canary Islands (eastern North Atlantic) during five research surveys carried out by the vessel R/V LA BOCAINA between 1997 and 2002 (Fig. 1). Depths ranging from 8 to 1,035 m were sampled. *Abralia veranyi* ($n = 763$) and *Abraliopsis morisii* ($n = 1{,}026$) were caught using a commercial semi-pelagic otter trawl net (5 mm mesh size at the cod-end). Trawling was carried out at different times of the day, and both diurnal and nocturnal trawls were conducted. The net used was an open net lacking closing doors. The net was dropped from the ship until it

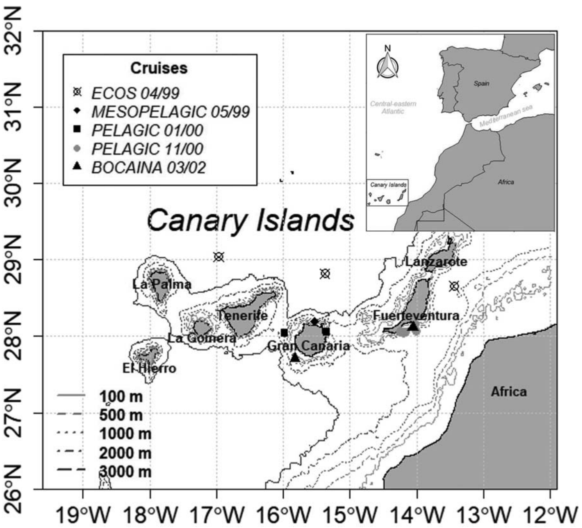

Figure 1. Map of the Canary Islands, showing locations sampled on the research cruises of the R/V LA BOCAINA.

sank to a particular trawl depth, after which trawling was carried out at a constant depth (capture depth). The trawls were monitored through acoustic telemetry using a SCANMAR net-sensor system; this system measured parameters such as depth, position, speed and both the vertical and horizontal opening of the net's mouth (see Bordes *et al*., 1997, 2002). Once the trawling was finished, the ship came to a complete halt and the net was hoisted vertically. At the moment of hoisting, the bulk of the net was pulled down by its own weight to form a bag and this closed the mouth of the net; the mouth of the net was demarcated by lines of buoys and plumbs. The hoisting speed was adjusted to prevent the mouth of the net from accidentally opening.

Captured cephalopods were classified and preserved in 70% ethanol for later analysis. Specimens of *Abraliopsis morisii* and *A. veranyi* were identified with the aid of the key developed by Nesis (1987). For each individual, the following measurements were taken in the lab: (1) dorsal mantle length (DML), measured to the nearest 0.1 mm; (2) total wet weight (TW) to the nearest 0.1 g; (3) head weight (HW), including the arms and tentacles, to the nearest 0.1 g; and (4) weight of the stomach contents (i.e. following extraction from the stomach) to the nearest 0.001 g. Length frequency distributions were quantified for the different depths of fishing, and the trawls were separated into nocturnal and diurnal captures. The DML data for the analysed specimens were not normally distributed in relation to depth; thus, a nonparametric test was used to determine if there were significant differences or not. The diet of the two species was analysed for samples of multiple individuals (*A. veranyi*, $n = 119$; *Abraliopsis morisii*, $n = 119$).

Breakpoint analysis

A model II piecewise linear regression (PLR) was carried out to detect possible ontogenetic shifts (Shea & Vecchione, 2002) in the growth of *Abraliopsis morisii* and *A. veranyi*. The relationship between TW and HW was analysed to detect possible growth-related differences in diet. This was done by $\log_e$ transforming the variable HW and plotting it against $\log_e$ TW. Following Shea & Vecchione (2002), we used the reduced major axis regression model and changed the LOSS default function to $\text{LOSS} = (\text{y}-(\text{a} + \text{bx}))^2/\text{ABS (b)}$, where x is the independent variable, y is the dependent variable and a and b are the intercept and slope of the line, respectively.

To analyse the breakpoints, a simple linear regression (SLR) was plotted using model II; *A. veranyi* and *Abraliopsis morisii* showed a patterned residual and this allowed possible breakpoints to be deduced. Subsequently, an iterative PLR model was employed, with the first test breakpoint being used to analyse multiple subsequent breakpoints (for each iteration the breakpoint increased by 0.1). The number of iterations performed was 22 for *Abraliopsis morisii* and 26 for *A. veranyi*. For each iteration, R2, LOSS and residues were saved.

As more than one breakpoint was observed for both species, the values of R2 and LOSS for each segment were analysed to see if the PLR segments were better adapted to the data than the SLR segment. After obtaining the two possible breakpoints, the equation for each segment and its 95% confidence intervals (CI) were calculated. The slopes were considered different if the slope of segment 2 was outside the CI of segment 1 and the slope of segment 3 was outside the CI of segment 2.

If the slope analysis showed that the R2 and LOSS values, along with their respective residuals, improved in comparison with SLR results, but the slope was within the 95% CI, the breakpoint was rejected. If, however, the new segments were associated with improved values of R2, LOSS and residuals of the SLR model, and the slope of the new segment was not in the 95% CI of the previous segment, the breakpoint was accepted. Allometric parameters were calculated for each segment (Table 1). All statistical analyses were carried out using R v. 3.4.2 (R Core Team, 2019).

Diet analysis

The stomach fullness index (SF) was calculated using the following equation:

$$\text{SF} = \left(\frac{\text{wet weight of stomach content}}{\text{wet weight of individual}}\right) \times 100$$

Prey items (hard and soft tissues) were identified to the lowest possible taxonomic level. However, due to the heavily digested state of food items, identification to the family or species level was usually not possible. Plankton and decapod taxa were identified using the guides by Zariquiey (1968), Estrada & Genicio (1970) and Newell & Newell (1970). The index of relative importance (% IRI) was calculated as described by Pinkas, Oliphant & Iverson (1971):

$$IRI_i = (N_i + WW_i) \times O_i,$$

where N = numerical frequency, WW = % wet weight, O = frequency of prey occurrence for all stomach analyses (including empty stomachs) and i = number of prey analysed.

A Kruskal–Wallis test was used to test for significant differences between the SF index of individuals captured during nighttime and daytime hours. This was followed by a post hoc Tukey honestly significant difference (HSD) test to determine at exactly which hours there were significant differences in the SF index. On the basis of the breakpoint analysis, individuals of both species were grouped into three length classes and growth-related differences in diet were analysed (See Results for further details); a $\chi 2$ test was used to assess if differences in diet were significant.

RESULTS

A total of 20 species of cephalopods were identified from the mesopelagic and epipelagic trawl samples taken at depths ranging from 8 to 1,035 m. Enoploteuthids represented 65.4% of the captured cephalopods, with *Abraliopsis morisii* being the most frequently captured species (35.1%). Other sampled enoploteuthid species included *A. veranyi* (26.1%) and *Enoploteuthis anapsis* (0.1%). Small individuals (DML <12 mm) were scarce in the trawl samples (11 and 4 individuals of *Abraliopsis morisii* and *A. veranyi*, respectively). This may possibly have been due to the fine mesh size of the trawl net, with specimens of DML <5 mm generally not been captured. Most of the small specimens captured had been damaged in the cod-end (i.e. due to the weight of the rest of the catch).

Table 1. Allometric parameters and breakpoints for *Abraliopsis morisii* and *Abralia veranyi* for the relationship between log_eTW and log_eHW.

Species	Breakpoints (TW, g)	Allometric parameters								
		Segment 1			Segment 2			Segment 3		
		Intercept	**Slope**	**95% CI**	**Intercept**	**Slope**	**95% CI**	**Intercept**	**Slope**	**95% CI**
Abraliopsis morisii	0.9 & 2.58	−0.83	0.94	0.47–1.12	−0.71	1.26	1.15–1.36	−0.88	0.67	0.49–0.87
Abralia veranyi	1.2 & 2.35	−0.99	0.58	0.27–1.14	−0.87	1.27	1.07–1.37	−0.48	0.70	0.37–1.22

The relationship consists of three segments: 1, points < breakpoint 1; 2, points between breakpoints 1 and 2; 3, points > breakpoint 2. Intercept and slope for the regression result for each segment are also given. When the slope = 1 the growth is isometric. 'CI' is the confidence interval.

Table 2. Number of individuals of *Abraliopsis morisii* and *Abralia veranyi* (by length class) caught at different depths during nighttime (00.00–06.30 and 18.30–00.00) and daytime (06.30–18.30) sampling.

Time (UTC)	Depth (m)		
Abraliopsis morisii	**DML <22.9 mm**	**DML = 22.9–35.3 mm**	**DML >35.3 mm**
00.00–06.30	38–40 m ($n = 11$)	38–40 m ($n = 2$)	38–40 m ($n = 2$)
06.30–18.30	356–402 m ($n = 5$)	356–402 m ($n = 10$)	–
18.30–00.00	38–49 m ($n = 7$)	38–90 m ($n = 49$)	38–90 m ($n = 33$)
Abralia veranyi	**DML <20.6 mm**	**DML = 20.6–30.9 mm**	**DML >30.9 mm**
00.00–06.30	–	–	–
06.30–18.30	308–1,035 m ($n = 19$)	308–1,035 m ($n = 39$)	308–1,035 m ($n = 15$)
18.30–00.00	98–219 m ($n = 4$)	98–219 m ($n = 27$)	98–219 m ($n = 15$)

We analysed the capture depth of *Abraliopsis morisii* and *A. veranyi* as a function of hour of the day (Table 2). Specimens of *Abraliopsis morisii* were caught during the night at depths of 38–90 m. While this represented 87.4% of the total number of individuals obtained for this species, 12.6% were caught during the day at depths ranging from 356 to 402 m. Similarly, for *A. veranyi*, 63.0% of individuals were captured during the night (between depth of 98–219 m) and 37.0% were obtained during the day (depth of 308–1,035 m). A Kruskal–Wallis test indicated nonsignificant differences in the vertical distribution of the DML of *A. veranyi* ($H = 116.11$, df = 114, $P = 0.43$) and *Abraliopsis morisii* ($H = 113.22$, df = 111, $P = 0.42$). Both enoploteutid species were caught during nighttime hours by deep-water trawls and during daytime hours by near-surface trawls, indicating that these cephalopods show a clear diel migratory pattern.

The breakpoint analysis showed significant morphometric changes during ontogeny for both *Abraliopsis. morisii* (SLR: $R^2 = 0.95$, LOSS = 1.43; PLR: $R^2 = 0.97$, LOSS = 1.38; Fig. 2) and *A. veranyi* (SLR: $R^2 = 0.96$, LOSS = 2.51; PLR: $R^2 = 0.97$, LOSS = 2.01; Fig. 3). The relationship between $\log_e$ TW and $\log_e$ HW showed that for both species there were two morphometric changes during growth. *Abraliopsis morisii* had two ontogenetic changes at a TW of 0.68 g and 2.29 g, respectively, while for *A. veranyi* these occurred at a TW of 0.81 g and 2.27 g, respectively (Figs 2, 3). In both species, the rate of increase of HW relative to TW was high after the first slope change, but declined after the second slope change (Figs 2, 3). These ontogenetic changes show that *Abraliopsis morisii* has its first morphometric change at 22.9 mm and the second one at 35.3 mm DML, while in *A. veranyi* they occur at 20.6 mm and 30.9 mm DML (Figs 2, 3). On the basis of the breakpoint analysis, each of the two species was grouped into three length classes: small (corresponding to data points occurring in the plot up to the first slope shift), medium-sized (data points between the first and second slope change) and large (data points after the second/last observable slope change).

Study of stomach contents showed that prey belonged to four taxa (Table 3). While a maximum of three prey items was found in a single stomach (this stomach appeared to be distended to maximum capacity), the stomach of 79.7% and 86.8%, respectively, of *Abraliopsis morisii* and *A. veranyi* individuals contained only a single prey item. Stomach fullness was quite variable, but typically lower during the day than at night (Fig. 4), indicating nocturnal feeding. A Kruskal–Wallis test showed significant differences in stomach fullness between nighttime and daytime for both *A. veranyi* ($H = 54.51$, $n = 119$, $P < 0.00001$) and *Abraliopsis morisii* ($H = 12.30$, $n = 119$, $P = 0.015$). A Tukey HSD *post hoc* test ($\alpha = 0.05$) also found significant differences between daytime and nighttime in both species ($P < 0.03$; Fig. 4).

Crustaceans were the most abundant prey items in the stomachs of both species. Food items, when present, were heavily digested, making identification of prey species difficult. Nonetheless, we found that decapods constituted a large proportion of the crustaceans. A $\chi 2$ test showed highly significant differences in the diet of the three length (DML) classes of *Abraliopsis morisii* ($P < 0.01$). The smallest specimens (DML <22.9 mm) of *Abraliopsis morisii* were shown to feed mainly on copepods (IRI = 83.7%), unidentified crustaceans (IRI = 14.4%) and mysids (IRI = 1.9%), while individuals in the medium-sized length class (DML = 22.9–35.3 mm) preyed almost exclusively on decapods (IRI = 91.0%). The largest specimens (DML >35.3 mm) also preyed mainly on crustaceans (IRI = 78.3%), but fish (IRI = 16.7%) and cephalopods (5.0%) were prevalent components of their diets. The possibility that the cephalopods were preyed upon when the captured study animals were in the net was rejected. This was because prey items were found to be in an advanced state of digestion, despite the fact that the stomachs containing them were extracted and preserved (in 70% ethanol) immediately after the capture of individuals of *Abraliopsis morisii* and *A. veranyi*. *Abraliopsis morisii* showed a high stomach fullness index at night, indicating that this species feeds preferentially during nocturnal hours (Table 3).

As with *Abraliopsis morisii*, a $\chi 2$ test showed highly significant differences in diet among the three length classes of *A. veranyi* ($P < 0.0001$). The diet of the smallest individuals (DML <20.6 mm) consisted mainly of copepods (IRI = 59.9%), other

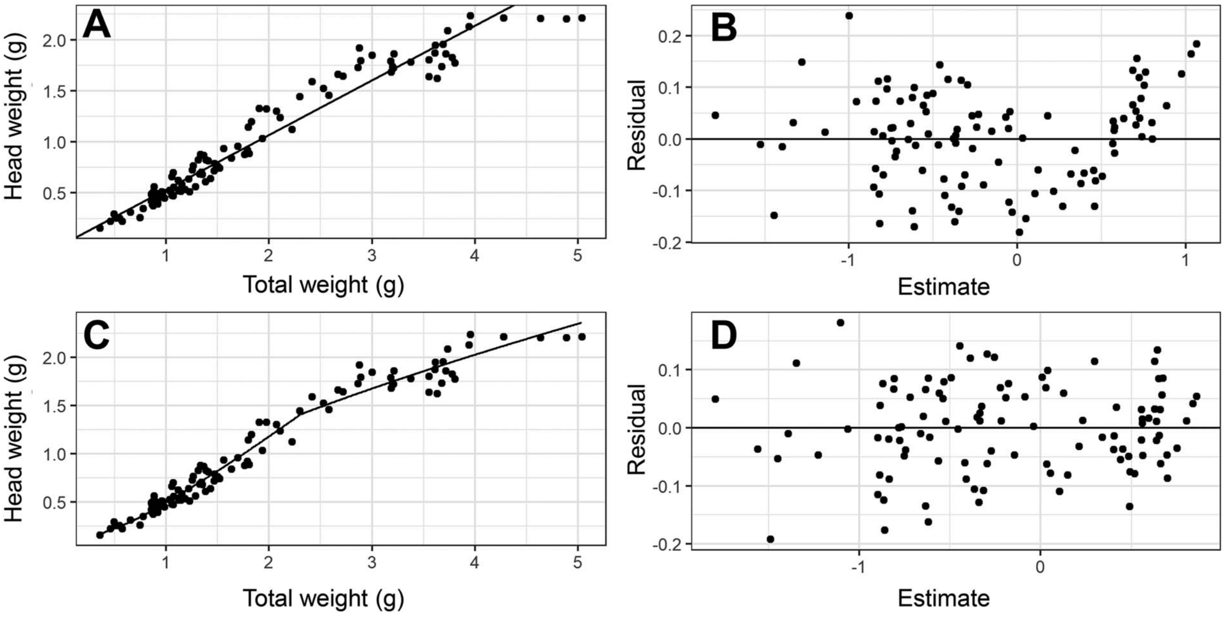

Figure 2. Breakpoint analysis for *Abraliopsis morisii*. **A.** Linear regression (SLR) for the relationship between total weight and head weight ($R^2 = 0.946$, LOSS = 1.43). **B.** Plot showing residuals from the SLR. **C.** PLR showing regression line with two breakpoints at 0.68 g and 2.29 g TW (corresponding to 22.9 mm and 35.3 mm DML, respectively; $R^2 = 0.967$, LOSS = 1.38). **D.** Plot showing residuals from the PLR. Note the lack of a pattern. Graphs shown in **A** and **B** are plotted with untransformed data for clarity; graphs **C** and **D** are plotted with $\log_e$ transformed data.

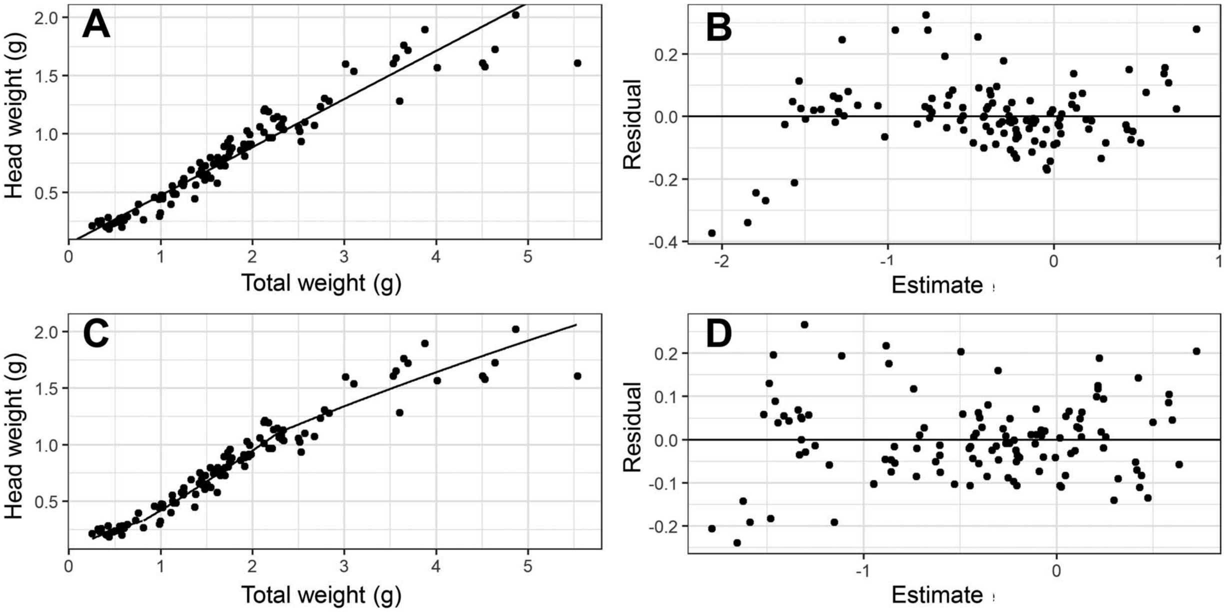

Figure 3. Breakpoint analysis for *Abralia veranyi*. **A.** Linear regression (SLR) for the relationship between total weight and head weight ($R^2 = 0.957$, LOSS = 2.51). **B.** Plot showing residuals from the SLR. **C.** PLR showing regression line with two breakpoints at 0.81 g and 2.27 g TW (corresponding to 20.6 mm and 30.9 mm DML, respectively; $R^2 = 0.969$, LOSS = 2.012). **D.** Plot showing residuals from the PLR. Note the lack of a pattern. Graphs shown in **A** and **B** are plotted with untransformed data for clarity; graphs **C** and **D** are plotted with $\log_e$ transformed data.

unidentified crustaceans (IRI = 18.0%) and mysids (IRI = 7.0%), while medium-sized individuals (DML = 20.6–30.9 mm) preyed more frequently on decapod crustaceans (IRI = 85.3%), other crustaceans (IRI = 10.7%) and, to a much lesser extent, fish (IRI = 2.5%). The diet of the largest specimens (DML > 30.9 mm) of *A. veranyi* consisted of fish (IRI = 49.3%), crustaceans, mainly in the form of decapods (IRI = 26.8%), and cephalopods (IRI = 10.6%; Table 3). In contrast to *Abraliopsis morisii*, medium-sized individuals and adults of *A. veranyi* preyed on fish at any time of the day, but on cephalopods only during daylight hours (Table 3).

Figure 4 shows the prey composition of the diet in relation to depth for both species. Crustaceans were recovered from the stomach of individuals caught across the whole depth range sampled (8–1,035 m depth). While copepods (27% and 42% IRI for *A. veranyi* and *Abraliopsis morisii*, respectively) were the most abundant prey in the diet of individuals caught in the upper 200 m of the sea, decapods predominated in the diet of individuals from waters between 200 and 500 m, reaching an IRI value of 88.7% for *A. veranyi*, but only 1% for *Abraliopsis morisii* at that same depth interval. In relation to depth intervals, fish were more abundant in

Table 3. Relative importance index (IRI) for the different prey taxa found in the stomach contents of *Abraliopsis morisii* and *Abralia veranyi* during daytime and nighttime.

	DML <22.9 mm			**DML = 22.9–35.3 mm**			**DML >35.3 mm**		
	% IRI			**% IRI**			**% IRI**		
	Total (*n* = 20)	**Night (*n*=15)**	**Day (*n* = 5)**	**Total (n = 64)**	**Night *n* = 51)**	**Day (*n* = 13)**	**Total (*n* = 35)**	**Night (*n*=35)**	**Day (*n* = 0)**
Abraliopsis morisii									
Copepods	83.7	35.3	80.0						
Mysids	1.9	12.7							
NI crustacea	14.4	1.8	20.0	76.2	98.6	98.1	78.3	80.2	
Decapod crustacea				23.5	0.0	1.9			
Cephalopods				0.2	0.7		5.0	5.6	
Fish				0.1	0.7		16.7	14.2	

	DML <20.6 mm			**DML = 20.6–30.9 mm**			**DML >30.9 mm**		
	% IRI			**% IRI**			**% IRI**		
	Total (*n* = 23)	**Night (*n* = 4)**	**Day (*n* = 19)**	**Total (*n* = 66)**	**Night (*n*=27)**	**Day (*n* = 39)**	**Total (*n* = 30)**	**Night (*n*=15)**	**Day (*n* = 15)**
Abralia veranyi									
Copepods	59.9		59.9	0.8		0.9			
Mysids	7.0		7.0	0.7		0.8			
NI crustacea	18.0		18.0	10.7	78.6	5.0	13.2	57.3	9.6
Decapod crustacea	15.1		15.1	85.3	14.5	91.5	26.8		31.3
Cephalopods				0.04		0.1	10.6		12.4
Fish				2.5	6.9	1.7	49.3	42.7	46.7

Data are presented in relation to the length classes of the two species. ‘NI crustacea’ indicate non-identified crustacea.

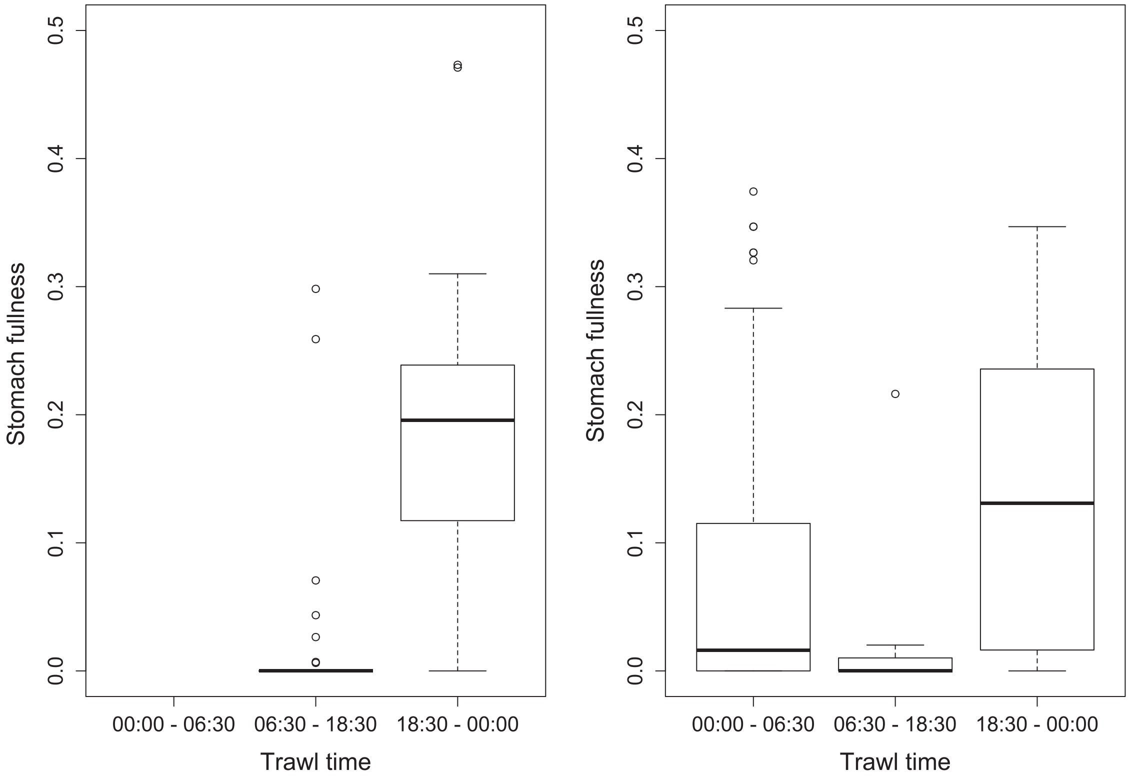

Figure 4. Relationship between stomach fullness and trawl time. **A.** *Abralia veranyi* (*n* = 119). **B.** *Abraliopsis morisii* (*n* = 119).

the stomach contents of *A. veranyi* caught between depths of 500–1,000 m (18.2% IRI) than in the stomach contents of individuals from shallower waters. In the case of *Abraliopsis morisii*, fish were only present in the stomach contents of individuals caught in shallower waters (0–200 m depth; IRI of 5.7%). Mysids and cephalopods were relatively scarce in the diet of both species; they were most common in *A. veranyi* caught at depths of 500–1000 m. For *Abraliopsis morisii*, cephalopods were found only in the stomachs of individuals from depths between 0 and 200 m and mysids were recorded only from individuals caught between depths of 200–500 m (Fig. 5).

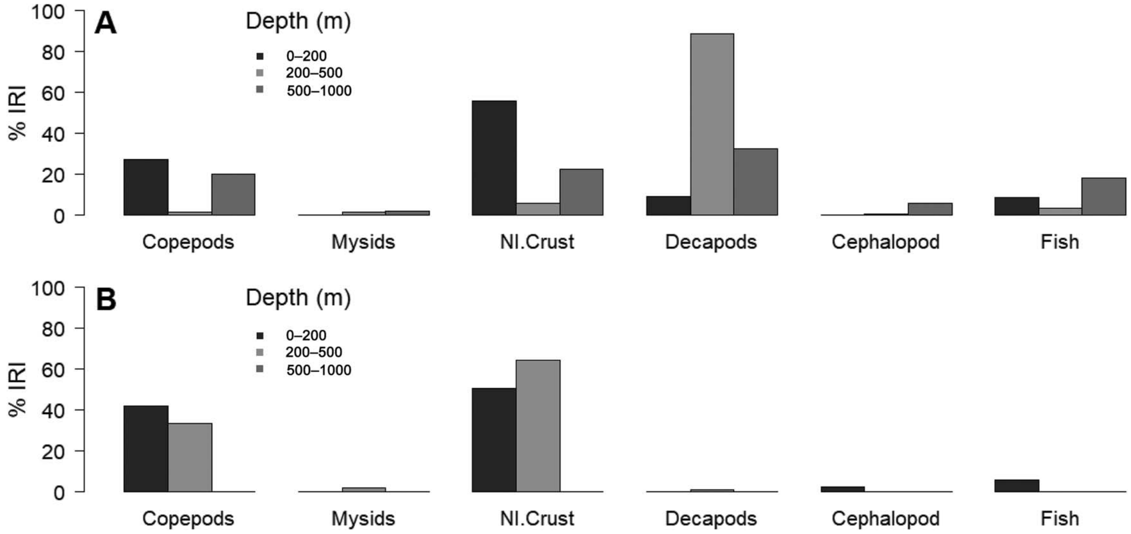

Figure 5. Relationship between taxa found in the stomach contents and depth. **A.** *Abralia veranyi* ($n = 119$). **B.** *Abraliopsis morisii* ($n = 119$). Non-identified crustacea are indicated by 'NI.Crust'.

DISCUSSION

Abralia veranyi and *Abraliopsis morisii* feed mainly on zooplankton, particularly on copepods, mysids and the early growth stages of decapod crustaceans. Despite similar feeding behaviour, these two enoploteuthid species differ in the prey composition of their diets. Moreover, the diet of both species showed variability in relation to their circadian cycles; this was particularly marked in *Abraliopsis morisii*.

Our observations indicate that the diet of both species changes significantly with growth, with the diets of larger individuals containing a greater share of other cephalopods and fish than smaller individuals. During ontogeny, individuals of both enoploteuthid species undergo two changes in the growth cycle and these probably relate to rapid changes in the ecology of these species; similar changes have been described by Castro & Hernández-García (1995) and Shea & Vecchione (2002) for other cephalopod species. As the body and head increase in size during growth, the buccal mass also increases in size. This facilitates the capture and consumption of larger, more robust prey, and studies have shown a direct relationship between the size of individuals and the type of prey consumed (Castro & Hernández-García, 1995; Sugimoto & Ikeda, 2013). The capacity to feed on larger prey is also associated with a significant increase in swimming speed and mode of hunting (Sugimoto & Ikeda, 2013). These changes in ontogenetic growth and diet may also be indicative of growth-related habitat shifts or the capacity for greater vertical movement through the water column (Shea & Vecchione, 2010).

The presence of copepods in the diet of smaller individuals of *Abraliopsis morisii* and *A. verany*i can be explained by the relatively high abundance of this zooplankton group in surface waters. Hernández-León, Gómez & Arístegui (2007) have shown that copepods are extremely abundant in the shallow waters off the Canary Islands, where they represent *c.* 90% of the zooplankton community. Although the presence of members of the family Enoploteuthidae in epipelagic waters (0–200 m depth) has been reported by Roper (1972), our observations indicate that smaller individuals (DML <12 mm) of both *Abraliopsis morisii* and *A. verany*i occur in surface waters, particularly at night. However, we did not find significant differences in depth distribution among small, medium-sized and large individuals of the two species. Nevertheless, it is obvious that increases in body musculature allow these species to migrate into the deeper mesopelagic layer (Röpke, Nellent & Piatkowski, 1993). This ontogenic change in behaviour is believed to result from reduced visual predator–prey interactions in the light-limited deep sea, as has been described for other cephalopod species (Hunt & Seibel, 2000).

Changes in the prey composition of the diet in relation to ontogenetic shifts have been reported for mesopelagic fish (Watanabe, Kawaguchi & Hayashi, 2002; Bernal *et al*., 2015) and epipelagic cephalopods (Castro & Hernández-García, 1995; Mouat, Collins & Pompert, 2001). As we observed, *Abraliopsis morisii* and *A. veranyi* are distributed throughout the mesopelagic layer during the daytime and ascend at night to the epipelagic region to feed (the two species feed at different depth levels and this may reduce interspecific competition). This feeding migration resembles that described by Sassa *et al.* (2002), Yatsu *et al*. (2005) and Takagi *et al.* (2009) for mesopelagic fish.

We found heavily digested prey items in the stomach of most of the individuals investigated and this suggests that most individuals had fed during the hours prior to capture. Contrastingly, we also found that many individuals had empty stomachs, indicating that these individuals had yet to feed. Sassa *et al*. (2002) has reported vertical migratory behaviour for mesopelagic fish, with some myctophid fish species being shown to have a diel vertical migratory pattern related to feeding. Most studies of vertical migration have focused on fish (McClatchie & Dunford, 2003; D'elia *et al*., 2016) and comparable data on the migration of mesopelagic cephalopods are scarce (Young, 1995; Hernández-García, Bordes-Caballero & Almonacid, 2006). Vertical migration to feed during nocturnal hours is common in mesopelagic fish (Yatsu *et al*., 2005; Takagi *et al*., 2009), but has been less extensively described in mesopelagic cephalopods (Passarella & Hopkins, 1991). Our study has shown that the cephalopods *Abraliopsis morisii* and *A. veranyi* feed between dusk and dawn in the epipelagic zone (0–200 m depth), pointing to the possibility that these species play a key role in the oceanic food web (Clarke, 1996; Ariza, 2015) and in the sequestration of carbon. We found that individuals of both species exhibited greater stomach fullness during nighttime hours compared with daytime hours, and this observation is consistent with vertical migration to the surface at night to feed.

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First assessment of the spearfishing impact in the Canary Islands

David Jiménez-Alvarado[a,*], Airam Guerra-Marrero[a], Airam Sarmiento-Lezcano[b], Eva K.M. Meyers[c], José J. Castro[a]

[a] *Instituto Universitario EcoAqua, Edf. Ciencias Básicas, Campus de Tafira, 35017 Las Palmas de Gran Canaria, Canary Islands, Spain*
[b] *Instituto de Oceanografía y Cambio Global, Universidad de Las Palmas de Gran Canaria, 35214 Telde, Spain*
[c] *Zoological Research Museum Alexander Koenig, Adenauerallee 160, 53113, Bonn, Germany*

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ABSTRACT

An onsite survey was conducted between June and December 2017 to characterize recreational spearfishing in the Canary Islands. This activity takes place throughout the entire year with higher catches in the summer and autumn months. The total estimated effort in 2017 was 658,798 fishing journeys; 34.5% of these journeys had no captures. The average catch per fisherman was 0.654 kg/h. It has been estimated that recreational spearfishing lands were approximately 480.8 t per year throughout the entire archipelago (not including non-resident fishermen). The discards were less than 10%, but in several cases they exceeded 25%. Fishermen make an average initial investment of €484.4 in fishing equipment and have an average annual expenditure of €245.14 for travel, maintenance, equipment replacement, insurance and a fishing license. In 2017, spearfishing mobilized €9.9 million only on travel and subsistence. The majority of fishermen estimate that 78.3% of the fishing areas that they visit are moderately degraded or highly degraded and that fishing resources have decreased by 25%–60% or more since they began to participate in this activity. They also indicated that the abundance and the average length of the target species increases with depth. It is noteworthy that 66.7% of the main target species have a high or very high intrinsic vulnerability index. However, spearfishermen do not assume responsibility for the possible deterioration of the permitted underwater fishing areas, and further evaluation is needed to assess the impact of all fishing activities conducted in these areas.

1. Introduction

Globally, commercial and professional fishing have been responsible for a significant reduction in stocks of various fish and invertebrate species (Swartz et al., 2010; Couce Montero et al., 2019). FAO (2018) estimated that in 2015, 93% of the fish stocks were either fully exploited or overexploited, which represents an increase compared with data from 1974. However, recent data suggests that recreational fishing also has an impact on the decline of local fisheries (Arlinghaus et al., 2002; McPhee et al., 2002; Strehlow et al., 2012).

Recreational fishing is expanding, both economically and socially. In 2015, it was estimated that 8.7 million European recreational sea anglers annually spend approximately 77.6 million days fishing, and their expenditures represent over €5.9 billion annually. The numbers of fishers, days fished and the expenditure are greater in the Atlantic than in the Mediterranean, but the Mediterranean estimates are generally less robust (Hyder et al., 2018).

In Majorca (western Mediterranean), Morales-Nin et al. (2005) estimated that the extractive capacity of this sector was approximately 34% of the total catch landed on the island. Similarly, a report from the Spanish Ministry of Agriculture, Fisheries and Food (MAPyA) on the Canary Islands (Central-eastern Atlantic) documented the extraction capacity at 40% of the total catch landed, but on highly populated islands such as Grand Canary, the proportion reached up to 63% (MAPyA, 2006). In addition, the Canary archipelago is characterized by very narrow, abrupt, volcanic, discontinuous shelves, and despite having the largest coastline perimeter (1.583 km) of Spain, it also has the lowest fishable neritic areas (Bas et al., 1995).

During the last decade, the recreational fishing sector in the Canary Islands has experienced a notable increase in the number of practitioners, exceeding 90,000 licenses (approximately 6.7% are for spearfishing) in the last 8 years (4.3–5.2% of the inhabitants of the island (s) (Table 1). This represents up to 10% of all licensed recreational fishermen in Spain (Gordoa et al., 2019).

Due to the lack of records on catches associated with recreational fishing, it is impossible to verify the contribution of non-professional fishing to the current status of overexploited stocks

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[*] Corresponding author.
E-mail address: david.jimenezalvarado@gmail.com (D. Jiménez-Alvarado).

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Table 1
Number of licenses of recreational fishing and spearfishing per year (Source: Fishing Directorate of the Canary Island Government).

	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Nº of Spearfishing licenses	–	–	–	7,838	8,166	7,307	7,106	6,794	6,353	6,085	6,225
Nº of Total recreational fishing licenses	57,622	71,697	87,000	96,190	104,084	95,786	98,134	99,445	98,089	91,437	91,046
Canary Islands inhabitant (x10^6)	1,946	1,992	2,025	2,045	2,065	2,086	2,105	2,115	2,126	2,135	2,155

in the archipelago (González, 2008; Castro et al., 2019). No quantification of the extractive power of recreational fishing activities has been performed, and there is no reliable assessment of the target species or catch levels for each recreational fishing modality. Therefore, there is a need to assess the importance and impact of recreational fishing relative to impacts from professional fishing, in regard to overfishing in the archipelago (MAPyA, 2006; Couce-Montero et al., 2015; Jiménez-Alvarado et al., 2019). Spearfishing is an underwater fishing modality that is practised using free-diving techniques (Sbragaglia et al., 2016). It would be necessary to evaluate the impact that this activity has on the 32 coastal fishing areas (18% of the total coastline of the archipelago) where it has been allowed since 1986. These data are essential to generate management strategies. However, alleging discrimination, in the last decade there has been substantial pressure on the government by spearfishing associations to open all areas to this fishing modality. It is important to note that the areas that are currently open to spearfishing are also open to other recreational fishing modalities and to professional fishing, but the reverse is not true.

In the Canary Islands, the absence of a record of catches associated with recreational fishing, including spearfishing, makes it impossible to verify the direct impact of this fishing modality on fish stocks. Moreover, it is assumed that spearfishing has a greater capacity for species selection, focusing effort on larger specimens of particular species with a higher ecological value. Therefore, in the absence of official catch data or other sources of information that allow the reconstruction of historical events to understand the direct impact of this fishery, innovative survey methods, which have their own strengths and weaknesses, should be applied (Dowling et al., 2015; Kokkalis et al., 2015; Gordoa et al., 2019).

Fishermen possess great knowledge and experience that is extremely valuable for fisheries research and management, particularly in cases where scientific data are often scarce (Fischer et al., 2015). However, a major impediment to the integration of this knowledge into the ecosystem approach to fisheries is the lack of formal guidance on this subject. For this reason, surveys, when data from more formal sources is lacking, can provide an adequate first approximation of the situation. In addition, the perception of fishermen regarding the status of these resources and ecosystems could be a valuable source of data. The validity of this type of method is widely recognized, although limitations are also acknowledged (Berkson et al., 2011; Dowling et al., 2015). This type of information is also useful to monitor catches (Machado-Martins et al., 2018).

In this context, the aim of this study was to conduct an initial characterization of spearfishermen, the fishing activity, costs associated with fishing, and catch composition.

2. Materials and methods

To obtain information on spearfishing activities, an on-site survey was used to interview recreational spearfishermen (Appendix). The form consisted of 34 questions. The survey was structured with 7 thematic blocks, the most important being those questions designed to define the fishing activity (8 questions) and the state of the target species (7 questions). The fisherman's impression of conservation status of the habitats was also evaluated (5 questions). In addition, 8 questions defined the social and economic profile of the fishermen, and another 4 questions established the way in which the fishing activity is conducted and the areas where it is typically performed. The last two questions recorded the impression of fishermen regarding the effectiveness of the existing management measures.

The surveys were conducted directly in the spearfishing areas both on working days, in the morning and afternoon, and on holidays, on all the islands of the archipelago between June and December 2017. After making a preliminary selection of the areas that were theoretically those most frequented by spearfishermen on each of the islands, the on-site surveys were conducted by groups of up to 5 interviewers. Most spearfishermen were reticent about answering the questions, but 93 interviews were completed and analysed.

A total of 144 visual scuba diving censuses (census Labrosse, 2002) of fish communities were conducted in 9 of the 32 areas where spearfishing is allowed (Fig. 1) and in 9 areas where it is prohibited as a control at depths from 0 m to 15 m on the islands of Lanzarote, Fuerteventura, Grand Canary, Tenerife and La Palma. The fishing areas visited were selected based on previous surveys that determined the areas most frequented by spearfishermen on each island. The control areas were randomly selected from nearby areas. The censuses were conducted by two divers with extensive knowledge of the common species in the shallow waters of the islands. Four linear underwater transects were completed for each sampled area (50 m × 5 m), and all the species were recorded on a PVC tablet. The information recorded by the divers included: (i) local or scientific name, (ii) number of individuals counted within the field of vision, (iii) approximate length of the recorded individuals, (iv) characteristics of the bottom, (v) depth of the transects (depth at the beginning and the end of the transect), (vi) water temperature, and (vii) sea conditions (visibility, wave action, etc.). Generally, the visibility was greater than 15 m.

The fish biomass was estimated from length–weight relationships of the identified species (Table 2). In most cases, the length–weight relationships were obtained from the literature based on research conducted in the Canary Islands or authors' own unpublished data.

The comparison of the ecological characteristics of the different fishing areas relative to the control areas was accomplished using the similarity index (Diversity β) of Jaccard ($Ij = c/(a + b - c)$) and the Sørensen index ($Is = 2c/(a + b)$), where a is the total number of species in community A; b is the total number of species in community B, and c is the number of species in common between the communities (Washington, 1984). Moreover, for each sampled area, the Shannon–Wiener diversity index was calculated, which combines species richness and relative abundance ($\mathrm{H} = -\Sigma_{\mathrm{i}=1}^{\mathrm{S}}\, p_{\mathrm{i}} \ln p_{\mathrm{i}}$), where p is the proportion (n/N) of individuals of each species found (n) divided by the total number of individuals found (N), ln is the natural logarithm, Σ is the sum of the calculations, and s is the number of species (Spellerberg and Fedor, 2003).

The vulnerability index (VI) was determined based the intrinsic characteristics of the biology of the species such as the life cycle or ecological variables that increase the sensitivity to or inhibit the recovery from a threat. For example, late maturity may increase the sensitivity to and inhibit species recovery from

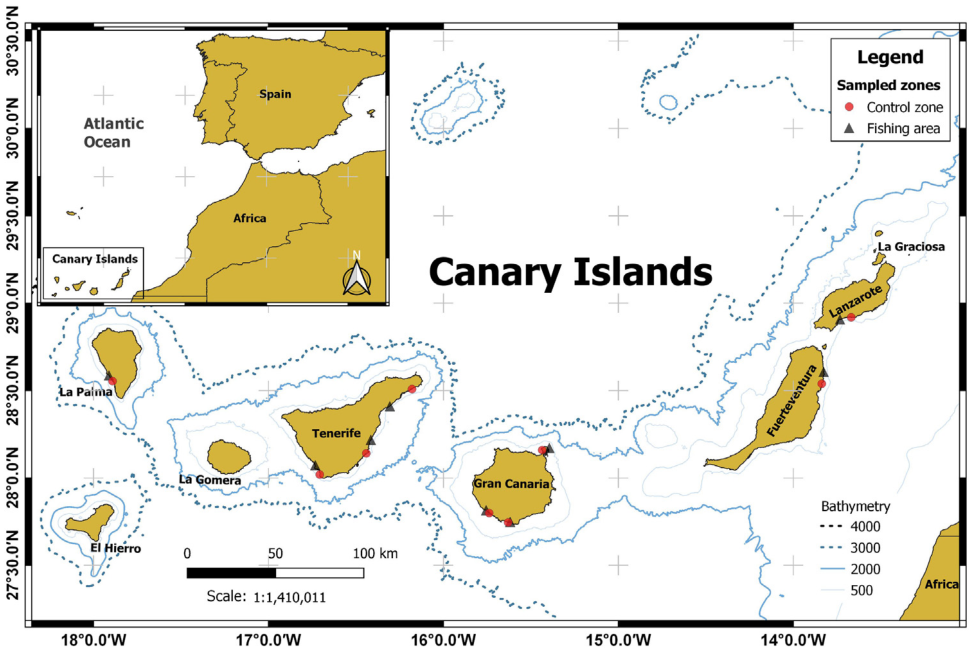

Fig. 1. Geographical distribution of the evaluated areas around the Canary Islands. QGIS Development Team (2020).

fishing pressure because individuals are more likely to be caught before spawning, which extends the time that populations require to rebuild their biomass after it has been removed (Stearns, 1992). The VI values were obtained from FishBase (Froesen and Pauly, 2018). The VI ranges from 1 and 100; the closer to the maximum value, the greater the vulnerability (between 0 and 30 the vulnerability is low, between 30 and 50 the vulnerability is moderate, between 50 and 70 the vulnerability is high, and above 70 the vulnerability is very high) (Cheung et al., 2005).

Different non-parametric statistical tests were conducted to clarify if there were differences in the biodiversity, biomass and status of target species of spearfishers between fishing grounds or islands (Kruskal–Wallis ANOVA). In a same way, a similarity in species diversity between areas was also tested carrying out a PERMANOVA analysis.

3. Results

3.1. Profile of the spearfisherman

The age range of the spearfishermen interviewed in the Canary Islands was between 16 and 63 years old; 89.9% were 18–45 years old and the mean age was 32.5 years old (SD = 6.2). All respondents were males and only 9.3% were unemployed. Most spearfishermen (82.8%) fished in the company of others. Their fishing method consisted predominantly of visits to holes/crevices, which are used as a refuge by large fish species. In total, 6.9% of the interviewed candidates did not hold a compulsory fishing license.

The majority of spearfishermen (89.2%) fished in rocky areas no deeper than 35 m, and typically accessed the fishing grounds from land (only 16.2% of respondents used a boat to access their fishing grounds). Almost 76% of the spearfishermen alternated between different fishing areas, although they showed a certain fidelity towards specific areas. More than 70% of spearfishermen fished in the same areas more than 7 times a year.

3.2. Target species

The spearfishermen targeted a wide diversity of fish and cephalopod species, but the majority exert more pressure on bento-demersal species (Table 3). Among the target species, the parrotfish (*Sparisoma cretense*), dusky grouper (*Epinephelus marginatus*) and octopus (*Octopus vulgaris*) were caught most frequently. More than half of the interviewed fishermen recognized the dusky grouper (*E. marginatus*) as a rare species in their catches along with the dentex species (*Dentex* spp.) and the island grouper (*Mycteroperca fusca*). However, although they were considered an occasional catch, seabreams (primarily *Diplodus sargus cadenati*) were a main target species along with the dusky grouper (*E. marginatus*), island grouper (*M. fusca*), parrotfish (*S. cretense*) and common octopus (*O. vulgaris*) (Table 4).

3.3. Fishing effort

Recreational spearfishing in the Canary Islands is conducted throughout the entire year. However, 55.2% of the fishermen indicated that the volume of catches shows some seasonality with the highest captures during October and November.

On average, 75.7% of spearfisherman fish once or twice a week, although 3% claimed to go fishing almost daily. The average number fishing days per week was 1.9 (± 1.2). However, not all fishing days were productive; in approximately 34.4% (± 21.7) of cases, the catch was zero. The average number of days of fishing per year was 99, but only on 64.8 days did fishermen report catching fish. Moreover, each fisherman dedicated between one and seven hours per fishing journey with an average of 3.3 (± 1.5) fishing hours per journey.

3.4. Captures

The current fishing regulation (Decree 182/2004) establishes a maximum catch of 5 kg per person per day (as several individuals or as a single individual of greater weight). The catches obtained by spearfishermen were generally in compliance with the current regulation with an average capture per successful fishing journey of 3.3 kg (± 2.3). This capture rate translates to a performance of 0.654 kg/hour.

Overall, recreational spearfishing extracted approximately 930,6 t in 2017 along the entire archipelago. If non-resident fishers (674 people, primarily tourists) are excluded, the total

Table 2
Parameters (a and b) of the length–weight relationships used to estimate fish biomass recorded during visual census.

SPECIES	a	b	STUDY AREA	SOURCE
Sarpa salpa	0.0000134	3.011	Canary Islands	Villamil et al. (2002)
Thalassoma pavo	0.0092	3.111	Azores	Morato et al. (2001)
Sparisoma cretense	0.0157	3.0128	Canary Islands	Espino et al. (2016)
Mullus surmuletus	0.0074	3.1826	Canary Islands	Pajuelo et al. (1997)
Pagrus pagrus	0.017947	2.9583	Canary Islands	Pajuelo and Lorenzo (1996)
Diplodus sargus cadenati	0.000023	2.96	Canary Islands	Pajuelo and Lorenzo (2004).
Pagellus erythrinus	0.0117	3.0609	Canary Islands	Espino et al. (2016)
Spondiliosoma cantharus	0.012	3.0921	Canary Islands	Espino et al. (2016)
Canthigaster capistrata	0.0353	2.8488	Canary Islands	Espino et al. (2016)
Diplodus anularis	0.0217	2.9025	Canary Islands	Espino et al. (2016)
Similiparma lurida	0.0344	2.813	Azores Is.	Morato et al. (2001)
Chromis limbata	0.0142	3.058	Azores Is.	Morato et al. (2001)
Bothus podas	0.0082	3.124	Azores Is.	Morato et al. (2001)
Synodus saurus	0.0034	3.332	Azores Is.	Morato et al. (2001)
Lithognathus mormyrus	0.0000275	2.9071	Canary Islands	Lorenzo et al. (2002)
Trachinotus ovatus	0.0000428	2.662	Canary Islands	Moreno-Moreno (1999)
Sphoeroides marmoratus	0.0204	2.9026	Canary Islands	Espino et al. (2016)
Stephanolepis hispidus	0.0218	2.93	Canary Islands	Mancera-Rodríguez and Castro-Hernández (2015)
Serranus atricauda	0.03898	2.764428	Canary Islands	Santana and Castro (2007)
Serranus scriba	0.01	3.1	Canary Islands	Tuset et al. (2005)
Epinephelus marginatus	0.212	3.444	Kenya	Mbaru et al. (2010)
Myteroperca fusca	0.00000713	3.098	Canary Islands	Bustos-Leon (2009)
Pagrus auriga	0.0086	3.014	Canary Islands	Pajuelo et al. (2006b)
Xyrichtys novacula	0.0148	2.9668	Canary Islands	Espino et al. (2016)
Oblada melanura	0.00000127	3.404	SW-Portugal	Gonçalves et al. (1997)
Balistes carolinensis	0.0088	3.152	S Portugal	Santos et al. (2002)
Pseudocaranx dentex	0.02	3.006	Azores	Afonso et al. (2008)
Sphyraena viridensis	0.0036	3.016	Azores	Morato et al. (2001)
Pomadasys incisus	0.0000039	3.264	Canary Islands	Moreno-Moreno (1999)
Scorpaena maderensis	0.0111	3.19	Sicyli	La Mesa et al. (2005)
Heteropriacanthus cruentatus	0.026	2.84	Guam (USA)	Kamikawa et al. (2015)
Bodianus scrofa	0.01	3.133	Cape Verde Is.	Pereira et al. (2012)
Atherima presbyter	0.004521	3.0771	Canary Islands	Pajuelo and Lorenzo (2000)
Boops boops	0.00000030	3.237	Canary Islands	Moreno-Moreno (1999)
Centrolabrus trutta	0.0092	3.0658	Azores	Azevedo et al. (1999)
Mugil cephalus	0.000005	3.086	Canary Islands	Moreno-Moreno (1999)
Diplodus vulgaris	0.00001756	2.987	SW Portugal	Gonçalves et al. (1997).
Diplodus cervinus cervinus	0.00000838	3.14	SW Portugal	Gonçalves et al. (1997)
Dentex gibbosus	0.01014	3.0812	Canary Islands	Pajuelo and Lorenzo (1995)
Henteroconger longissimus	0.00102	3.06	FISHBASE	Froese et al. (2014)
Gymnothorax unicolour	0.00095	3.09	FISHBASE	Froese et al. (2014)
Octopus vulgaris	0.0007	3.096	Canary Islands	Hernández López (2000)
Sepia officinalis	0.2871	2.6308	Canary Islands	Almonacid-Rioseco (2006)
Serranus cabrilla	0.00007337	2.661	SW Portugal	Gonçalves et al. (1997)
Squatina squatina	0.00871	3.02	FISHBASE	Froese et al. (2014)
Thachinus draco	0.00001921	2.930	SW Portugal	Gonçalves et al. (1997)
Aulostomus strigosus	0.002	3.19	FISHBASE	Froese et al. (2014)
Apogon imberbis	0.0124	3.1079	SE Spain	Valle et al. (2003)
Ophioblennius atlanticus	0.00000135	2,379	Gulf of México	Bohnsack and Harper (1988)
Myliobatis Aquila	0.0008	3.34	North Egean	Filiz and Bilge (2004)
Dasyastis pastinaca	0.00238	3.248	Central Egean	Özaydin et al. (2007)

catch was 836.5 t. Assuming that the respondents in this study were the most active fishers and introducing the correction by Ruiz et al. (2014), the total catch obtained was 480.8 t.

3.5. Discards

A total of 81% of spearfishermen reported injuring fish during fishing activities. It is important to point out that although this fishing modality is considered highly selective, there is a level of discard that is generated by the catches due to misfiring or practice shooting on low-value species. Although the majority of estimates of the discard, when generated, were less than 10% of the catch, in some cases it exceeded 25%. In general, the discarded species were those with low economic value such as mullet (*Liza aurata*), flounder (*Bothus podas*), damselfish (*Chromis limbata* and *Similiparma lurida*) and bogue (*Boops boops*). Some high value species that did not reach the minimum legal length such as parrotfish (*Sparisoma cretense*), sea bream (*Diplodus* spp.), dusky grouper (*Epinephelus marginatus*), island grouper (*Mycteroperca fusca*), and glasseye (*Heteropriacanthus cruentatus*) were also reported, among others. Only 33% of respondents indicated that their fishing activity generated no discards.

3.6. Economic valorization

Spearfishing required an average initial investment of €484.4 (± €427.6), primarily for the acquisition of neoprene suits, flippers and mask, weights, spear gun, and the fishing license (valid for 3 years). The average annual expenditure for spearfishing was €245.1 (± €257.5), which includes short trips, maintenance costs, renewal of part of the equipment, and sport-related accident insurance. On each fishing day, the average spending was approximately €16.0 (± €11.4), which was primarily related to travel and maintenance costs but also to a lesser extent it was used for spare parts for the fishing equipment, batteries, etc. and in some cases the costs associated with using a boat.

Table 3
Occurrence per fishing journey of target species in the catches of spearfishermen in the Canary Islands and vulnerability index of each species.

Species	Frequent (>25%)	Usual (10%–25%)	Rare (< 10%)	Dk/Da	VI
Acanthocybium solandri	–	7.1	–	92.9	46
Balistes capriscus	7.1	14.3	–	78.6	49
Bodianus scrofa	–	14.3	7.1	78.6	53
Dentex spp. (*D. gibbosus*)	–	–	57.1	42.9	60
Dicentrarchus labrax	–	14.3	7.1	78.6	69
Diplodus spp. (*D. sargus cadenati*)	–	7.1	14.3	78.6	57
Epinephelus marginatus	28.6	21.4	50.0	0	72
Muraena spp. (*M. augusti*)	7.1	–	–	92.9	59
Mycteroperca fusca	7.1	7.1	57.1	28.7	58
Pomatomus saltatrix	–	21.4	–	78.6	63
Pseudocaranx dentex	–	–	14.3	85.7	74
Seriola spp. (*S. dumerili*)	–	7.1	28.6	64.3	54
Serranus spp. (*S. cabrilla*)	–	7.1	–	92.9	36
Sparisoma cretense	42.8	42.8	–	14.4	36
Sphyraena viridensis	–	7.1	7.1	85.8	69
Spondyliosoma cantharus	7.1	–	–	92.9	37
Octopus vulgaris	21.4	7.1	–	71.5	78
Sepia officinalis	–	7.1	–	92.9	30

Table 4
Percentage of fishermen that have different target species during spearfishing in the Canary Islands.

Species	Frequently targeted	Occasionally targeted	Not target	Dk/Da
Acanthocybium solandri	7.1	–	–	92.9
Dentex spp.	7.1	5.1	–	87.8
Dicentrarchus labrax	21.4	21.4	–	57.2
Diplodus spp.	64.3	7.1	7.1	21.5
Epinephelus marginatus	42.9	28.6	14.3	14.2
Mycteroperca fusca	50.0	14.3	7.1	28.6
Pomatomus saltatrix	7.1	14.3	7.1	71.5
Seriola spp.	21.4	7.1	–	71.5
Sparisoma cretense	43.8	56.2	–	0
Sphyraena viridensis	7.1	–	–	92.9
Octopus vulgaris	35.7	14.3	–	50.0

Table 5
Percentage of reduction of captures declared by fishermen since the year that they began to fish.

Species	<10%	10%–25%	25%–60%	>60%
Bodianus scrofa	–	100	–	–
Dentex spp.	33.3	–	33.3	33.3
Diplodus spp.	7.1	42.9	50	–
Epinephelus marginatus	14.3	14.3	64.3	7.1
Mycteroperca fusca	20	20	60	–
Pseudocaranx dentex	50	25	25	–
Seriola spp	25	25	25	25
Sparisoma cretense	–	57.1	42.9	–
Sphyraena viridensis	100	–	–	–
Octopus vulgaris	–	33.3	66.7	–

Table 6
Tendency of presence of target species in the catches of spearfishing during the last 5 years.

Species	Decreasing	Increasing	Stable	Dk/Da
Acanthocybium solandri	5.6	–	–	94.4
Balistes capriscus	5.6	–	5.6	88.8
Dentex spp.	16.7	–	5.6	77.7
Dicentrarchus labrax	–	16.7	5.6	77.7
Diplodus spp.	50.0	–	27.8	22.2
Epinephelus marginatus	55.6	16.7	5.6	22.1
Mycteroperca fusca	33.3	5.6	11.1	50.0
Pseudocaranx dentex	11.1	–	–	88.9
Seriola spp.	16.7	5.6	5.6	72.1
Sparisoma cretense	33.3	16.7	50.0	0.0
Sphyraena viridensis	11.1	–	–	88.9
Spondyliosoma cantharus	–	–	5.6	94.4
Octopus vulgaris	5.6	–	16.7	77.7

3.7. Status of fishing grounds according to spearfishermen

In the fishing grounds where spearfishing is allowed, the accessibility of the habitats was unequal. The majority of the respondents (75.7%) indicated that only 50% of the habitat was accessible to their spearfishing. However, they also indicated that 78.3% of the habitats were moderately or highly degraded.

Half of the respondents believed that fishing had decreased by 25%–60% or more since they had begun fishing (Table 5). Moreover, 43.2% of spearfishermen indicated that their catches had declined in the last 5 years (Table 6). The majority of individuals indicated that the abundance of the target species increased with depth and that for some species, particularly the dusky grouper (*Epinephelus marginatus*), island grouper (*Mycteroperca fusca*), and dentex species (*Dentex* spp.), it was very unusual to encounter large specimens (Tables 7 and 8). Most respondents indicated that the size of the fish specimens increased with depth, particularly in the previously mentioned species (Table 9). Most spearfishermen (86.2%) associated the symptoms of resource depletion with excessive fishing pressure. This was attributed in particular to the

Table 7
Variation in relative abundance of target species with depth.

Species	Increase abundance with depth	Decrease abundance with depth	Dk/Da
Dentex spp.	42.8	–	57.1
Dicentrarchus labrax	–	28.6	71.4
Diplodus spp.	21.4	28.6	50.0
Epinephelus marginatus	92.9	7.1	0.0
Mycteroperca fusca	78.6	–	21.4
Pseudocaranx dentex	28.6	7.1	64.3
Sparisoma cretense	35.7	28.6	25.7
Seriola spp.	21.4	–	78.6
Sphyraena viridensis	35.7	–	64.3

Table 8
Difficulties of find large specimens of target species.

Species	Difficulties to find large specimens	Dk/Da
Acanthocybium solandri	11.1	88.9
Bodianus scrofa	11.1	88.9
Dentex spp.	33.3	66.7
Diplodus spp.	5.6	94.4
Epinephelus marginatus	100.0	0.0
Mycteroperca fusca	66.7	33.3
Pomatomus saltator	22.2	77.8
Pseudocaranx dentex	16.6	83.4
Sparisoma cretense	27.8	72.2
Seriola spp.	33.3	66.7
Sphyraena viridensis	5.6	94.4

artisanal fishery but also to a lesser extent to the presence of fish farms, loss of water quality and climate change. None identified spearfishing as a cause of overfishing. In addition, 54.1% of these fishermen believed that more than 25% of the target species were overfished.

3.8. Status of fishing grounds by visual census

The Jaccard and Sørensen similarity indices between the fishing areas and their respective control zones were relatively high (over 75%) except at Fuerteventura (Table 10). This indicates that the selected control zones had an ichthyofauna similar to the areas where spearfishing was allowed, so it was reasonable to use these zones to assess the ecological and population parameters. These controls allow an assessment of the level of exploitation of the selected fishing grounds. According to Brito et al. (2002) and Espino et al. (2006), all fish and invertebrate species recorded in the visual censuses are relatively common in the shallow coastal waters of the Canary Islands. No significant differences were observed in the Shannon–Wiener diversity index (Table 10) between the fished and control areas (Mann–Whitney U test; $Z = 0.293$; $P = 0.769$; $N1 = 18$; $N2 = 18$) or among the islands (Kruskal–Wallis ANOVA, $H = 8{,}44$; $P = 0.767$). This similarity in species diversity between areas was also found after a PERMANOVA analysis using the island, area and census-taker as cofactors ($P = 0.179$).

Overall, there were no significant differences in the mean length of the fish species observed in the fishing areas compared with the control areas (Table 11). An exception was *Sarpa salpa* in the waters around Gran Canary Island, where significantly larger specimens were found in the fishing areas (ANOVA, $F = 10.56$; $P = 0.009$). However, the total fish biomass estimated in the fished areas was significantly higher than that reported in the control zones (Mann–Whitney U test, $Z = -3.948$; $P < 0.0001$; $N1 = 56$; $N2 = 72$). There were also significant differences in the biomass censed on the different islands (Kruskal–Wallis ANOVA, $H = 21.024$; $P = 0.0003$). However, it is important to note that the mean lengths estimated for the majority of the species in both areas (fishing and control areas) were smaller than the length of first maturity for those species.

4. Discussion

To date, the impact of non-professional fishing activities in the Canary Islands has been very difficult to quantify due to a lack of data on catches associated with recreational fishing (González, 2008; Castro et al., 2019). The MAPyA (2006) estimated that in 2005, 40% of the total catch in the waters around the archipelago was attributed to recreational fishing. On some islands, recreational fishing exceeded 60% of the total catch. If it is extrapolated the obtained estimations of mean fishing effort and yield per fishing journey to the entire population of spearfishermen (6.225 in 2017) this minority fishing modality alone landed over 836 t in the archipelago in 2017, although this should be confirmed with additional surveys. However, due to the level of uncertainty associated with this survey method, the total catch may have been overestimated (Gordoa et al., 2019). If the same correction factors described by Ruiz et al. (2014) in the Basque Country (North of Spain) are applied, the total capture may be much lower (480.8 t). However, in both cases, the estimates are within the range given by Gordoa et al. (2019) (914 t and 478 t, respectively). The fish that were targeted in these catches were large individuals of a few species (i.e., white seabream (*D. sargus*), pink dentex (*D. gibbosus*), parrotfish (*S. cretense*), dusky grouper (*E. marginatus*) and island grouper (*M. fusca*)). This selective capacity can accentuate the impact of this extractive activity, particularly on those more vulnerable species (Russell, 1977; Audzijonyte et al., 2013).

The selection of specific species by spearfishing is driven by either remarkable gastronomic value or the physical characteristics of the species (size, colour, etc.). As a result, the species are transformed into special trophies that stimulate the competitive desire of fishermen. As a consequence, information about the impact of this fishing activity on the target species becomes distorted and restricted. In addition, in the Canary Islands, all species targeted by spearfishers overlap with those targeted by professional fishermen and other recreational fishermen (Santana-Ojeda, 2014). The same situation has been described in other areas (Van Der Elst, 1989; Coleman et al., 2004). In certain cases, this selective action may have contributed to the problems caused by overfishing. It should be noted that 66.7% of the main target species of these fishermen have a high or very high intrinsic vulnerability index (Cheung et al., 2005), which increases their sensitivity and inhibits the recovery of these species in the face of high fishing pressure (Stearns, 1992).

It is important to note that the censuses conducted in the areas with underwater fishing activity did not show significant differences in the faunal composition or in the length distribution of the target fish species compared with other areas that are closed to spearfishing, which is evidence that overfishing is a general problem. However, the average values of fish biomass were significantly higher in these areas, probably because due to differences in habitat quality that have not been assessed in this study, weak spatial control of this fishing activity in neighbouring areas (i.e., control areas) where spearfishing is not allowed, and due to the difficult accessibility from land to many of the areas where spearfishing is allowed in the Canary Islands. For these reasons, the estimated average length for the majority of the species within the evaluated areas was lower than the length established for first maturity. This is cause for concern, because the lack of large reproductive animals is a clear symptom of overfishing that threatens the resilience of the population and causes ecological disturbances (Pennisi, 2018).

Table 9
Increase in length of specimens of target species with depth.

Species	Increase of length with depth	Decrease of length with depth	No variation in length with depth	Dk/Da
Dentex spp.	50.0	–	–	50.0
Diplodus spp.	68.8	6.3	18.8	6.1
Epinephelus marginatus	100.0	–	–	0.0
Mycteroperca fusca	81.3	–	–	18.7
Pomatomus saltator	6.3	–	–	93.7
Pseudocaranx dentex	12.5	–	6.3	81.2
Sciaena spp.	12.5	–	–	87.5
Seriola spp.	31.3	–	–	68.7
Sparisoma cretense	43.8	12.5	31.3	12.4
Octopus vulgaris	–	–	6.3	93.7
Sepia officinalis	–	–	6.3	93.7

Table 10
Values of the similarity indexes and Shannon–Wiener diversity index obtained between the different spearfishing areas and the respective control zones in each of the islands.

Island	Nº of species in the control areas	Nº of species in the fishing areas	Nº of species in both areas	Jaccard index	Sørensen index
Lanzarote	25	27	22	0.73	0.85
Fuerteventura	6	22	5	0.22	0.35
Gran Canaria	18	18	14	0.64	0.78
Tenerife	16	25	18	0.78	0.88
La Palma	12	20	12	0.60	0.75
	Shannon Index Control areas		Shannon Index Fishing áreas		
Lanzarote	2.9124		1.9492		
Fuerteventura	1.5338		3.2899		
Gran Canaria	3.6094		2.4580		
Tenerife	3.6893		3.0221		
La Palma	3.6634		3.4029		

Table 11
Average lengths and standard deviation of the most representative fish species in the control and spearfishing areas studied in the Canary Islands.

Species	Length at the control areas (cm ± SD)	Length at the fishing areas (cm ± SD)	Length at 1st maturity (cm)
Sparisoma cretense	18.1 ± 6.0	21.5 ± 7.1	23.3
Diplodus sargus cadenati	15.4 ± 4.6	19.8 ± 6.3	22.0
Diplodus vulgaris	15.9 ± 6.3	16.5 ± 5.2	22.0
Oblada melanura	18.0 ± 2.7	22.0 ± 4.5	–
Lithognathus mormyrus	20.7 ± 1.9	22.5 ± 2.7	24.6
Sarpa salpa	10.9 ± 4.3	18.0 ± 2.7	29.4
Mullus surmuletus	13.3 ± 8.3	19.0 ± 4.2	16.6
Stephanolepis hispidus	10.0 ± 0.0	9.5 ± 1.6	14.9

In the Canary Islands, it has been found that spearfishermen have a high preference for species such as the dusky grouper (*E. marginatus*), island grouper (*M. fusca*) and pink dentex (*D. gibbosus*) (which are relatively scarce in the artisanal catches) as well as large specimens of parrotfish (*S. cretense*) and seabreams (*Diplodus sargus c.*), some of which are currently classified as at risk of overfishing (Aguilera Klink et al., 1993; Tuya et al., 2006a,b; González, 2008) or are species in which sexual reversal processes occur in large specimens (Pajuelo and Lorenzo, 1995, 1996; Pajuelo et al., 2003, 2006a,b). In this sense, because spearfishing is more efficient than the other fishing modalities (in terms of catch per fishing journey, Pascual Fernández et al., 2012; Jiménez-Alvarado, 2016), it may have a more severe impact on vulnerable fish stocks. There are several examples in the scientific literature that highlight the impact of spearfishing on fish stocks (Johannes, 1978; Dayton, 1998; Pogonoski et al., 2002; Frisch et al., 2012), including the Canary Islands (Jiménez-Alvarado, 2016). In addition, it is striking that despite the high selectivity, this fishing method generates discards, although they are less than 10% of the total catch. Discards are primarily low-value species or individuals smaller than the legal length. The causes of discards are errors in shooting, multiple captures, or an overestimation of the size of the target fish. Similar effects have been described in Portuguese (Rangel and Erzini, 2007) and South African waters (Mann et al., 1997).

Caution is advised when using estimates of effort and catch that are obtained from data-poor fisheries. The information obtained from the surveys approximates the subjective perception that the fishermen have on the development of their fishing activity over a period of years, which in some cases may be more than a decade. It is therefore a mere approximation or trend in the catches over an undefined period of time rather than a quantification of actual catch volumes. However, it provides a measure of the relative impact that the activity is having within the global context of the fishery. It also establishes its socioeconomic importance and provides a realistic approximation of the conservation status of the exploited resources.

It is worth mentioning that more than half of the spearfishermen indicated that fish abundance had decreased by 25% to 60% since they began fishing (mostly before the year 2000). In addition, they declared that they had observed decreasing trends in the biomass of target species over the last five years. Moreover, the majority affirmed that almost 50% of these species are overfished and that both the abundance and the size of the specimens increase with depth. However, as indicated by Santana-Ojeda (2014), the spearfishermen did not relate these clear symptoms of the impact of fishing with their own extractive activity (there was no self-criticism), even when they described that some of the symptoms of resource exhaustion (i.e., an increase in the abundance target species and an increase in mean length with depth; questions 20 and 21 of the survey) are partially reversed at the depths where they exert less fishing pressure (deeper than 20 m); these depths are not accessible to the majority of divers due to individual differences in physical conditions. Moreover, when asked about the causes behind the decrease in catches, they do not identify their fishing activity as a part of the problem.

Recreational spearfishing in the Canary Islands occurs throughout the year, although the fishery appears to show some seasonality. Thus, the highest catches were obtained in the summer and autumn months with a peak in October and November when marine conditions are likely to be ideal, including a large number of flat days with light trade winds. The majority of these fishermen engage in this activity once or twice a week, but they do not obtain catches on 34.4% of these days. However, it is very possible that the number of fishing days per week is overestimated, because it is higher than those estimated by Pascual Fernández et al. (2012) on the island of Tenerife, which estimated 0.4 days/week. Nevertheless, those authors suggested that the level of effort appeared abnormally low, which led them to infer a tendency for spearfishermen to not declare their activity. The estimated effort in the hereby study is very close to that estimated by Santana-Ojeda (2014) for Grand Canary Island, which was up to 1.5 days/week.

Based on the surveys, each fisherman invests between one and seven hours with an average of 3.3 fishing hours per day. This is similar to the 4 h estimated by Pascual Fernández et al. (2012). These authors included preparation time, displacement and effective fishing into their time calculations. Santana-Ojeda (2014) estimated the average time dedicated to fishing at 4.29 h per journey. The estimated fishing yields in this study (0.654 kg/h) are similar to those documented by Pascual Fernández et al. (2012) for the island of Tenerife (0.542 kg/h). The authors considered this the most productive activity of all the recreational fishing modalities on the island. In comparison, Pita et al. (2018) indicated that in Galician waters, underwater fishing in 2015 landed a total annual catch of 758 t, which is very similar to that estimated for the Canary Islands (776.3 t/year), but with a fishing population that is less than half of the census in the Canary Islands. The fishing yields obtained in the Canary Islands are approximately half of those recorded in Galicia. The present results are also within the range given by Gordoa et al. (2019) of 2.42 (±0.17) kg per fishing day.

An important consideration is the economic contribution that spearfishing represents in the context of fishing in the archipelago. It is assumed that recreational fishing represents an important local economic activity, similar to other sports activities that mobilize a large number of participants. However, in the Canary Islands, there is no quantification that gives us certainty about this claim. In a study on recreational fishing in the Canary Islands conducted in 2005, the Spanish Ministry of Agriculture, Fisheries and Food (MAPyA, 2006) estimated the economic contribution of the entire recreational fishing sector at approximately €117 million per year. Much of this valuation is related to the costs associated with the acquisition of boats, moorings, equipment, fuel and insurance. Spearfishing is practised by a relatively small number of fishermen, representing less than 7% of the total recreational fishing licenses in 2017, in contrast to 83.4% shore fishermen (using fishing roads) and almost 10% of fishermen using a boat (with hook and line). Thus, its economic contribution must also be less than the other two modalities, because it does not have the costs associated with boats and their maintenance or the high numbers compared with anglers who fish from the shore (75,988 in 2017). According to the estimates obtained here, in the entire archipelago, recreational spearfishing annually mobilizes a capital of only €9.9 million in travel and subsistence. If the cost of the equipment (without accounting for depreciation) and the fishing licenses is added, this totals €12.7 million, which is almost 2.5 times higher than the estimate of Pita et al. (2018) for Galicia.

In conclusion, despite the caution that should be used with estimates of effort and catch obtained from data-poor fisheries, the estimations made indicate that recreational fishing does not play a marginal role in the status of target fish stock. Spearfishing, although it involves a small number of practitioners, could have a significant impact on more vulnerable species due to its high selectivity, particularly when species are overfished, thus accentuating the impact of global fishing. This impact could be more significant in areas such as the Canary Islands where weather conditions permit fishing year-round. The censuses of the fishing and control areas revealed a concerning scarcity of large reproductive fish in waters less than 30 m deep. Regardless, spearfishers do not assume responsibility for the possible effects of their collective fishing actions, although they are aware that abundance and length of target fish increases with depth, particularly below the depths where they exert fishing pressure. A major effort should be made by local fishery administrations to assess the actual role of recreational fishing on the status of target species and ecosystems in the Canary Islands, despite its positive social and economic impacts.

CRediT authorship contribution statement

David Jiménez-Alvarado: Conceptualization, Methodology, Investigation, Supervision, Writing - original draft. **Airam Guerra-Marrero:** Software, Investigation, Formal analysis. **Airam Sarmiento-Lezcano:** Software, Investigation, Formal analysis. **Eva K.M. Meyers:** Writing - review & editing, Data curation. **José J. Castro:** Conceptualization, Methodology, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix. Spearfishermen survey

1. How old are you?

....

2. When did you began spearfishing (year)?

....

3. Do you have a fishing license?

☐Yes ☐ No

4. Which type of licence do you have?

☐ 2nd Class ☐1st and 2nd Class ☐2nd and 3rd Class

5. Do you fish alone or with a partner?

6. In what area do you usually practise this activity? Indicate all areas.

☐G1: San Cristobal – Jinamar beach

☐G2: Punta de Tenefe – Matorral beach

☐G3: Faro de Maspalomas - Pasito Blanco

☐G4: Tauro beach – Taurito beach

☐G5: Punta Descojonado - Baja del Trabajo

☐G6: Punta de la Palma - Punta Gorda

☐G7: Punta Guanarteme - Puertito Bañaderos

☐G8: Punta del Confital - Punta del Palo

☐F1: La Puntilla - Cabo del Agua

☐F2: Punta Toneles - Gran Tarajal

☐F3: Roque del Moro - Punta de Amanay

☐F4: Caletones Mansos – Tebeto beach

☐L1: Punta Pasito - Punta Piedra Negra

☐L2: Punta Tiñosa - Punta Papagayo

☐L3: Punta Jurado - Punta la Gaviota

☐T1: Santo Domingo - Las Aguas

☐T2: Punta del Sol - Punta del Viento

☐T3: Roques de Antequera – Pta los Órganos

☐T4: Boca Cangrejo – Punta del Morro

☐T5: Roques de Fasnia – Poris de Abona

☐T6: San Miguel de Tajao – Miedo beach

☐ T7: Medano beach – Punta del Confital

☐ T8: Guincho – Colmeneras beach

☐ T9: Punta del Camisón – Barranco Erques

☐ P1: Punta la Gaviota – Punta Salvajes

☐ P2: Punta Malpais – Caleta Ancón

☐ P3: Punta Ganado – Punta Arenas Blancas

☐ P4: Puerto Naos – Roques Gabaseras

☐ G1: Punta del Viento – Punta del Peligro

☐ G2: Punta Majona – Punta Gaviota

☐ H1: Punta Norte – El Tamaduste

☐ H2: Punta de Orchilla – Punta de la Sal

7. Where do you practice your fishing activity?

☐ Rocky coasts ☐ Sandy coasts

☐ Far from the coast ☐ Other

8. Have you observed changes in your fishing areas?

No changes Half disturbed Highly disturbed Dk/Da

9. Are the fishing habitats accessible in your fishing areas?

50% accessible 50-75% accessible >75% accessible Dk/Da

10. Do you always visit the same area?

☐ Same ☐ Several ☐ All

11. In your opinion, what form of spearfishing is the most effective?

☐ Wait fishing ☐ Ambush fishing ☐ Descending ☐ Couple

☐ Hole fishing ☐ Ocean foam ☐ Deep fishing ☐ Indifferent

12. In which month is your catch largest?

13. When do you began and end your fishing season?

14. At what depth do you usually fish?

15. Can you identify the species that you catch?

☐ Yes ☐ No

16. Which are your target species and with which frequency do you catch them? (always, occasionally, rarely).

....

17. In the last five years, have you noticed a change in abundance (increase/decrease) of species in areas designated for spearfishing? (indicate species).

☐ Increase ☐ Decrease ☐ No change

18. Since you began fishing, to what degree has your catch decreased? (indicate species)

<10% 10-20% 25-60% >60% DK/Da

19. How would you describe the status of the target species? (indicate species)

<10% overfished 1-25% overfished >25% overfished Dk/Da

20. At greater depths, does species abundance increase or decrease ? (indicate the species)

Increase ☐ Decrease ☐ No change ☐

21. At greater depths, does specimen length increase or decrease? (indicate the species)

☐ Increase ☐ Decrease ☐ No change

22. It is difficult to find large specimens? (indicate de species)

☐ Yes ☐ No

23. How many kilograms do you catch per fishing journey?

24. How many times do you practice this activity during the week?

☐ 1x/year ☐ 1x/6 months ☐ 1x/3 months ☐ 1x/month ☐ 1x/2 weeks

☐ 0-1x/week ☐ 1-2x/week ☐ 2- 4x/week ☐ 4-7x/week

25. How many hours do you spend in this activity per fishing trip?

26. What proportion of fishing journeys result in zero catch?

27. When diving, have you observed damage to fish caused by this fishing activity? If yes, indicate which type of damage.

☐ Yes ☐ No

☐ Speargun ☐ fishing hooks ☐ Others.............. ☐ DK/Da

28. Do you generate discards? (indicate species)

<10% 10-20% >25%

29. Is there a seasonality in the catches? (indicate species)

☐ Yes ☐ No ☐ Dk/Da

30. In your opinion, what are the causes behind the decrease in catches?

☐ Overfishing ☐ Pollution ☐ Habitats Deterioration

☐ Spearfishing ☐ Recreational fishing ☐ Professional fishing

31. Do you start spearfishing at the coast or do you use a boat?

32. What do you spend on fishing equipment?

33. How much do you expend per fishing trip?

34. What methods can be used to recover populations?

☐ Regulated fishing ☐ Change the mentality of fishermen (information)

☐ New laws ☐ Fishing restrictions ☐ Changes of areas

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Preliminary assessment of the impact of Covid-19 Pandemic in the small-scale and recreational fisheries of the Canary Islands

Airam Guerra-Marrero [a,*], Lorena Couce-Montero [a], David Jiménez-Alvarado [a], Ana Espino-Ruano [a], Raibel Núñez-González [a], Airam Sarmiento-Lezcano [b], Ángelo Santana del Pino [c], José J. Castro [a]

[a] Instituto Universitario Ecoaqua, Universidad de Las Palmas de Gran Canaria, Edf., Ciencias Básicas, Campus de Tafira, Gran Canaria, Canary Islands, 35017 Las Palmas de Gran Canaria, Spain

[b] Instituto de Oceanografía y Cambio Global, IOCAG, Universidad de Las Palmas de Gran Canaria, Unidad Asociada ULPGC-CSIC, Campus de Taliarte, Gran Canaria, Canary Islands, 35214 Telde, Spain

[c] Department of Mathematic, Universidad de Las Palmas de Gran Canaria, Campus de Tafira, Gran Canaria, Canary Islands, 35017 Las Palmas de Gran Canaria, Spain

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ABSTRACT

Covid-19 pandemic has affected worldwide in many different ways. Fisheries around the world are not an exception due to the long-term isolation and the non-activities period suffered. To do an evaluation of its impact on the fishing sectors in the Canary Islands, 87 online and phone questionnaires were carried out between July and September 2020, conducting the interviews to artisanal fishermen, fishmongers, recreational charter boats fishermen and tackle shops along the archipelago. Both, the artisanal and recreational fishing sectors have been affected by this pandemic, but in an unequal manner. The drop of the demand of fresh fishing products in the islands markets due to the closure of hotels, restaurants and other services, and the highly significant decreasing in the number of tourists, provoked an estimated income loss for the artisanal fishermen about the 40% on average, but the majority of vessels continued their activities during the pandemic, with very limited effects on direct employment. However, the fishmonger's activity apparently was not affected and increased their monthly income in relation to the previous year. Likewise, the infeasibility of fishing charter companies due to the great reduction in the number of tourists contrasted with the significant increase in the number of recreational fishing licenses immediately after the confinement ended. Even though that fishing tackle shops increased sales by over 60% in relation to the similar period of the year before, only 4.4% of these shops declared not to have had economic losses.

1. Introduction

The COVID-19 generated a global health crisis that has forced governments to take measures to contain the pandemic that meant a restriction or limitation of the movements of people, as well as of the economic activity at various scales and intensities. This is causing a global economic recession not yet adequately dimensioned, which has also been associated with a humanitarian and food crisis [1]. The responses of different governments have been very disparate, and not always more related to face the health crisis than the economic one. Thus, while some countries responded initially with a home confinement of the population to limit the spread of the virus, with greater or less temporal length and severity, in others the normal social activity continued [2]. In the specific case of Spain, where the population was confined between March 14th and June 21st, 2020, most of the commercial activity was deeply affected by the closure, except for those that were considered essential (e.g., supermarkets, agriculture, livestock, fishing, etc.). The initial closure affected the entire tourism industry, not only in hotels and apartments, but also all businesses related to catering (restaurants, bars, etc.) and leisure (theatres, cinemas, museums, sports facilities, etc.); once this initial confinement phase was completed, tourism and leisure activity has not been fully reactivated with its modulated reopening to the public according to the variations in the intensity of infection that the population has shown in the different regions.

In almost all the countries which restrict the movement of citizens,

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* Corresponding author.
E-mail address: airam.guerra@ulpgc.es (A. Guerra-Marrero).

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fishing was considered from the beginning an essential activity aimed at guaranteeing the supply of fresh food to the population. However, this did not necessarily imply a solution to the social and economic crisis that directly affected the rest of economic sectors due to the closure. According to the [1], the protection measures taken by governments to contain the spread of the disease, have impacted all the seafood supply chain, from fishing production, to processing, the transport of input supplies and of products to wholesale and retail markets, as well as demand. Fishing activities have decreased in both artisanal and recreational sectors during the pandemic, but the impacts of the crisis have been not equal in both sorts of fisheries, and between the different groups of fishermen. According to Global Fishing Watch, global industrial fishing activity had dropped globally by about 6.5 percent at the end of April 2020, compared with previous years, because of restrictions and closures related to COVID-19 [3]. Nevertheless, in those areas more affected by the pandemic the drop was much severe. In this way, the [4] estimated that Mediterranean and Black Sea fisheries suffered reductions of up to 80% in the number of operating vessels. But, while small-scale/coastal vessels less than 10% still operated, large-scale vessels operated between 40-100% depending on the cases. At the beginning of the pandemic, the immediate response was a general decrease in captures, greater than 75% in most of the Mediterranean countries, with the exception of Turkey, where production continued at pre-crisis levels thanks to a constant demand, encouraged by decreasing prices and dedicated consumer campaigns [4]. In April, some signs of improvement were evident, due to the adaptation of some fisheries to market demand. In contrasts, in those countries where fisheries were also totally closed at the beginning of the confinement, because they were not considered essential activities [5,6], the economic losses were larger due to the underestimation of the role of fish in the food chain [7].

In those places where tourism is the main economic industry, just as is the case of the Canary Islands, a fall in demand of fish took place due to the closure of hotels and restaurants [8], as well as restrictions on exports. In addition, changes in consumer preferences caused a drop in prices [1,4]. Data from the European Market Observatory for Fisheries and Aquaculture indicated a significant price decline in European countries fisheries of 20-70%, particularly in those of the Mediterranean region, with price varying significantly across products and countries. But the oversupply and its consequent price drop seems to be a factor that has increased the demand for locally sourced fish [1].

In the Canary Islands, the artisanal fishing sector is a low intensity economic sector with a decreasing trend, which contributes around 0.04% of GDP in 2018 and supports 0.16% of the active population of the Archipelago (J. Macias, Canaest Consultores, Comm. Pers.). In spite of the importance of fresh fish in the islander diet, there is an inefficient distribution chain of fresh products of high economic value depending on the small-scale fishery, made up of intermediaries, small fish markets, restaurants, and taverns, as well as some large supermarkets that value the local product. However, the market penetration of artisanal fresh fish in the sphere of the large tourist industry of the Canaries traditionally has been very small, which limits its market possibilities. The main reason for this is that the artisanal fleet is unable to guarantee the regular supply of the domestic market, among other reasons due to the overexploitation of islands fishing grounds [9]. The high demand of imported fishing products competes with local ones, which reduce the profit of Canary fishermen due to lack of competitiveness and an effective commercial organization of the artisanal fishing industry. Thus, local artisanal fishing only contributes 1/6 of the total fishery products that enter the Archipelago's markets. However, it should not be forgotten that the vast majority of fish products imported are not destined to satisfy the demand of islands markets, and are immediately re-exported to other national, European and Asian markets, particularly to China [10], acting the main Canarian ports (i.e. Puerto de La Luz and Las Palmas and Santa Cruz de Tenerife) as mere transhipment platforms to Asian markets or to entry to the EU of the catches of fleets from third countries.

In the Canary Islands, social distancing and confinement measures have not resulted in the closure of local fish markets, while trade has been affected by border closures and significant declines in the availability and increases in the cost. These impacts have created further challenges for the sale of fresh fish products, even where demand still exists domestically. In addition, in this context, it is possible to suppose that it could be an opportunity to promote the value of artisanal fleet fishing products, and to temporarily recover loss market niches due to lack of competitiveness. In the same way, this confinement has made impossible for citizens to practice their recreational fishing activity, since it has been considered and regularized as a leisure sport, being totally prohibited. A different case has been that of the fishing charters vessels, which have seen their activity limited during much of the pandemic, but once they reactivated their businesses they remained without the necessary influx of clients to carry out their normal activity, since the majority of their customers have been tourists [11]. So, the aim of this paper is to assess the initial impacts of the COVID-19 pandemic on the Canary Islands local fishing sector (artisanal fisheries and fishmonger), including the recreational tackle shops and charters.

2. Material and methods

The effects evaluation of the Covid-19 pandemic on the small-scale fishery at the Canary Islands was carried out through online and telephone surveys between July and September 2020. The survey was addressed to estimate the economic repercussions caused on the local fishing sector during social confinement, non-essential activities closure, and movement restrictions due to the declaration of Health Alert Status (HAS) by the Government of Spain [12] on March 14th, 2020. The survey was focused on fishermen (artisanal and recreational), fishmongers and recreational tackle shops that were working prior to that date.

An online snowball recruitment-style survey model [13] was used to assess the situation of the fishing sector in the Canary Islands. As already described by [14] for the Ontario fisheries sector, this assessment method is gaining traction with increasing research proving its validity [15,16]. Even so, we agree with [14], that the scope of this type of survey is limited, so we must consider our results as exploratory and preliminary and not make inferences from the results obtained to the entire population of the fishing sector of the Canary Islands. In the same way, an evaluation was carried out to check the evolution of recreational fishing licenses in the archipelago, to see if the current pandemic has had any effect on them. The data were obtained from the General Directorate of Fisheries of the Government of the Canary Islands.

The questionnaire was designed in a brief way with a total of 13 questions for artisanal fisheries, 7 for fishmonger, and 10 and 11 questions for tackle shops and charters, respectively (see Supplementary Materials). Data from artisanal fishermen come from 9 fishing associations (36% of fishing associations/cooperatives of the Canary Islands), where 91.67% of survey participants were vessel owners, 15 from fishing charters (35.7% of the Canary Islands fishing charters) and 26 from fishmonger from Canarian archipelago

2.1. Survey design

The survey was composed by 3 thematic blocks, in order to structure and analyse different segments of the local fishing sector and their dependence on each other. The questionnaire was designed following the recommendations of FAO [17].

2.2. Employee analysis

In order to know the impact of the HAS by the pandemic on the local fishing sector, it was mainly sought to analyse whether the closure of non-essential economic activities was caused by unemployment in the fishing sector, through temporary employment regulation (ERTE in

Spanish) or layoff (ERE in Spanish). In addition, it was requested that, in the event of an activity closure, detail the time during the closure was effective. These labour regulations (ERTE or ERE) refer to self-employed workers or company workers too. The responses of this block try to measure the impact of COVID-19 on employment in the local fishing sector.

2.3. *Supply/demand relationship*

This question block was addressed to detect the impacts of confinement and closing/limitations on hotels and restaurant services have had on fresh fish demand, but also its effects on the relationship between supply from the small-scale fishery and the demand in local fresh fish markets and supermarkets. This block also assesses the effect of HAS on the recreational tackle shops and recreational fishing charters, that were considered as non-essential activities.

2.4. *Analysis of the company's activity*

The HAS limited the activity of companies related with the fishing word that were considered as non-essential (i.e., fishing charters and tackle shops), and the objective of this block of questions was to obtain information on the economic losses during closure, but also if when they were reopening their sales increased or decreased in relation the same period of 2019, and if prices were modified (up/down). On the other hand, there was also requested if companies that were not closed (i.e., supermarkets) had problems to obtain fresh fish or other fishing products, directly by fishermen or fishmongers, and if this also affected the prices of these products.

2.5. *Statistical analysis*

In social research, it is common to work with variables or qualitative data, by means of which a group of individuals are classified into two or more mutually exclusive categories. When the intention is to compare two or more groups of subjects with respect to a categorical variable, data are usually submitted as double-entry tables that are called contingency tables.

The surveys contain questions common to the four groups surveyed, so to analyse if there were differences between the answers offered by each one, the Chi-square test of independence was applied. This test evaluates if there exists a relationship between two categorical variables, comparing the frequencies observed in the sample with the expected frequencies if there was no relationship between the two categorical variables. Null (H_0) and alternative (H_1) hypotheses are detailed below:

H_0. : the variables are independent, so there was no relationship between the two categorical variables. Knowing the value of one variable does not help to predict the value of the other variable.

H_1. : the variables are dependent, so there was a relationship between the two categorical variables. Knowing the value of one variable helps to predict the value of the other variable.

The Chi-square test analysis, as well as its corresponding graphic representations, were performed using the *vcd* package [18] developed for the R software [19].

To make inferences about the population, measures of statistical significance were provided to certify that the results found were not attributed to chance. The Pearson residuals measure the departure of each cell from independence, and they were calculated as following:

$$rij = \frac{Oij \quad - Eij}{\sqrt{Eij}}$$

where subscripts i and j represent the rows and columns of the contingency table respectively, Oij is the observed frequency and Eij represents the value fitted under the model. When data do not fit a model, examination of the Pearson residuals often helps to diagnose where the model has failed.

3. Results

A total of 87 surveys were obtained, of which 27.58% were answered by artisanal fishermen or representatives of artisanal fishermen's associations, 28.74% by fishmonger, 26.44% by tackle shops, and 17.24% by fishing charter.

Figs. 1–5 show the results obtained combining a mosaic plot (to visualize each contingency table) with its corresponding result of the Chi-square test of independence. Each mosaic plot with coloured cases shows where the observed frequencies deviate from the expected frequencies, if the variables were independent. The red cases mean that the observed frequencies were smaller than the expected frequencies, whereas the blue cases mean that the observed frequencies were larger than the expected frequencies.

It can be noted a strong positive association between fishermen and fishmonger respondents and the option "None" for answer, while for tackle shops and charter groups it is the only category with a negative association (Fig. 1). All respondents from the tackle shops and charter groups were forced to cease their activity for different periods; most tackle shops were closed for 1–2 months, while fishing charter went out of business for 2–3 months. In addition, only 30% of the fishermen and 8% of fishmongers stopped working (from mid-March to end-May).

Regarding employment regulation (Fig. 2), the most notable results were those referring to ERTE; fishing charters embraced the ERTE as the main measure of employment regulation (60%), following by recreational tackle shops (52.2%) while this was the option least adopted by artisanal fishermen and fishmongers.

Fishmongers have not observed noticeable economic losses during the confinement when compared with a similar period in previous years or in previous months, declaring most respondents an increase in their income (Figs. 3–4). About 93% of fishing charters declared having suffered economic losses over 50%, however when they were asked if they had suffered changes in their income, 67% of respondents refused to answer (Figs. 3–4). The 70% of recreational tackle shops respondents reported losses over more than 25%, while 54% of artisanal fishermen reported economic losses greater than 50% (Fig. 3). The differences between the frequencies observed versus those expected in the N/A option regarding economic losses were because only members of fishermen's group declined to answer this question (Fig. 3). Regarding changes in income, more than 80% of artisanal fishermen such as

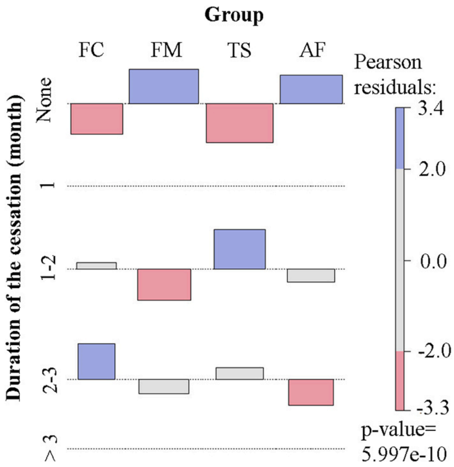

Fig. 1. Duration of closure activity. (FC, fishing charter; FM, fishmongers; TS, tackle Shops; AF, artisanal fishermen). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

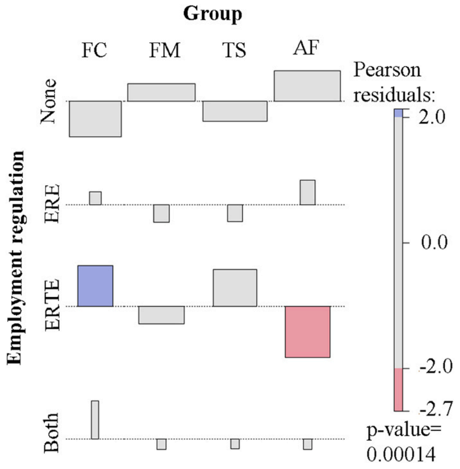

Fig. 2. Employment regulation measures adopted during the HAS. (FC, fishing charter; FM, fishmongers; TS, tackle Shops; AF, artisanal fishermen). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

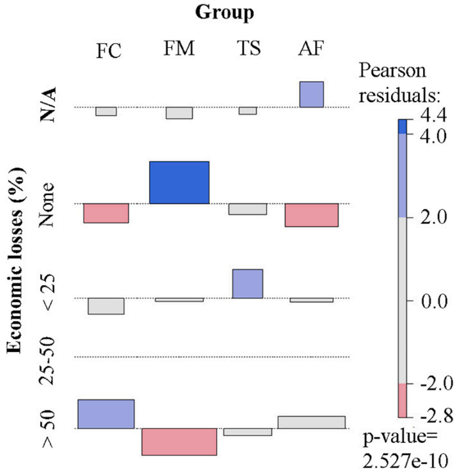

Fig. 3. Estimate of economic losses compared to a previous period. (FC, fishing charter; FM, fishmongers; TS, tackle Shops; AF, artisanal fishermen). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

recreational tackle shops surveyed indicated that these declined compared to a similar period prior to HAS (Fig. 4).

Relative to changes in prices, the strong positive association observed between this variable and artisanal fisherman (Fig. 5) was because it was the only group where some respondents declined to answer, although the most common response from fishermen was that there was a drop in prices. In the rest of the groups, the responses were more distributed, and the proportion of each option was more similar between groups, as shown in the contingency table (Fig. 5). In this case, most of the respondents (79%) indicated that there was no variation in prices.

Overall, considering the *p*-values obtained (Figs. 1–5), we can conclude that chosen variables turned out to be dependent: duration of cessation activity, employment regulation, economic losses, changes in prices and income changes depends on the respondent groups.

About 74% of fishmongers also declared that their marketing lines were altered because of the impact that HAS had on fish distributors. Most fishermen have not reported differences in their captures per unit of effort in relation to a similar period of the year before; however, the 90% of respondents indicated that their captures were reduced. Fishermen reduced the selling price of fresh fish in about 0.50€/Kg from January 2020 to April 2020, and in about 1.00 €/Kg from January 2020 to December 2020 (reduced by 14.6% on average from January to September 2020). Restaurants, bars, and retailing represent the 64.9% of the recipients of fresh fish from the small-scale fishery, while the other 35.1% was commercialized through fishmongers and supermarkets. Although the seconds ones were considered as essentials during HAS, particularly the commercialization and supply of middle-sized pelagic fish, as chub mackerel (*Scomber colias*), was more affected due not only the reduction of the demand, but because the high volumes of captures that normally were distributed and sell in markets of different islands, that was more difficult for limitations imposed during HAS to movements and transport.

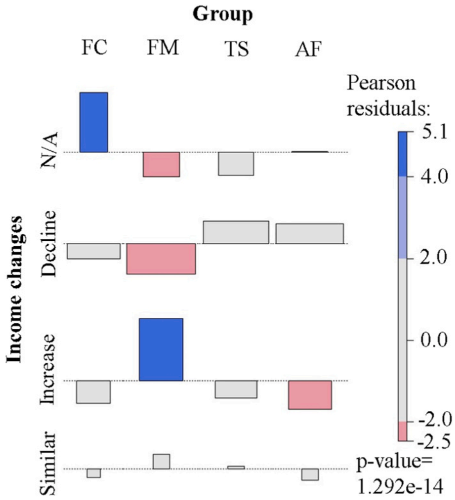

Fig. 4. Estimate of income changes compared to a previous period. (FC, fishing charter; FM, fishmongers; TS, tackle Shops; AF, artisanal fishermen). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

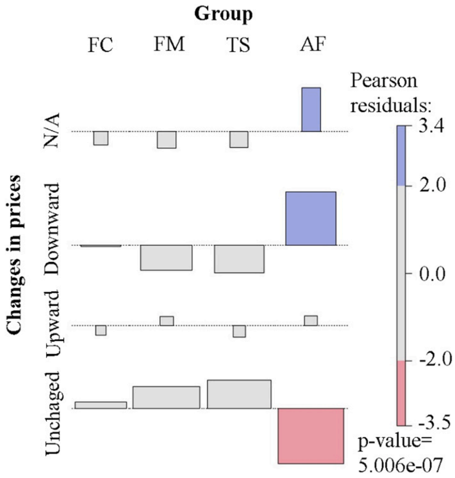

Fig. 5. Changes in prices to adapt them to the new demand situation. (FC, fishing charter; FM, fishmongers; TS, tackle Shops; AF, artisanal fishermen). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

The number of weekly charter fishing trips decreased according to 73.3% of the surveyed staff, although 60% also stated that catch yields per fishing day had not been affected during the confinement, maintaining this trend after the end of the HAS. After that, the recreational tackle shops were reopened and 82.6% of traders reported that their sales increased considerably, mainly in equipment to perform shore angling (69.6%). Among the products most demanded by anglers were reels, nylon, buoys, hooks, and other fishing tools, followed by spearguns, masks and fins used by spearfishermen.

To assess the impact of the pandemic on recreational fishing, the number of licenses granted has also been considered; since these licenses are valid for three years in the Canary Islands, the analyses cover the 2018-2020 period. The total number of active licenses at the end of 2020 was 104,828 and throughout that year, 39,620 recreational fishing licenses have been granted, being, in proportion, 8% and 6% higher than 2018 (31,407 licenses) and 2019 (33,801), respectively (Fig. 6). The effects of the pandemic can be clearly seen in the drastic decrease in the number of licenses during the months of March and April, coinciding with the strictest part of the isolation, obtaining only 39 fishing licenses in April, a practically negligible number compared to the licenses obtained in the same months of years 2018 and 2019. In the same way, an increase was observed during the months between May and July, being June the month with the highest number of registered licenses in the full period (three years), with 7,085, almost the double of those obtained during the same period of the years 2018 and 2019 and coinciding with the end of confinement (Fig. 6).

4. Discussion

To our knowledge, this study contributed to obtaining a perspective on the impact of COVID-19 pandemic on the fishing organization of the Canary Islands. Both, the professional and recreational fishing sectors have been affected by this pandemic, but in an unequal manner. Although, the closure of non-essential activities due to HAS has produced an important decline in the islands economy (the GDP drop in the archipelago has been estimated to be over the 20%; [20]), particularly for its negative effects on the touristic industry. The drop of the demand of imported fishing products in the Canarian market was about 30% in relation to 2019, with falls over the 60% in April and May (Mr. J. Sola, Decoexsa Ltd., Pers. Comm.). This drop of demand also impacted on the local fresh fish markets due to the closure of hotels, restaurants and other services, particularly during the social confinement (14th March–21th May), but also due to the negative effects of the pandemic on the touristic industry of the islands. However, in this context artisanal fishing has shown a greater economic resilience than those fishing activities related with recreational fishing (i.e.: fishing charters).

Thirty percent of the Canarian artisanal fishing vessels stopped their activity during confinement, due to their strong dependence on fresh fish demand from restaurants and other similar establishments. According to the opinion of fishermen this provoked an income loss of about the 40% on average during the confinement period, but the majority of vessels continued their activities during the pandemic, with very limited effects on direct employment (the ISM -Marine Social Institute- indicated that, from March to June 2020, only 48 fishermen - 3% - of a total population of 1600, requested the extraordinary benefit of cessation of activity -ERTE). This situation was similar to that described for some Caribbean and Pacific small-scales fisheries of Mexico, where 48% of fishermen stopped fishing during confinement, and 41% that continued working reduced their catches by around 30–80% [21].

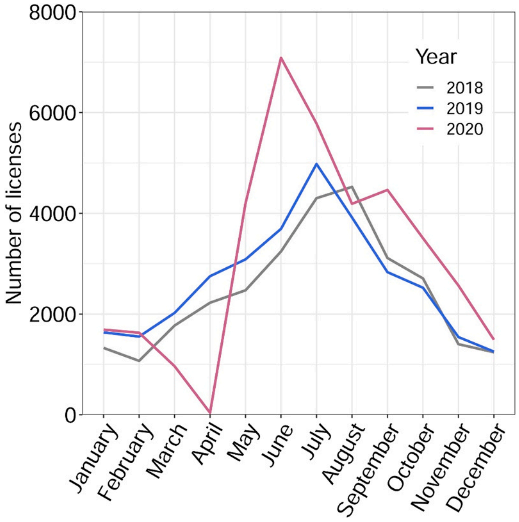

Fig. 6. Monthly evolution of recreational fishing licenses between 2018 and 2020 in the Canary Islands.

Fishmongers' activity has been apparently not affected by the pandemic, even though a minority of companies have had to make temporary closures because their volume of transactions (supply/demand relationship) dropped considerably, making it impossible to keep the service open. This was described by [22] as a pragmatic approach of local-scale vulnerability and for planning appropriate adaptations within the context of multiple interacting exposure to the reduction in demand and dependence to the touristic sector [23]. That is, the multilateral capacity to operate in scenarios with limited capacity [24]. Even so, the majority of local fish markets remained open during confinement, without a significant reduction in the prices of fishing products, but with a part of them (21.7%) using the ERTE as an instrument to reduce the number of workers employed and consequently, the costs. In this context, 72% of fishmongers indicated an increase of their monthly income in relation to the previous year, despite that they needed to change their marketing lines during HAS.

Regardless that price per kilogram of fish of demanded species slightly decreased during the confinement, as occurred in the general context described by [25], and mainly because momentary overproduction due to closure of hotels and restaurants, its effects in the economical balance of the local fresh fish markets of the islands was apparently negligible, despite the 16.4% of fish price decreasing. According to [26], around 68 million euros of net profit were looser in relation to 2019 in the country as a whole, although the most impacted fisheries were those of the Mediterranean and northwest coast of the Iberian Peninsula. In these two last fishing grounds the decreasing in sales was about 40% (between March 14 and the end of May), with losses estimated at 34 million euros and a price drop of about 37%. It is possible that the reported lower price reductions of fresh fishing products of the Canary Islands were probably related to the already limited productivity of small-scale fishing fleets due to overfishing [9], that all captures (except those of tuna species) are consumed by the local population of the islands, and/or the capacity of local markets to quickly adjust their offer to demand, controlling the prices, and passing it cost to fishermen. Price reduction of fishing products during the pandemic has been reported in other countries, where fishermen has reduced their catches by not being able to sell their products due to lack of merchants or storage space [21,27], modifying their market to online sales systems or door-to-door sales [21,28–31].

On the other hand, because of the decree of the Spain Government [12], activities associated with recreational fishing (i.e. tackle shops) were seriously affected during confinement. However, immediately after the confinement ended the number of recreational fishing licenses showed a significant increase (in June 2020 were granted 7.085 fishing licences, almost twice than given in June of 2018 or 2019), so in 2020 the number of active licences were 104,828, more than in the ten previous years. A similar effect was also described by [32] who reported that The Pennsylvania Fish and Boat Commission sold 150,000 fishing licences more than the previous year, due to the boom in the population to engage in outdoor activities. In this way, immediately after the confinement ended (June-August) occurred an important increase of demand for reels, nylon, buoys, hooks, and other fishing tools, followed by spearguns, masks and fins used by spearfishermen. However, and despite that fishing tackle shops increased sales by over 60% in relation to the similar period of the year before, only 4.4% of these shops declared not to have had economic losses. Similar economic losses also has been reported in other areas, where post-confinement measures (cancellation of fishing tournaments, prohibition of operating fishing charters, or prohibition of fishing or temporary suspension of the licenses sales for non-residents) affected negatively in the recreational companies [33]. Nevertheless, the post-confinement increase in selling of tackle shops seems to be a worldwide effect of the pandemic, and international companies, such as "Angling Direct" (United Kingdom), that closed its 36 physical shops in the UK during HAS, has increased its online sales by 27% (reaching profits up to 59.16 million euros) in relation to the year 2019 [34].

Probably, the significant increase in the number of recreational fishing licences in the Canaries were influenced not only by the possibility to carry out this outdoors activity, but to obtain fresh and quality food in a simple way. A similar effect was observed after the financial crisis of 2008, when unemployment in the archipelago was over 250.000 people [35], and the number of active fishing licences was close to 100.000, because many people used fishing as a source of food and/or incomes. Another face of the pandemic in the recreational fishing sector was the fishing charter companies, whose reduction of tourists has made keeping the vessels operating normally economically unfeasible.

As a conclusion, we must recognize the limitations of online snowball-style surveys [36], so the data obtained refers to our sample population, without intending to extrapolate to the entire fishing sector of the Canary Islands. Therefore, the information obtained in this study is shown as exploratory in order to know and identify the experiences, perspectives and consequences generated by the HAS. Even without extrapolating these results for the entire fishing sector, this assessment is useful to understand the effects of this pandemic and provide preliminary results to administrations or organizations that assess the consequences and generate opportunities after COVID-19 pandemic. In general terms, all the fisheries sectors related with fishing (artisanal or recreational) in the Canary Islands had been affected in some way by the COVID-19 Pandemic, but in different intensity, according to their consideration as essential services during HAS or its dependence on the touristic industry in the archipelago.

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CRediT authorship contribution statement

AGM: Conceptualization, Methodology, Interviews, Data curation, Writing – review & editing. **LCM**: Conceptualization, Methodology, Data curation, Software and Writing. **DJA**: Conceptualization, Methodology, Interviews, Data curation and Writing. **AER**: Interviews, Data curation and Writing. **RNG**: Interviews, Data curation and Writing: **ASL:** Data curation, Software and Writing. **ASP:** Data curation. **JJC:** Conceptualization, Supervision, Writing – review & editing.

Declarations of interest

None.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.marpol.2021.104712.

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Fotografía contraportada: Threatening Broadclub Cuttlefish Displaying Tentacles on Black Background. Edward Rowland/Alamy Stock Photo.

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