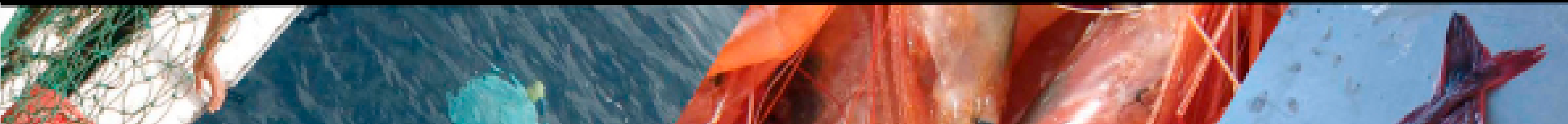
UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA
Programa de Doctorado en Calidad Ambiental y Recursos Naturales (DOCARNA)
Escuela de Doctorado

Doctoral Thesis

Ecology of *Plesionika edwardsii* (Decapoda, Pandalidae) and *Physiculus cyanostrophus* (Osteichthyes, Moridae) in the eastern-central Atlantic

Raül Triay Portella



Las Palmas de Gran Canaria

September 2019

UNIVERSIDAD DE LAS PALMAS
DE GRAN CANARIA

D PABLO MARTEL ESCOBAR COORDINADOR/A DEL PROGRAMA DE DOCTORADO EN CALIDAD AMBIENTAL Y RECURSOS NATURALES (DOCARNA) DE LA UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA,

INFORMA,

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 "Ecology of *Plesionika edwardsii* (Decapoda, Pandalidae) and *Physiculus cyanostrophus* (Osteichthyes, Moridae) in the eastern-central Atlantic" presentada por el doctorando D. Raül Triay Portella y dirigida por el Doctor José M. González Pajuelo y el Doctor José Antonio González Pérez.

Y para que así conste, y a efectos de lo previsto en el Artº 11 del Reglamento de Estudios de Doctorado (BOULPGC 7/10/2016) de la Universidad de Las Palmas de Gran Canaria, firmo la presente en Las Palmas de Gran Canaria, a……de …………………… de dos mil diecinueve

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA

Doctoral School

PhD Programme in Environmental Quality and Natural Resources (DOCARNA)

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ESCUELA DE DOCTORADO

Programa de doctorado en Calidad Ambiental y Recursos Naturales (DOCARNA)

Título de la Tesis

ECOLOGY OF *PLESIONIKA EDWARDSII* (DECAPODA, PANDALIDAE) AND *PHYSICULUS CYANOSTROPHUS* (OSTEICHTHYES, MORIDAE) IN THE CENTRAL-EASTERN ATLANTIC.

ECOLOGÍA DE *PLESIONIKA EDWARDSII* (DECAPODA, PANDALIDAE) *Y PHYSICULUS CYANOSTROPHUS* (OSTEICHTHYES, MORIDAE) EN EL ATLÁNTICO CENTRO-ORIENTAL

Tesis Doctoral presentada por D. Raül Triay Portella

Dirigida por el Dr. D. José M. González Pajuelo

Codirigida por el Dr. D. José Antonio González Pérez

El Director,	**El Codirector,**	**El Doctorando,**
(firma)	**(firma)**	**(firma)**

Las Palmas de Gran Canaria, a 17 de septiembre de 2019

Note:

It has been considered necessary to specifically introduce a special paragraph on the thesis' title. The original title of the present thesis was "Biology of *Physiculus cyanostrophus* (Osteichthyes, Moridae) in Cape Verde". However, in the course of the research process the topic has been expanded considerably, including aspects of the semi-floating shrimp-trap fisheries and the study of life history traits of *Plesionika edwardsii* (Crustacea, Decapoda, Pandalidae) among others. The pre-doctoral fellowship that supports the present thesis does not allow substantial changes in thesis' title, so the present title has been adapted as the less bad option. Not without being aware that it may not fully reflect the content of this document, this has been compensated with the abstract and the introductory chapter.

A sa meva fía ,Vera

Agradecimientos

Quiero agradecer a la Universidad de Las Palmas de Gran Canaria la oportunidad de realizar la presente tesis a través de un contrato pre-doctoral. Siento agradecimiento por todos los conocimientos, formación y oportunidades que me ha ofrecido esta institución y por el apoyo y facilidades que he recibido en este largo camino que aquí culmina. Del mismo modo, agradezco al Instituto Canario de Ciencias Marinas (ICCM) y en concreto al grupo de Biología Pesquera haberme acogido en su seno cuando apenas había finalizado mis estudios de Licenciatura y del que formé parte hasta su clausura.

La tesis ha sido respaldada y financiada parcialmente por un gran número de proyectos de investigación, sin ellos la tesis no se podría haber llevado a cabo: PROACTIVA, PROACTIVA-2, MARPROF, MARPROF-CV, MARISCOMAC y MACAROFOOD. Detrás de estos proyectos están las personas que los han hecho posibles y a los cuales extiendo mi gratitud. La mayoría de estos proyectos implican la participación de grupos de investigación de diversos países, como son Portugal y el Archipiélago de Cabo Verde. Países a los que les agradezco que me permitieran estudiar sus ecosistemas marinos, especialmente a través de inolvidables campañas oceanográfico-pesqueras, formarme como investigador y además permitirme realizar las estancias internacionales en el Museo de Historia Natural de Madeira e Instituto de Desenvolvimiento das Pescas de Cabo Verde.

A quienes me han formado como futuro investigador, mis dos directores, Pajuelo y Pepe. Les debo todo, me siento afortunado de seguir aprendido de ellos. Me han dejado hacer y trabajar con quien he querido, equivocarme y siempre han estado a mi lado. Mi mayor regalo es su respeto. A Nespereira, director del grupo y a quien considero un amigo. Siempre me ha apoyado y respaldado. Todos juntos conformamos el Grupo de Ecología Marina Aplicada y Pesquerías. A Pepe Ignacio, un gran apoyo en mi estancia en el ICCM y en el transcurso de las campañas en Cabo Verde. Me siento afortunado de contar con su amistad. A Fernando, por su amistad y sus enseñanzas, cuenta con mi admiración y es uno de mis referentes como investigador. Me ha ayudado y apoyado en momentos clave. He aprendido mucho de él y espero seguir haciéndolo. A Ángel y Jose, por su amistad, ayuda y por contar conmigo en sus proyectos. Por enseñarme lo que sé de buceo científico. A Castro, por ayudarme y aconsejarme, por saber escuchar y por animarme a seguir. A Manuel Biscoito, por sus inestimables enseñanzas y clases de taxonomía. Por contar conmigo en sus trabajos y ofrecerme siempre su ayuda. A todos los coautores de los trabajos científicos que componen la tesis y de aquellos que no la componen. Todos han aportado una parte de la presente tesis. A los dinosaurios, especialmente a los supervivientes, Pep, Pablo, Tachi, Maite, Ico, Alejandro, Óscar y Aketza. A todo el personal del departamento de Biología y del edifico de Ciencias básicas. A todos los pescadores profesionales, especialmente a Adexe, Rayco y al Majorero, me han permitido trabajar en sus barcos. Siento un profundo respeto y admiración por su trabajo.

Por último, a mi familia y amigos, la menorquina y la canaria. A mis padres y a mi hermano, por apoyarme en todo. A Esmeralda por quererme, entenderme y ayudarme.

Thesis preview

The present thesis, entitled *Ecology of* Plesionika edwardsii *(Decapoda, Pandalidae) and* Physiculus cyanostrophus *(Osteichthyes, Moridae) in the eastern-central Atlantic*, was conducted under the supervision of Dr. José G. Pajuelo and Dr. José A. González. The initial idea germinated at the extinct Canary Institute of Marine Sciences (ICCM), and posteriorly continued at the Institute for Environmental Studies and Natural Resources (i-UNAT) at the University of Las Palmas de Gran Canaria (ULPGC), within the Doctoral Programme of Environmental Quality and Natural Resources (DOCARNA). This thesis was supported by a pre-doctoral fellowship of the ULPGC. Pre-doctoral training has partially founded by the project RESIGRASS (CGL2014-58829-C2-1-R) granted to Dr. Fernando Tuya Cortés. This thesis compiles six original research works published in peer-reviewed journals of the Journal Citation Report (Q1 = 3, Q2 = 2, and Q3 = 1) and another paper currently under revision (1), in the framework of the projects granted to Dr. González and Dr. Pajuelo PROACTIVA (A-51/2009) and PROACTIVA-2 (A-44/2010) of the Canary Government, and MARPROF (MAC/2/M065), MARPROF-CV (MAC/03/C124), MARISCOMAC (MAC/2.3d/097) and MACAROFOOD (MAC/2.3d/015) co-funded by the EU ERDF of the Programme INTERREG V-A (Madeira, Açores, Canarias). Furthermore, this study has benefited from our active participation in fishery series of fishing cruises on board the R/V "Profesor Ignacio Lozano" that resulted from the research projects mentioned above, resulting in more than 125 working days on board. Research surveys were headed by Dr. José A. González. In addition, two research stays have been carried out by the candidate. Once at the "Instituto Nacional de Desenvolvimento das Pescas" (INDP) in Cape Verde during four months, and the other at the "Museu Municipal (História Natural) do Funchal" (MMF) in Madeira, Portugal during three months. Both visits resulting in a seven month of international research stays.

This thesis has been organized according to the ULPGC structure of thesis by compendium of publications (BOULPGC, XII nº 3, Chap. 3, 2019): A general introduction provides the essential background information, and outlines the objectives and hypothesis to be examined in the study; then, the seven scientific contributions validate the stated hypothesis; finally, the main conclusions. All these sections have been entirely written in English to comply with the valid regulation for obtaining the Mention of International Doctor (BOULPGC, XII nº 3, 2019), which dictates that at least the abstract and conclusions must be presented in a language other than Spanish. Likewise, it has been included a final section summarizing in Spanish the general aspects of the thesis, as required from the PhD Thesis Regulations from the ULPGC (BOULPGC, XII nº 3, 2019). Additionally, other nine contributions integrated in the pre-doctoral learning process have also been included in section VII to provide a broader and deeper view about thesis contributions on deep-sea species in the Central east Atlantic.

Abstract

Composition and bycatch of semi-floating shrimp-trap fisheries (SSTF) were compared among areas with different levels of anthropogenic alteration of marine ecosystems. The three areas selected were Madeira, the Canary and the Cape Verde Islands. Mean species richness and diversity of the SSTF did not show significant differences among areas. The dominant species in catches of the SSTF for all regions studied was the main target species, *Plesionika edwardsii*, which accounted for 96.0% of the catch in Cape Verde, 75.8% in Madeira, and 59.1% in the Canary Islands. Targeted pandalid shrimps accounted for more than 96.8% of total catches for all areas combined. The present results suggest that the selectivity of traps for the main target species, *P. edwardsii*, in SSTF changes due to changes in species dominance, which are probably linked to the degree of human fishing exploitation of the marine ecosystems in each area.

Life-history traits of the pandalid shrimp *Plesionika edwardsii* are studied for the first time in three isolated Atlantic populations (Madeira, Canaries and Cape Verde Islands) to gain an understanding of their latitudinal variations**.** Ovarian maturity, egg development and brood size were analysed. Synchronic ovarian maturation was observed during the embryo incubation process, and ovigerous females bearing embryos at the final stage of development were found throughout the year. Females produce multiple spawning's during the reproductive season, after which the reproductive process ends and a rest period begins. The mean number of embryos carried by females decreased from Madeira to the Cape Verdes, where less energy was invested in reproduction. The patterns observed may be a consequence of the temperature experienced by shrimps during development. A latitudinal north-south pattern was also observed in the maximum size of ovigerous females, with larger sizes found in the Madeira area and lower sizes observed in the Cape Verde Islands. The relative size at sexual maturity is not affected by latitude or environmental factors and is the same in the three areas studied. *Plesionika edwardsii* had a long reproductive season with ovigerous females observed all year round, although latitudinal variations were observed. Seasonally, there were more ovigerous females in spring and summer in Madeira and from winter to summer in the Cape Verde Islands. A new taxonomic trait able to determine sex in pandalid shrimps of the genus *Plesionika* and an indicator of functional maturity in females was described. Thoracic teeth were located on the 7th thoracic sternite. Each species presents characteristic teeth. This structure could be used as a tool in the systematics of this genus. Sex determination through thoracic teeth shall represent a faster alternative to the classical appendix masculina sexing method. Functional maturity of females is linked to the fading of immature thoracic teeth. Thoracic teeth open a new window to different fields of research in *Plesionika* species.

A new species of *Physiculus*, *P. caboverdensis* n. sp., is described from the outer shelf and upper slope of the Cape Verde Islands. This species differs from all other congeners from the Atlantic Ocean by its dentition.

Among of 917 individuals of *Physiculus cyanostrophus* caught from the outer shelf and upper slope of the Cape Verde Islands, a total of 258 specimens (28.1%) showed caudal region regeneration. Morphometric and meristic data obtained have significantly broadened the known ranges of morphology variables for this species. An updated table comparing the relative position and size of the light organ among Atlantic species of *Physiculus* is given, representing a taxonomic tool for species identification. Finally, a remarkable caudal regeneration capacity of *Physiculus cyanostrophus* was described. This trait reveals the ability of this particular morid to survive attacks that would be lethal in other species. In *P. cyanosytrophus* the larger sized individuals the greatest amount of tissue loss occurred in the caudal region. The amount of regenerated tissue was independent of body losses and ranged between 5 and 19% of total length for the entire range of sizes. The frequency of regenerated individuals in the population increases with ontogeny. Tissue losses represent a significant allocation of costs in terms of growth and offspring production. Nevertheless, regeneration capability decreases mortality in the large breeding females of a population, maximizing maternal fitness.

Resumen

La composición de especies y las capturas accesorias de las pesquerías con nasas camaroneras semi-flotantes (SSTF, de sus siglas en inglés) se compararon entre áreas con ecosistemas marinos sometidos a diferentes niveles de presión pesquera. Estas tres áreas seleccionadas fueron Madeira, las Islas Canarias y las Islas de Cabo Verde. La riqueza media de especies y la diversidad en las SSTF no mostró diferencias entre las distintas áreas. La especie dominante en las capturas de SSTF, para todas las regiones estudiadas, fue la especie objetivo, *Plesionika edwardsii*, que representó el 96.0% de la captura en Cabo Verde, el 75.8% en Madeira y el 59.1% en las Islas Canarias. Los camarones pandálidos de aguas profundas representaron más del 96.8% de las capturas totales para todas las áreas combinadas. Los resultados actuales sugieren que la selectividad de las nasas para la especie objetivo, *P. edwardsii*, en SSTF cambia debido a los cambios en el dominio de las especies, que probablemente estén vinculados al grado de explotación pesquera de los ecosistemas en cada área.

Los rasgos del ciclo biológico del camarón soldado, *Plesionika edwardsii*, se estudian por primera vez en tres poblaciones atlánticas aisladas con el objetivo de comprender sus variaciones latitudinales. Para ello, se analizó la madurez ovárica, el desarrollo embrionario, el tamaño de las puestas y la sincronización entre maduración ovárica y el proceso de incubación de embriones. Se encontraron hembras ovígeras que llevaban embriones en la etapa final de desarrollo durante todo el año. Las hembras producen múltiples desoves durante la temporada reproductiva, al finalizar el proceso reproductivo comienza un período de reposo. El número medio de huevos que portan las hembras disminuyó desde Madeira hasta las Islas de Cabo Verde, donde se invirtió menos energía en la reproducción. Los patrones observados pueden ser consecuencia de la temperatura que experimentan los camarones durante el desarrollo. También se observó un patrón latitudinal norte-sur en el tamaño máximo de las hembras ovígeras, observándose tallas grandes en el área de Madeira y tallas menores en las Islas de Cabo Verde. El tamaño relativo en la madurez sexual no se ve afectado por la latitud o factores ambientales y es el mismo en las tres áreas estudiadas. *Plesionika edwardsii* tuvo un largo periodo reproductiva con hembras ovígeras durante todo el año, aunque se observaron variaciones latitudinales. Estacionalmente, hubo más hembras ovígeras en primavera y verano en Madeira y de invierno a verano en las islas de Cabo Verde. Se describió un nuevo rasgo taxonómico capaz de determinar el sexo en camarones pandálidos del género *Plesionika* y un indicador de madurez funcional en las hembras. Los dientes torácicos se ubican en el séptimo esternito torácico. Cada especie presenta dientes característicos. Esta estructura podría usarse como una herramienta en la sistemática de este género. La determinación del sexo a través de los dientes torácicos representará una alternativa más rápida al método de sexado clásico a través de los apéndices masculina e interna. La madurez funcional de las hembras está relacionada con la desaparición progresiva

de los dientes torácicos inmaduros. Los dientes torácicos abren una nueva ventana a diferentes campos de investigación en especies las especies del género *Plesionika*.

Se describe una nueva especie de *Physiculus*, *P. caboverdensis* González, Triay-Portella & Biscoito, 2019, presente desde la plataforma exterior hasta el talud superior de las islas de Cabo Verde. Esta especie se diferencia de todos los demás congéneres del Océano Atlántico por su peculiar dentición. Entre los 917 individuos de *Physiculus cyanostrophus* capturados en las Islas de Cabo Verde, un total de 258 especímenes (28.1%) mostraron la región caudal regenerada. Los datos morfométricos y merísticos obtenidos de estos ejemplares, han ampliado significativamente los rangos conocidos de variables morfológicas para esta especie. Se proporciona una tabla actualizada que compara la posición relativa y el tamaño del órgano luminosos entre las especies atlánticas de *Physiculus*. Esto representa una herramienta taxonómica eficaz para la identificación de estas especies. Finalmente, se describió la notoria capacidad de regeneración de *Physiculus cyanostrophus*. En *P. cyanosytrophus*, los individuos de mayor tamaño presentaron las pérdidas mayores de tejido en la región caudal. La cantidad de tejido regenerado fue independiente de las pérdidas corporales y varió entre 5 y 19% de la longitud total para todo el rango de tallas estudiado. La frecuencia de individuos regenerados en la población aumenta con la ontogenia. Las pérdidas de tejido representan una asignación significativa de costos en términos de crecimiento y fecundidad. Sin embargo, la capacidad de regeneración disminuye la mortalidad en las grandes hembras reproductoras de una población, maximizando el *fitness* maternal.

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Chapter 1

General Introduction

1.1 Preamble

Over the last several decades, depletion on shallow coastal waters resources has resulted in an expansion of fishing activities to deeper waters (Morato et al. 2006; Norse et al. 2012; Wehrtmann et al. 2012). An unprecedented development of deep-sea fisheries has triggered an early overexploitation of several species (Koslow et al. 2000; Roberts 2002). This fact has increased the interest of the scientific community seek to achieve sustainability in deep-sea fisheries (Norse et al. 2012). In this regard, deep-sea ecosystems are challenging in some fields, due to be poorly known and vulnerable to fishing activity (Pajuelo et al. 2016). Deep-water pandalid shrimps of the genus *Plesionika* Spence Bate, 1888 are the main targets of some commercial and small-scale fisheries conducted in the Mediterranean Sea and eastern-central Atlantic islands (González et al. 1992). Large gaps on the impact of this fisheries and the life cycle of deep-water species are certainly worthwhile discussing and studying in detail.

The first part of the present thesis aims to know the impact of semi-floating shrimp-trap fishery (SSTF) on the shallowest deep-sea ecosystems (100-450 m) (Pajuelo et al. 2018). The approach is based on SSTF's behaviour throughout three eastern-central Atlantic archipelagos: Madeira, Canary Islands and Cape Verde. Catch composition analysis concerning different bioregions and oceanographic characteristics was described. Relationship between by-catch and the degree of human exploitation were discussed, addressing one of the biggest problems concerning fisheries (Wilcox & Donlan 2007). The Chapter 2 introduces the main actors of the present thesis. Semi-floating shrimp-traps as a small-scale fishery and exploratory sampling method. Deep-water pandalid shrimps (Chapter 3) represented by *Plesionika edwardsii* (Brandt, 1851) as the main target species of the SSTF, and finally morid codlings (Chapter 4) represented by the genus *Physiculus* Kaup, 1858 as a part of by-catch of SSTF in Cape Verde.

Second part of the present thesis aims to know the main life-history traits of *Plesionika edwardsii*. Indeed, methodologies used in the literature are discussed and improved with the aim to contribute in a better parameters' estimation (Triay-Portella et al. 2017). The study on secondary sexual characteristics of these species concluded in a new morphological structure in genus *Plesionika*. This structure can be useful in several ways such as: taxonomy, sexual assignment, maturity condition and reproductive strategies (Triay-Portella et al. 2018). Finally, variation in the life-history traits of *Plesionika edwardsii* are analysed as an indicator of biogeographic trends along a latitudinal gradient in the three eastern-central Atlantic archipelagos (González et al. 2018; Triay-Portella et al. 2018). From a fisheries perspective, information about reproductive strategies, offspring generation, growth and mortality are essential for the population's sustainability. Latitudinal variation in life-history traits of deep-water shrimps allows to scientific cooperation at global, regional and national scale.

While *Physiculus* group are the most diverse within the family Moridae Moreau, 1881, until the present thesis ecological studies were almost entirely absent. The last part of the present document aims to expand knowledge of the genus *Physiculus* in the Atlantic, highlighting aspects on its ecology that makes it particularly exceptional. First approach was based in taxonomic studies, which have resulted in the discovery of a new species, *Physiculus caboverdensis* González, Triay-Portella & Biscoito, 2019, an endemism of the Cape Verde (González et al. 2018). Thus, new morphological data of *Physiculus* species occurring in the Atlantic Ocean provide new identification tools in a poorly known group (Triay-Portella et al. submitted). Lastly, remarkable caudal regeneration capacity in *Physiculus cyanostrophus* Anderson & Tweddle, 2002 has been described and evaluated, including consequences in their natural population dynamics, growth and fitness (Triay-Portella et al. 2019).

1.2 Spatial dimension: Twilight zone and eastern-central Atlantic archipelagos

The present thesis has two spatial dimensions. From an ecological viewpoint, bathymetric extension belonging to the continental margin covers approximately from 175 to 500 m depth, the habitat so called twilight zone. This habitat is the frontier between mesophotic and aphotic (bathyal) ecosystems. Secondly, a latitudinal dimension integrates three archipelagos of the eastern-central Atlantic Ocean: Madeira, Canary Islands and Cape Verde (Fig. 1).

In the twilight zone, species are adapted to a transitional environment between light and darkness (Marshall et al. 1971). In this habitat, bioluminescence is a resource used by organisms to communicate, to predate and to avoid predation (Herring 1996; Haddock et al. 2010). At these depths, large gaps in fundamental aspects of ecological knowledge remain.

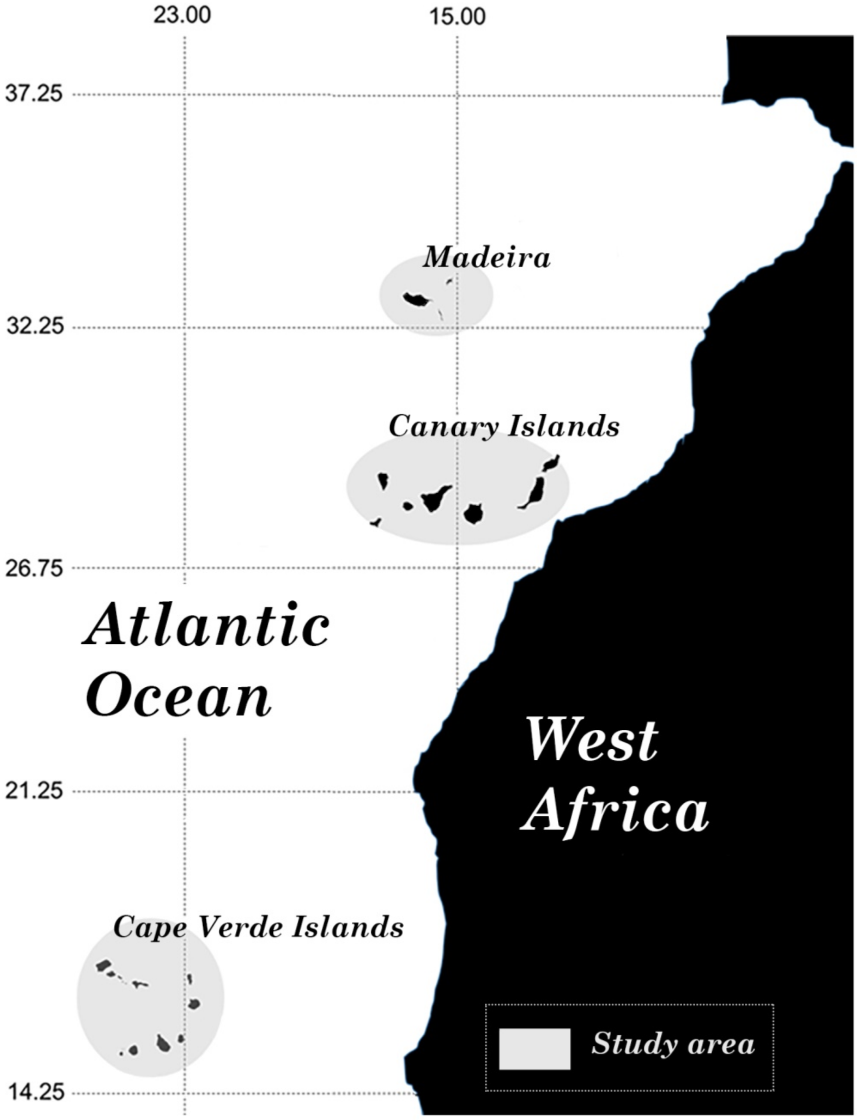

Figure 1. Latitudinal dimension integrates three archipelagos of the eastern-central Atlantic Ocean: Madeira, Canary Islands and Cape Verde.

Latitudinal study runs along the Canary Current System, which is one of the Large Marine Ecosystems of the World and Linked Watersheds (LMEs) across global oceans (Sherman & Hempel 2009). They are characterized by their singular bathymetry, hydrography and productivity, as well as their ability to support marine populations that have adapted their life-history traits (Hernández-León et al. 2007). The region of Madeira is dominated by the Canary Current system, which induces a southward net transport (Caldeira & Sangrà 2012). The presence of a seamount at the southeast end of Madeira produces a localized island upwelling of cold nutrient-rich waters around the coasts (Caldeira et al. 2002). The Canary Islands are characterized by the presence on the first 500 m of depth of Eastern North Atlantic Central Water (Hernández-Guerra et al. 2002). Meanwhile, the seawaters off the Cape Verde are under the influence of the North Equatorial Counter-Current and the Canary Current. The seasonal circulation patterns of this Counter-Current mainly show their influence in the south-eastern part of the archipelago (Lázaro et al. 2005).

1.3 Semi-floating shrimp-traps: fishery and sampling technique

In recent years, shrimp small-scale fisheries (SSF) are considered a good example to promote the prosperity of fishing communities in the Mediterranean Sea (Kalogirou et al. 2017; Vasilakopoulos et al. 2019). These fisheries have often been described as more selective and sustainable than commercial fishing activities (Zimmerhackel et al. 2015). Moreover, SSF are currently in a substantive discussion within the European Union, due to incompleteness and low quality of existing data in this fleet sector (STECF 2018).

Since 1975 shrimp species of the *Plesionika* genus have been fished with highly selective semi-floating shrimp-traps (SST) (Fig. 2) operating between 100 and 500 m depth throughout the Mediterranean Sea (González et al. 1992; García-Rodríguez et al. 2000). The success of these fisheries produced its expansion to the archipelagos of the eastern-central Atlantic (Santana et al. 1997), where a small-scale fishery has been developed, in the Azores (Martins & Hargreaves 1991), Canary archipelago (González et al. 2001), and Madeira (Sousa et al. 2014). In Cape Verde, only experimental fishing has been conducted, where the deep-water populations and habitats remain at pristine levels.

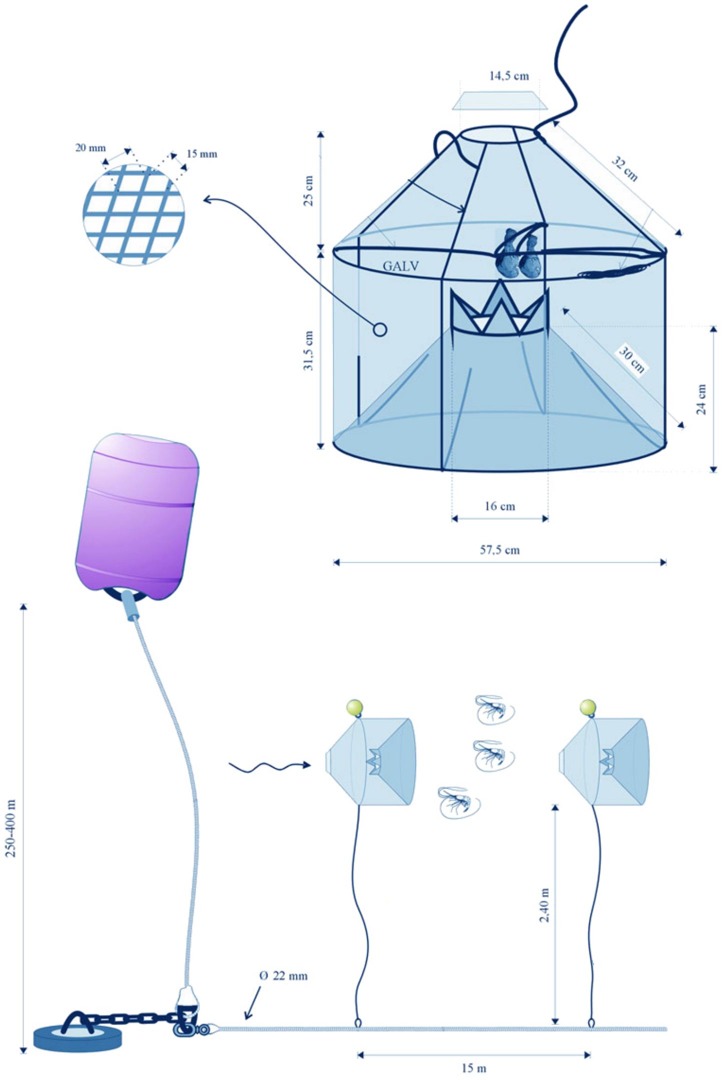

Figure 2. Semi-floating shrimp traps (SST) are the main sampling technique of the present thesis.

The aim of the second chapter is to evaluate the catch composition of the shrimp fishery with semi-floating shrimp-traps off Madeira, Canary Islands and Cape Verde. In addition, the quantification and diversity of bycatch species is relevant for the current fisheries policy of the European Union, which tie down to reduce the catches (landings) of some species groups to zero until 2019 (EU 2018). A second objective of this chapter is to evaluate the behaviour of the fishing system at different levels of ecosystem exploitation.

Environmental impact of demersal trawling on deep ecosystems exceeds ethical and ecological limits (Thrush & Dayton 2002). For this reason, it is reasonable that respectful sampling methods are used for deep ecosystems studies. Among the fishing methods, traps are less destructive of deep-water habitats than bottom trawling (Roberts 2002). Semi-floating shrimp traps (SST) are the main sampling technique of the present thesis. The traps were suspended 2.4 m above the bottom. The single semi-floating trap is a cylinder conical trap with a base length of 56 cm and a height of 57 cm, covered with 15×20 mm plastic mesh. Each trap has one truncated cone-shaped opening with a 23 cm outer diameter and 19 cm inner diameter (Pajuelo et al. 2018). The fishing gear consisted of 75 traps on a fishing rope separated from each other by 15 m. Atlantic chub mackerel (*Scomber colias*) was used as bait, and immersion times was around 20 h.

1.4 Deep-water shrimps (Pandalidae)

Species of the genus *Plesionika* play an important ecological role in benthic ecosystems, and the life-history traits of species living in these habitats, such as *Plesionika edwardsii* (Fig. 3), may need to adapt to deep environmental features (Carbonell & Abelló 1998; Vafidis et al. 2005). *Plesionika edwardsii* has a circumtropical distribution (absent in the eastern Pacific) and inhabits a variety of bottoms including mud, sand, rocks and corals at depths between 110 and 680 m, chiefly at 250–380 m (González et al. 2001). In the eastern Atlantic, this species has been found from south-western of Spain to Angola, including the Macaronesian archipelagos, Cape Verde and the entire Mediterranean region (García-Rodríguez et al. 2000; González et al. 2001). The life-history traits of *P. edwardsii*, such as reproductive strategy, growth, diet and mortality, were studied in the Pacific (King & Moffitt 1984; King 1987), Indian Ocean (Intès et al. 1989) and in the Mediterranean (Cartes 1993a, 1993b; García-Rodríguez et al. 2000; Colloca 2002; Vafidis et al. 2005; Possenti et al. 2007). However, information about ovarian maturation, egg development and brood size are scarce in general and lacking for the Atlantic populations of this species.

The first objective of the third chapter is to contribute to the knowledge of ovarian and egg development, estimate the brood size and establish a maturity scale for this species in the eastern-central Atlantic. The second goal examines the latitudinal variations in the life-history traits of *P. edwardsii*, including depth distributions and demography. A complete understanding of their ecology, mainly the reproductive, growth and brood size strategies, and their latitudinal differences would be of great interest considering that deep-water species are especially vulnerable to exploitation. Finally, considerable insight has been gained with regard to ecology of genus *Plesionika* discovering a new morphological structure.

Figure 3. Ejemplars of *Plesionika edwardsii*.

1.5 Codlings (Moridae)

Codlings are distributed in all tropical, subtropical, and warm-temperate seas of the world at depths of 100–600 m (Paulin 1989). They are mainly known from a taxonomic perspective, but few data concerning their ecology and population structure are available. Most species are very similar externally and are not easily identifiable. For these reasons, in general they are poorly known (Paulin 1989; Prokofiev 2006). The genus *Physiculus* is represented by 42 valid species (Froese &

Pauly 2019), but 41 according to Biscoito & González (2018), distributed worldwide, nine of which occurring in the Atlantic Ocean. Of these, seven occur in the eastern Atlantic Ocean: *P. cyanostrophus* (Fig. 4); *P. dalwigki* Kaup, 1858; *P. helenaensis* Paulin, 1989; *P. huloti* Poll, 1953; *P. karrerae* Paulin, 1989; *P. maslowskii* Trunov, 1991 and *P. microbarbata* Paulin & Matallanas, 1990.

First aim of the fourth chapter is the description of a new species, *Physiculus caboverdensis* (Fig. 4), which is an endemism of the Cape Verde Islands (González et al. 2018). A morphometric and meristic of *Physiculus cyanostrophus* study was accomplished herein based on a wide sample of individuals. Another objective was an update of distinctive traits among *Physiculus* species occurring in the Atlantic Ocean. Thus, an updated comparative table on size and position of the light organ of *Physiculus* species occurring in the Atlantic Ocean was performed.

Although the existence of fishes with a pseudo-hypural plate (or false tail) has been still poorly investigated in the deep-sea, the occurrence of individuals with regenerated caudal region is a characteristic trait in some species of *Physiculus*. Brüss (1986) described it for the first time in *P. marisrubri* Brüss, 1986. Later, some authors described this phenomenon in other *Physiculus* species (Paulin 1989; Paulin & Matallanas 1990; Prokofiev 2006). The final part of the present thesis describes remarkable caudal regeneration capacity of *P. cyanostrophus* and evaluates its importance through the main life-history traits.

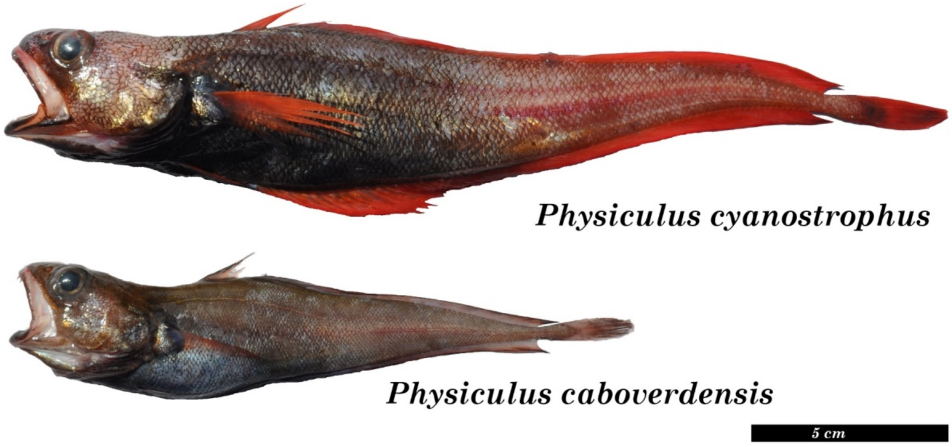

Figure 4. Individuals of *Physiculus cyanostrophus* and *Physiculus caboverdensis*.

1.6 Layout of the thesis

In the present compendia thesis, there are two main protagonists: *Plesionika edwardsii* and *Physiculus cyanostrophus*. The relationship between both species, beyond the habitat they share, can be summarized as the main target species of a fishery and one of the main by-catch species, respectively. Accordingly, second chapter is composed by one article introducing the semi-floating shrimp-trap fishery and its by-catch associated as a link between the consecutive chapters. Chapter three is composed by three published articles on ecology of *P. edwardsii* in particular and genus *Plesionika* in the eastern-central Atlantic in general. Similarly, chapter four is composed by three papers on ecology of *P. cyanotrophus* and ichthyologic contributions on genus *Physiculus* in the eastern-central Atlantic. General conclusions were provided based on these three differentiate chapters.

Finally, in addition to this story line, other contributions have been integrated in the pre-doctoral learning process. Despite they do not fall within the main scope, nine published articles have also been included as section VII, without the main body, to provide a broader and deeper view about thesis contribution on deep-water species in the eastern-central Atlantic. These contributions can be classified into three large blocks. A first block would include the contributions to the biodiversity of deep and shallow marine ecosystems in the archipelagos of Macaronesia and Cape Verde (Articles; Section VII, Art. 9, 10, 11, 13 & 16). A second block would combine the work related to the spatial distribution and abundance of benthic decapod crustaceans in the deep ecosystems of the Canary Islands and the importance of underwater canyons (Articles; Section VII, Art. 8 & 12). And finally, the contributions to the ecology of two species of deep water brachyuran crabs (Articles; Section VII, Art. 14 & 15).

III. Copy of the articles

Chapter 2

Semi-floating shrimp-trap fishery

(Article 1). Changes in catch and bycatch composition and in species diversity of a semi-floating shrimp-trap fishery in three eastern Atlantic island ecosystems with different degrees of human alteration.

Discards regulation vs Mediterranean fisheries sustainability
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Changes in catch and bycatch composition and in species diversity of a semi-floating shrimp-trap fishery in three eastern Atlantic island ecosystems with different degrees of human alteration

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Summary: Composition and bycatch of semi-floating shrimp-trap fisheries (SSTF) were compared among areas with different levels of anthropogenic alteration of marine ecosystems. The three areas selected were Madeira, the Canary Islands and Cape Verde. Mean species richness and diversity of the SSTF did not show significant differences among areas. The dominant species in catches of the SSTF for all regions studied was the main target species, *Plesionika edwardsii*, which accounted for 96.0% of the catch in Cape Verde, 75.8% in Madeira and 59.1% in the Canary Islands. Targeted pandalid shrimps accounted for more than 96.8% of total catches for all areas combined. Numbers of non-target species caught were 18 (Madeira), 14 (Canary Islands) and 16 (Cape Verde), of which 13 (Madeira), 8 (Canary Islands) and 11 (Cape Verde) were always discarded. Bycatch accounted for 0.5% (Madeira), 0.7% (Canary Islands) and 3.1% (Cape Verde) in numbers. Shark species accounted for 0.11% of all individuals caught. A total of 5 species in Madeira, 6 in the Canary Islands and 4 in Cape Verde, accounting for 0.2% to 0.8% of total catches, were not landed due to the small size of individuals or low numbers of individuals caught (self-consumption). The present results suggest that the selectivity of traps for the main target species, *P. edwardsii*, in SSTF changes due to changes in species dominance, which are probably linked to the degree of human fishing exploitation of the marine ecosystems in each area.

Keywords: abundance; diversity; bycatch; semi-floating shrimp traps; *Plesionika edwardsii*.

Cambios en la composición de la captura y de la captura accesoria y en diversidad específica en una pesquería con nasas camaroneras semi-flotantes en tres ecosistemas insulares del Atlántico oriental sujetos a distinta presión antrópica

Resumen: Se comparó la composición de las capturas y la captura accesoria de la pesquería de camarones con nasas semi-flotantes (SSTF) entre áreas con diferentes niveles de alteración de sus ecosistemas marinos por la acción humana. Se seleccionaron tres áreas: Madeira, Canarias y Cabo Verde. La riqueza de especies y la diversidad de la pesquería no mostraron diferencias significativas entre áreas. La especie dominante en las capturas de la SSTF fue la principal especie objetivo, *Plesionika edwardsii*, en las tres regiones estudiadas, variando desde 96.0% (Cabo Verde) hasta 59.1% (Canarias), con 75.8% en Madeira. Los camarones pandálidos objetivo de la pesca representaron más del 96.8% de la captura total en el conjunto de las tres áreas. El número de especies no-objetivo capturadas fue 18 (Madeira), 14 (Canarias) y 16 (Cabo Verde), de las cuales siempre fueron descartadas 13 especies en Madeira, 8 en Canarias y 11 en Cabo Verde. El porcentaje de individuos (en número) de las capturas accesorias en relación con las capturas totales representó el 0.5% en Madeira, 0.7% en Canarias y 3.1% en Cabo Verde. Las especies de tiburones representaron solo el 0.11% de los individuos capturados. Cinco especies en Madeira, seis en Canarias y cuatro en Cabo Verde representaron entre 0.2 y 0.8% del total de las capturas no desembarcadas debido a su pequeño tamaño o al bajo número de individuos capturados (auto consumo). Los resultados obtenidos sugieren que las nasas de la SSTF cambian sus características de selectividad con respecto a la especie objetivo principal, *P. edwardsii*, debido a cambios relativos entre las especies dominantes, lo que probablemente está relacionado con la explotación pesquera de los ecosistemas marinos en cada área.

Palabras clave: abundancia; diversidad; captura accesoria; nasas semi-flotantes; *Plesionika edwardsii*.

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INTRODUCTION

The impact of the fishing activity on non-target species or bycatch species, together with overexploitation of target species and impacts on habitats, is considered one of the main problems of marine ecosystems (Dulvy et al. 2003, Kappel 2005, Shester and Micheli 2011). At a global level, bycatch has been estimated at 27 million t per year (Alverson et al. 1994), but more recently Kelleher (2005) estimated worldwide discards at an average of 7.3 million t per year. Increasing awareness of the potential impacts of such high levels of unwanted catch on marine ecosystems is becoming an issue of global importance (Stobutzki et al. 2001, Bellido et al. 2011).

Small-scale fisheries have often been described as more selective and more sustainable than industrial fisheries (Chuenpagdee et al. 2006, Jacquet and Pauly 2008, Zimmerhackel et al. 2015). However, the bycatch level in small-scale fisheries can cause major ecological impacts and, when scaled to per-unit of total catches, be comparable to that in industrial fisheries (Bellido et al. 2011, Shester and Micheli 2011, Zimmerhackel et al. 2015).

In view of these findings, two priority goals emerge: a) to determine and reduce the impact of fishing activity on bycatch species, and b) to find a selective gear that minimizes the capture of non-target species. These goals are of particular importance when the fishing activity is focused on shrimp species, for which the biomass discarded is higher than the marketable biomass (33.0% of all world fishery discards) (Alverson et al. 1994, Stobutzki et al. 2001, Bellido et al. 2011), and attaining them will help the search for alternatives to bottom trawling.

Continental shelves are among the richest ecosystems of the sea (e.g. Stobutzki et al. 2001), supporting more than 95.0% the world's fisheries (Pauly and Christensen 1995, Pauly 2008, Sadovy et al. 2013), so they are among the marine ecosystems with the clearest signs of overexploitation. Although subjected to a lower fishing intensity, deep ecosystems, including the ones on the slope, are extremely sensitive to fishing activity (Cartes et al. 2007, Pajuelo et al. 2010, 2016), and bycatch has become a major conservation issue (Harrington et al. 2005).

Since 1975 shrimp species of the *Plesionika* genus have been fished with highly selective semi-floating shrimp traps operating between 100 and 500 m depth throughout the Mediterranean Sea (González et al. 1992, García-Rodríguez et al. 2000). Since 1997 (González 1997), this fishery has expanded to the northeastern Atlantic islands, where a small-scale fishery developed, first in the Canary archipelago (González et al. 2001) and many years later in Madeira (González et al. 2016). Only experimental fishing has been conducted around Cape Verde to date. However, the development of these fisheries has not been monitored and information on its impact on target and non-target species (in particular sharks) has not been available.

To bridge this gap, a research programme was developed to evaluate the composition of the catch of the shrimp fishery with semi-floating traps off Madeira, the Canary Islands and Cape Verde. Of particular interest was the bycatch of top predators because of their importance for ecosystem functioning (Pajuelo et al. 2010). In addition, the quantification and diversity of bycatch species is relevant for the current fisheries policy of the European Union, which aims to reduce the catches of some species groups to zero over a short period (Clarke 2009). A second objective of this study was to evaluate the behaviour of the fishing system at different levels of ecosystem exploitation.

MATERIALS AND METHODS

Sample procedures

Fishing operations (n=90) were done during six research cruises (15 fishing operations each) carried out in the Madeira (n=30), the Canary (n=30) and Cape Verde (n=30) archipelagos, to compare the composition and bycatch of the semi-floating shrimp-trap fishery (SSTF). The research cruises were conducted in the same period of the year (May-July 2017).

Three areas with different levels of fisheries-impacted ecosystems were selected: (1) Cape Verdean waters, a pristine deep ecosystem with little anthropogenic alteration, where no benthic fisheries exist below 100 m; (2) Canary Islands waters, the most fisheries-impacted of the three archipelagos, with full fishing activity from 0 to 1000 m depth and multiple gears such as benthic traps, semi-floating shrimp traps, trammel nets, purse seines, longlines, hand lines and poles; and (3) Madeiran waters, an example of medium fisheries impact.

Fishing operations (n=90) were performed around the islands and not only on a particular side of them. Each fishing operation (n=90) was performed with one ground line (trap-line) with 75 traps equally spaced (25 m) along the length of the fishing rope. Each fishing operation was done at a particular location and a specific depth, with no replicates. Atlantic chub mackerel (*Scomber colias*) was used as bait in the traps. All fishing operations were conducted over approximately 24 h to include the entire distribution range of species affected by diel migrations. Each fishing operation (30 at each archipelago) was carried out covering a bathymetric range between 175 and 490 m depth, corresponding to the maximum abundance depth for the target species *Plesionika edwardsii* at the three archipelagos combined (González et al. 2016). The traps were suspended 2.4 m above the bottom. The semi-floating trap is a cylinder conical trap with a base length of 56 cm and a height of 57 cm, covered with 15×20 mm mesh. Each trap has one truncated cone-shaped opening with a 23 cm outer diameter and 19 cm inner diameter. The specimens caught were identified to species level according to the WoRMS Editorial Board (2018).

The species caught were classified as target species (*P. edwardsii* and other pandalids of the *Plesionika* and *Heterocarpus* genera) or bycatch. Bycatch is considered the incidental catch of non-target species (NMFS 2016) and was further classified into two categories: (1) catch of species or sizes that are discarded because they are not marketable or have no economic value, and (2) catch of regulated species or sizes that are discarded due to regulations (Dunn et al. 2011, Zimmerhackel et al. 2015, NMFS 2016).

Data analysis

For each species the abundance in number of individuals and percentage was estimated by areas. For each main group (crustaceans, osteichthyans and chondrichthyans) and for the target/non-target species, the number of species and the abundance were calculated by areas.

A dominance curve, a plot of percentage cumulative abundance by numbers against the species rank, was applied to investigate changes in species dominance in the SSTF by area (Clarke 1990).

The analyses focused on the macrofauna caught by the SSTF. For each trap-line, the species composition and abundance (expressed as the number of individuals per trap-line) were recorded. Standardization and logarithmic transformation were applied to data of each trap-line prior to the analysis (Clarke and Warwick 2001), after which a resemblance matrix using the Bray-Curtis similarity index was constructed (Clarke and Warwick 2001, Clarke and Gorley 2006). Of the total trap-lines of the SSTF (n=90), only valid fishing operations (n=87) were used to test differences in species composition and abundance among areas. This was done using a distance-based permutational multivariate analysis of variance, PERMANOVA (Anderson et al. 2008). The factor considered to explain the ordination of the trap-lines of the SSTF was the area (archipelagos). PERMANOVA was performed to test the null hypotheses of no differences among the assemblages of the SSTF among areas. The permutation method used was the unrestricted permutation of raw data with a maximum number of permutations of 9999 due to their good empirical results in the maximum discriminant power (Anderson and Legendre 1999, Anderson and ter Braak 2003). For each factor, a pseudo-F test (*p*-F) and a pairwise test for significant effects were estimated. Statistical analyses were performed using Primer v.6 with PERMANOVA+ software (Clarke and Warwick 1994, Anderson et al. 2008).

The Similarity percentage (SIMPER) analysis procedure was used to identify the species (within and between samples) that contribute the most for a significant intergroup dissimilarity between areas and for a significant intragroup similarity (Clarke and Warwick 1994, 2001). Statistical analyses were also performed with PERMANOVA+ (Clarke and Warwick 1994, Anderson et al. 2008).

Biodiversity was tested among areas. Species diversity of the SSTF was estimated for abundance data with the Shannon-Wiener diversity index (H') and species richness (S) (Magurran 1988) using the DIVERSE subroutine within the Primer v.6 software. Species diversity of the SSTF was tested for differences among areas by an ANOVA test, considering each trap-line as one observation. This analysis was used to evaluate the null hypothesis of equality in S and H' for the SSTF among areas with a critical value of $F_{0.05,2,86}=3.15$.

Abundance of the most important pandalid species (*H. ensifer, P. edwardsii, P. ensis* and *P. martia*), individually and as a whole, and sharks were compared using a catch per unit effort (CPUE) unit estimated as the average number of shrimps per trap at each line (for shrimps), and as the square root of the total count per line (for sharks). Data of abundance were compared by an ANOVA test. This analysis was used to evaluate the null hypothesis of equality in CPUE among areas with a critical value of $F_{0.05,2,86}=3.15$.

Statistical significance was set at $p<0.05$ for all statistical tests performed.

RESULTS

Of the 90 fishing operations carried out around the three archipelagos combined, 29 in Madeira, 28 in Canary Islands and 30 in Cape Verde were considered valid.

A total of 64332 individuals representing 17 crustacean species (63568 individuals, 98.8%) and 28 fish species (764 individuals, 1.2%) were recorded. Only three species of Elasmobranchii (belonging to 3 families and representing <0.1% of the individuals caught), and 23 species of Actinopterygii (16 families, 1.1% in number of individuals) were caught (Table 1). In number of individuals, shrimps of the family Pandalidae (98.7%) dominated the SSTF. By region, the SSTF in Madeira was dominated by pandalid shrimps (99.5%) followed by the fish family Congridae (0.1%). In the Canary Islands, pandalids (99.3%) dominated the catches of the SSTF, followed by the fish family Sparidae (0.2%). In Cape Verde Islands, pandalids represented 96.9% of the catches of the SSTF, followed by the fish family Moridae with 1.9%. In all three regions the dominant species in the catches of the SSTF was the main target species *Plesionika edwardsii*, which accounted for 96.0% in Cape Verde, 75.8% in Madeira and 59.1% in the Canary Islands. The pandalid target species accounted for more than 96.8% of the total catches.

Table 1. – Species composition of macrofauna in numbers and in percentage of the semi-floating shrimp-trap fishery in Madeira, the Canary Islands and Cape Verde.

Family	Species	Madeira		Canary Islands		Cape Verde	
		Numbers	%	Numbers	%	Numbers	%
Aristeidae	*Aristaeopsis edwardsiana* (Johnson, 1868)			4	0.016		
	Aristaeomorpha foliacea (Risso, 1827)	4	0.018				
Epialtidae	*Anamathia rissoana* (Roux, 1828)					3	0.018
Galatheidae	Galatheidae not id.			6	0.023		
Homolidae	*Homola barbata* (Fabricius, 1793)	12	0.055	4	0.016		
Lysmatidae	*Ligur ensiferus* (Risso, 1816)	3	0.014				
Majidae	Majidae not id.					1	0.006
Oplophoridae	*Systellaspis pellucida* (Filhol, 1884)	12	0.055	9	0.035		
Pandalidae	*Heterocarpus ensifer* A. Milne-Edwards, 1881	84	0.388	4789	18.625	35	0.207
	Plesionika edwardsii (Brandt, 1851)	16424	75.791	15197	59.102	16267	96.009
	Plesionika ensis (A. Milne-Edwards, 1881)	24	0.111	3150	12.251	83	0.490
	Plesionika gigliolii (Senna, 1902)	11	0.051				
	*Plesionika martia (*A. Milne-Edwards, 1883)	122	0.563	32	0.124	13	0.077
	Plesionika narval (Fabricius, 1787)	4210	19.428	2294	8.922	7	0.041
	Plesionika williamsi Forest, 1964	683	3.152	65	0.253	6	0.035
Polybiidae	*Bathynectes maravigna* (Prestandrea, 1839)			5	0.019		
	Bathynectes piperitus Manning & Holthuis, 1981					3	0.018
Centrophoridae	*Centrophorus squamosus* (Bonnaterre, 1788)					12	0.071
Etmopteridae	*Etmopterus pusillus* (Lowe, 1839)	3	0.014			6	0.035
Somniosidae	*Centroscymnus crepidater* (Barbosa Bocage & Brito Capello, 1864)	3	0.014	3	0.012		
Centriscidae	*Macroramphosus scolopax* (Linnaeus, 1758)			11	0.043		
Congridae	*Conger conger* (Linnaeus, 1758)	24	0.111	25	0.097	9	0.053
Labridae	*Acantholabrus palloni* (Risso, 1810)	2	0.009			7	0.041
	Lappanella fasciata (Cocco, 1833)					4	0.024
Moridae	*Gadella imberbis* (Vaillant, 1888)					2	0.012
	Gadella maraldi (Risso, 1810)	5	0.023				
	Laemonema laureysi Poll, 1953					2	0.012
	Physiculus caboverdensis González, Triay-Portella & Biscoito, 2018					44	0.260
	Physiculus cyanostrophus Anderson & Tweddle, 2002					269	1.587
	Physiculus dalwigki Kaup, 1858	8	0.037				
Muraenidae	*Muraena helena* Linnaeus, 1758	5	0.023	10	0.039	20	0.118
Myrocongridae	*Myroconger compressus* Günther, 1870					9	0.053
Nettastomatidae	*Nettastoma melanurum* Rafinesque, 1810	1	0.005				
Ophichthidae	*Echelus myrus* (Linnaeus, 1758)					8	0.047
Ophidiidae	*Benthocometes robustus* (Goode & Bean, 1886)	3	0.014				
Phycidae	*Phycis phycis* (Linnaeus, 1766)	6	0.028	6	0.023		
Scorpaenidae	*Neomerinthe folgori* (Postel & Roux, 1964)					3	0.018
	Pontinus kuhlii (Bowdich, 1825)	7	0.032	11	0.043	103	0.608
Sebastidae	*Helicolenus dactylopterus* (Delaroche, 1809)	4	0.018	17	0.066	4	0.024
Serranidae	*Anthias anthias* (Linnaeus, 1758)					5	0.030
	Serranus atricauda Günther, 1874					8	0.047
Sparidae	*Dentex macrophthalmus* (Bloch, 1791)			41	0.159		
Synaphobranchidae	*Synaphobranchus affinis* Günther, 1877	7	0.032				
	Synaphobranchus kaupii Johnson, 1862	3	0.014				
Tetraodontidae	*Sphoeroides pachygaster* (Müller & Troschel, 1848)			34	0.132	10	0.059
		21670	100	25713	100	16943	100

A total of 18 non-target species were caught in Madeira, 14 in the Canary Islands and 16 in Cape Verde, of which 13, 8 and 11 species, respectively, were always discarded. Bycatch (in numbers) accounted for 0.5% of catches in Madeira, 0.7% in the Canary Islands and 3.1% in Cape Verde. The bycatch can be divided into three types according to the reason for not landing them: regulatory discards, species that are not marketable and individuals that are not marketable due to size. Bycatch due to regulations included only three individuals of *Etmopterus pusillus* and three of *Centroscymnus crepidater* in Madeira, three of *C. crepidater* in the Canary Islands, and 12 of *Centrophorus squamosus* and six of *E. pusillus* in Cape Verde. The capture of deep shark protected species was low, accounting for 0.11% of all individuals caught. The most frequently caught non-marketable species were *Gadella maraldi*, *Physiculus dalwigki*, *Synaphrobranchus affinis* and *Synaphobranchus kaupii* in Madeira; *Macroramphosus scolopax*, *Systellaspis pellucida* and *S. affinis* in the Canary Islands; and *Acantholabrus palloni*, *Lappanella fasciata*, *Physiculus cyanostrophus* and *Physiculus caboverdensis* in Cape Verde. A total of 5 species in Madeira, 6 in the Canary Islands and 4 in Cape Verde, accounting for 0.2% to 0.8% of total catches, were not landed due to the small size of individuals or low numbers of individuals caught (self-consumption).

The k-dominance curves for species abundance (Fig. 1) showed that the distribution of the number of individuals among species at Cape Verde differed markedly from that at the Canary Islands or at Madeira, which had a smaller number of dominant species. The patterns of the dominance curves of the three areas indicated different patterns of distribution of individuals among species, with the highest number of individuals aggregated in a single species at Madeira.

The results of PERMANOVA analysis (Table 2) in abundance indicated significant differences in the catch assemblage of the SSTF among archipelagos (p<0.001).

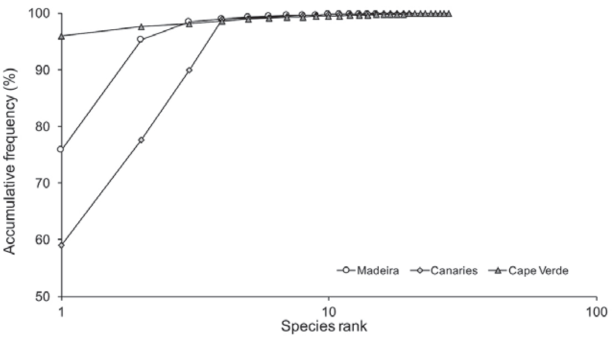

Fig. 1. – K-dominance curves of the number of individuals caught in Madeira, the Canary Islands and Cape Verde.

Pairwise comparisons showed that the trap-lines (assemblages) among archipelagos were significantly different in all cases (Canary Islands-Madeira p<0.0005; Canary Islands-Cape Verde p<0.0001; Madeira-Cape Verde p=0.0001).

The results of the SIMPER analysis of abundance showed that a few species provided the greatest contribution for defining the assemblages of the SSTF in each area, with an average similarity of 55.0 in Madeira, 44.3 in the Canary Islands and 73.8 in Cape Verde (Table 3). Considering the cumulative contribution roughly at 90%, the species that most contributed to intragroup similarity were the three pandalid species *Plesionika edwardsii*, *Plesionika narval* and *Plesionika williamsi* in Madeira; a more diverse set of four species including *P. edwardsii*, *Heterocarpus ensifer*, *P. narval* and *Plesionika ensis* in the Canary Islands; and the pandalid *P. edwardsii* and the fish *Physiculus cyanostrophus* in Cape Verde (Table 2). The target species of the SSTF, *P. edwardsii*, had a contribution of 80.8% in Cape Verde, 72.2% in Madeira, and 39.2% in the Canary Islands (Table 3).

Table 2. – Results of the PERMANOVA analysis. *values indicate significant differences at p<0.05; df, degrees of freedom; SS, sum of squares; p-F, pseudo F value; p, p value; t, t value.

Source	df	SS	p-F	p
Isles	2	42878	17.62	0.0001*
Res	84	1.02E5		
Total	86	1.45E5		
Groups			**t**	**p**
Canary Islands, Madeira			3.12	0.0005*
Canary Islands, Cape Verde			5.32	0.0001*
Madeira, Cape Verde			4.27	0.0001*

The comparison among areas, measured as the dissimilarity between each pair of areas, considering the number of species that cumulatively have a contribution of around 90%, is presented in Table 2. The values of dissimilarity ranged from 49.3% (between Cape Verde and Madeira) to 62.8% (between Canary Islands and Cape Verde). Five species, *H. ensifer*, *P. edwardsii*, *P. ensis*, *P. narval* and *P. cyanostrophus*, provided the greatest contribution (>76%) to discriminate the SSTF between the Canary Islands and Cape Verde. The pandalid species *H. ensifer*, *P. edwardsii*, *P. ensis*, *P. narval* and *P. williamsi* were found to contribute the most to the average dissimilarity between the SSTF of Canary Islands and Madeira. Six species, *P. narval*, *P. cyanostrophus*, *P. williamsi*, *P. edwardsii*, *H. ensifer* and *Pontinus kuhlii*, were found to be the discriminating species most contributing to the dissimilarity of the SSTF between Madeira and Cape Verde (Table 3).

By area, the greatest mean species richness (S) values of the SSTF was found in Cape Verde (S=6.71±1.73 [mean±sd]) and the lowest in the Canary Islands (S=6.26±33.13). The highest diversity values (H') for the SSTF were also recorded in Cape Verde (H'=1.20±0.36), being lower in Madeira (H'=1.19±0.45) and in the Canary Islands

Table 3. – Results of the SIMPER routine to analyse the contribution (C, in %; cut off=90.0%) in abundance of typifying species to within-group similarity and showing species that most contribute to intergroup dissimilarity.

Madeira Average similarity: 54.96		Canary Islands Average similarity: 44.34		Cape Verde Average similarity: 73.77	
Species	C%	Species	C%	Species	C%
Plesionika edwardsii	72.21	*Plesionika edwardsii*	39.23	*Plesionika edwardsii*	80.83
Plesionika narval	17.55	*Heterocarpus ensifer*	29.28	*Physiculus cyanostrophus*	10.86
Plesionika williamsi	5.29	*Plesionika narval*	14.99		
		Plesionika ensis	13.39		

Canary Islands - Cape Verde Average dissimilarity: 62.76		Canary Islands - Madeira Average dissimilarity: 59.06		Madeira - Cape Verde Average dissimilarity: 49.26	
Species	C%	Species	C%	Species	C%
Heterocarpus ensifer	20.26	*Heterocarpus ensifer*	20.37	*Plesionika narval*	21.17
Plesionika edwardsii	19.31	*Plesionika edwardsii*	20.13	*Physiculus cyanostrophus*	13.08
Plesionika ensis	13.74	*Plesionika narval*	16.67	*Plesionika williamsi*	13.07
Plesionika narval	13.14	*Plesionika ensis*	14.19	*Plesionika edwardsii*	10.02
Physiculus cyanostrophus	10.01	*Plesionika williamsi*	10.95	*Heterocarpus ensifer*	7.27
Pontinus kuhlii	4.31	*Plesionika martia*	4.05	*Pontinus kuhlii*	5.81
Physiculus caboverdensis	2.48	*Conger conger*	2.09	*Plesionika martia*	4.67
Plesionika williamsi	2.03	*Helicolenus dactylopterus*	0.52	*Plesionika ensis*	4.59
Plesionika martia	1.86	*Sphoeroides pachygaster*	0.39	*Physiculus caboverdensis*	3.24
Conger conger	1.57			*Conger conger*	2.03
Sphoeroides pachygaster	1.35			*Myroconger compressus*	1.25
				Muraena helena	1.23
				Homola barbata	1.20
				Centrophorus squamosus	0.91
				Helicolenus dactylopterus	0.84

(H'=1.17±0.41). The tests for homogeneity of variances for indexes of species richness (S) and diversity (H') were not rejected (p=0.124 and p=0.746, respectively). The ANOVA test showed no significant differences either in species richness (p=0.143) or in diversity (H') (p=0.438).

The standardized CPUEs, estimated as the average number of shrimps per trap in each trap-line (for shrimps) and as the square root of the total count per line (for sharks), showed that all pandalid species (*H. ensifer, P. edwardsii, P. ensis* and *P. martia*) individually had significant differences in CPUE level among areas (ANOVA Brown-Forsythe, p<0.033). However, when all species were analysed together, no significant differences in CPUE level among areas were found (ANOVA, Brown-Forsythe, p=0.055). Shark CPUE values were also significantly different among areas (ANOVA Brown-Forsythe, p=0.031).

DISCUSSION

Fishing produces ecological impacts on the biological community structure by exploiting non-target, high-trophic-level species that are important in the structure of the ecosystems, such as sharks (Myers et al. 2007, Shester and Micheli 2011, Zimmerhackel et al. 2015). The ratio of deep sharks increases with depth (Clarke et al. 2015), and their exploitation causes changes in the community via trophic cascades (Pauly et al. 1998, Lewison et al. 2004, Zimmerhackel et al. 2015). In the fishing system analysed herein, the bycatch volume varied from 0.5% to 3.2% in numbers. These values are in accordance with those of Kelleher (2005), who indicated that small-scale fisheries have a low or negligible discard rate (3.7% of total catches). The bycatch of the SFTF was diverse but showed a low number of individuals per species. Individuals of bycatch composition are mainly discarded because they are not marketable, but a low percentage are discarded because of regulatory restrictions. In addition, a very low proportion are discarded because they are undersized commercial species, but their bycatch makes an almost negligible contribution to the stock mortality.

The low number of individuals of non-target species caught confirmed the high selectivity of this fishing gear for a low number of target species of pandalid shrimps. Also, the overall bycatch of protected species such as sharks recorded in the present study was very low in comparison with that recorded in other small-scale activities in the area, such as the *Aphanopus* fishery, in which the ratio in number of individuals is one deep shark per target individual of black scabbardfish (Pajuelo et al. 2010). Cape Verde was the only area in which a single species, the morid *P. cyanostrophus*, was associated with the bycatch in the assemblage of the SSTF. Differences in the bycatch among areas can be best explained by a combination of local oceanographic factors and biogeographical patterns of the region considered. According to Spalding et al. (2007), Madeira and the Canary Islands belong to the Macaronesian ecoregion within the Lusitanian biogeographic province of the Temperate Northern Atlantic realm, whereas Cape Verde belongs to its own ecoregion within the West African transition province of the Tropical Atlantic realm.

Estimated bycatch ratios of between 0.5% and 3.2% in numbers were significantly much lower than the current global fisheries bycatch estimates of 40.4% (Davies et al. 2009), and lower than those recorded in many small-scale fisheries such as lobster traps (15.1%), drifting gillnets (18.5%), fixed gillnets (34.4%) or bottom longlines (42.0%-50.0%) (Pajuelo et al. 2011, Shester and Micheli 2011, Zimmerhackel et al. 2015). The level of bycatch recorded is in agreement with that reported by Shester and Micheli (2011), who pointed out that bycatch and habitat impacts of traps are non-significant. This low level of bycatch in a fishery is extremely positive, because a high level of bycatch has important ecological consequences at the species, population/stock (Hall et al. 2000, Lewison et al. 2004) and ecosystem levels (Dulvy et al. 2003, Kappel 2005, Read et al. 2006), particularly for shark species due to their life strategies (Hall et al. 2000, Stevens et al. 2000, Figueiredo et al. 2008). These impacts include reduction of the reproductive rates, reduction of population biomass, and less resilient marine ecosystems (Zimmerhackel et al. 2015).

Differences found in the catch assemblage of the SSTF among archipelagos indicate that the relative composition among species in the catches is different, and that the fishing system affects them in a different way.

These differences seem to be associated with the degree of human fishing exploitation of each area due to this fishing gear and particularly to other fishing systems used in the area, such as bottom traps, lines and longlines (Pajuelo and Lorenzo 1995, Pajuelo et al. 2011, Biscoito et al. 2015). In the area where there is no fishing exploitation, the main target species represented 96.8% of the catches but, when the exploitation increases in each area, there is a relative increase of the other pandalid target species that occupy the niche left by the species directly or indirectly affected by the fishing exploitation.

The archipelagos that showed the greatests differences were the Canary Islands and the Cape Verde, i.e. the most exploited and the unexploited marine areas, respectively, while Madeira was in an intermediate position in accordance with its moderate degree of exploitation. As the degree of exploitation changes from one area to another and as the communities are altered or degraded (Pajuelo et al. 2010, 2011, Shester and Micheli 2011, Zimmerhackel et al. 2015), the present results suggest that the structure of catches and their relative proportions change, and therefore the assemblages obtained with SSTF will change. These changes are supported by historical data. In the Canary Islands, the first fishing surveys with semi-floating shrimp traps in 1997 yielded 90.1% of *P. edwardsii* in the catches, with only 8.8% of other pandalids, mainly *P. narval* and *H. ensifer* (González 1997). In Cape Verde, the first fishing surveys with this selective fishing system in 2010 yielded 93.4% (Santiago island) and 96.9% (Boa Vista island) of *P. edwardsii* (unpublished data).

However, it is important to point out that these changes do not generate an increase in the species exploited, or a reduction in the standard mean abundance for each SSTF between areas, given that no changes are found in diversity, so there are only changes in the species dominance in the assemblage. CPUE data confirm these results, showing that values for each individual species differed among areas. However, pandalids as a whole showed no differences in CPUE values among areas.

The present results suggest that semi-floating shrimp traps do not change their selectivity for the main target species, *P. edwardsii*, because of a change in selective capacity or losses of selective capacity in an exploited marine ecosystem versus a pristine area such as Cape Verde, but because of changes in the community. Changes in the community produce changes in the species dominance, probably associated with the degree of human exploitation in the marine ecosystems, which is the case of the overexploited Canary Islands waters. In Madeiran waters, the situation seems to be intermediate. Despite these changes in relative abundance between the main target species and other target species, the bycatch rate is always very low regardless of the marine ecosystem conditions.

Taking into account that 22 million fishers work globally in small-scale fisheries and that these fisheries provide over 50% of the world's catches (Berkes et al. 2001, Chuenpagdee et al. 2006, Teh and Sumaila 2013), the use and development of this kind of selective fishing system makes an important contribution to reducing bycatch and conserving the community and habitat, especially in deep-sea marine ecosystems.

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Chapter 3

Deep-water shrimps from the eastern-central Atlantic

(Article 2). Ovarian maturity, egg development, and offspring generation of the deep-water shrimp *Plesionika edwardsii* (Decapoda, Pandalidae) from three isolated populations in the eastern North Atlantic.

(Article 3). Latitudinal patterns in the life-history traits of the three isolated Atlantic populations of the deep-water shrimp *Plesionika edwardsii* (Decapoda, Pandalidae).

(Article 4). Sex with the lights of: Can a morphological structure reveal the sex and functional maturity in the genus *Plesionika*?

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ORIGINAL ARTICLE

Ovarian maturity, egg development, and offspring generation of the deep-water shrimp *Plesionika edwardsii* (Decapoda, Pandalidae) from three isolated populations in the eastern North Atlantic

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ABSTRACT

Ovarian maturity, egg development and brood size were analysed for three isolated populations (Madeira, the Canary Islands and Cape Verde Islands) of *Plesionika edwardsii* (Decapoda, Pandalidae) in the eastern Atlantic. Multiple colour patterns were observed at the same ovarian maturity stage, which was verified histologically, invalidating the extensive use of ovarian colour as a maturity stage criterion. The physiological size at sexual maturity, based on the maturity of the ovaries, was higher in Madeira (carapace length of 19.73 mm) and decreased to the Cape Verdes (16.39 mm). Synchronic ovarian maturation was observed during the embryo incubation process, and ovigerous females bearing embryos at the final stage of development were found throughout the year. Females are multiple spawners during the reproductive season, after which the reproductive process ends and a rest period begins. The absence of females larger than the size at sexual maturity with ovaries in Stage 1, the incubation of embryos in the final developmental stages, suggests that the resting period begins with a process that reabsorbs the energy located in the ovaries and that the resting period occurs asynchronously in females in each of the studied populations. Embryo size was independent of female body size in the three populations studied, but increased with the developmental stage. A power equation was used to describe the relationship between brood size and female body size in the three areas studied. The mean number of external Stage I embryos carried by females decreased from Madeira ($n = 7868$) to the Cape Verdes ($n = 3781$), where less energy, in terms of the number of embryos and the size of the eggs, was invested in reproduction. Although female size decreases from north to south, the egg number was higher in Madeira than in the Cape Verdes for the same size range.

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Ovarian and embryo development; brood size; maturity scale; Pandalidae; central–eastern Atlantic

Introduction

In recent decades, the reduction of fishery resources in shallow coastal waters as a consequence of fishing has resulted in an expansion of fishing activities to deeper waters (Pauly et al. 2005; Morato et al. 2006; Echeverría-Sáenz & Wehrtmann 2011; Wehrtmann et al. 2012). Some pandalid species from deep habitats are the main targets of commercial fishing activities (for instance, *Pandalus borealis* Krøyer, 1838 in the north-western Atlantic, or *Heterocarpus reedi* Bahamonde, 1955 off Chile and Peru) (Araña-Espina & Nakanishi-Campos 1971; Holthuis 1980; Wehrtmann & Andrade 1998; Pérez & Defeo 2003; Pérez 2005; Wehrtmann & Nielsen-Muñoz 2009; Wehrtmann et al. 2012), and the deep-water shrimp species of the genus *Plesionika* Spence Bate occur and play an important ecological role in the benthic ecosystems of tropical and subtropical regions along the continental shelf and slope in the Atlantic and Mediterranean (Cartes 1993a, 1993b; Carbonell & Abelló 1998; Vafidis et al. 2005; Da Silva et al. 2013). The reproductive cycles and life histories of species living in these habitats may be adapted to an environment that is far from the photic zone, with patterns and abundances of organic inputs quite different from the near shore (Carbonell & Abelló 1998). *Plesionika edwardsii* (Brandt, 1851) was included in the FAO catalogue of species of interest to fisheries (Holthuis 1987), and it is currently the target species of specialized Spanish and Italian fleets that operate multiple selective semifloating shrimp traps throughout the entire Mediterranean basin (González et al. 1992). *Plesionika edwardsii* has a circumtropical distribution (except in the eastern Pacific) and inhabits a variety of bottoms including

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mud, sand, rocks and corals at depths between 110 and 680 m, but mainly at 250–380 m (González et al. 2001). In the eastern Atlantic, this species has been found from southwestern Spain to Angola, including the Macaronesian archipelagos, Cape Verde Islands and the entire Mediterranean region (García-Rodríguez et al. 2000; González et al. 2001).

The life-history traits of *P. edwardsii*, such as reproductive strategy, growth, diet and mortality, have been well studied in the Pacific (King 1984, 1986; Poupin et al. 1990), the Indian Ocean (Intès & Bach 1989) and in the Mediterranean (Cartes 1993a, 1993b; Company & Sardà 1997, 2000; García-Rodríguez et al. 2000; Colloca 2002; Vafidis et al. 2005; Possenti et al. 2007; Arculeo & Lo Bruto 2011). However, information about ovarian maturation, egg development and brood size are scarce in general and lacking for the Atlantic. Egg development plays a major role in the life-history traits of invertebrates because the energy contained in the eggs as nutrients must ensure the survival and development of the embryos (Begon et al. 1996; Figueiredo et al. 2008). Furthermore, from a fisheries perspective, knowledge of these characteristics is important for understanding the reproduction of the species, and in the case of brood size, it is essential for the estimation of reproductive potential and recruitment, one of the main aspects of population sustainability (King 1995; Begon et al. 1996; Mori et al. 1998; Figueiredo et al. 2008).

The goals of this study were to investigate ovarian and egg development, estimate the brood size and establish a maturity scale for this species in the eastern Atlantic.

Materials and methods

A total of 320 females of *Plesionika edwardsii*, 45 ovigerous and 35 non-ovigerous in each of the quarters of 2012, from each of the archipelagos of Madeira (MA), Canaries (CIS) and Cape Verdes (CVS) were analysed. The shrimps were collected using semifloating shrimp traps deployed at approximately 2.5 m above the sea floor between 100 and 350 m in depth. Each trap had base length dimensions of 56 × 57 cm and was 57 cm in height; they were covered with 15 × 20 mm plastic mesh with one truncoconical opening with an inner diameter of 19 cm (González et al. 1992). Atlantic chub mackerel (*Scomber colias* Gmelin, 1789) was used as bait, and immersion times ranged from 20 to 24 hours.

Carapace length (CL, from the posterior edge of the eye socket to the mid-dorsal rear edge of the carapace) was measured with a digital calliper to the nearest 0.01 mm, and total weight (TW) was measured to the nearest 0.01 g. Females were identified under a binocular microscope based on the absence of the appendix masculina on the endopod of the second pleopod and the shape of the endopod of the first pleopod (King & Moffitt 1984). Ovigerous condition was determined based on the presence of external or remaining eggs on the pleopods (King & Moffitt 1984).

Individual shrimps were dissected and their maturity stage was visually assessed macroscopically based on the structure, shape, position in the cephalothoracic cavity and colour of the dorsal and ventral faces of the ovaries. The mature ovary visibly extended anteriorly to the orbital margin and occupied most of the dorsal part of the cephalothorax. Ovaries were fixed and preserved in 4% buffered formaldehyde and subsequently processed histologically to verify the macroscopic stage. For histological analysis, the fixed tissues were dehydrated in a series of ethanol solutions, cleared in isoparaffin H, and then embedded in paraffin in a vacuum chamber (Triay-Portella et al. 2014). Tissue was sliced into 5 µm sections and stained with Harris' haematoxylin followed by an eosin counter-stain, and the histological morphologies of the ovary stages and the oocytes were described following the scale proposed by ICES (2010).

The percentage of mature females for each 10 mm CL class was determined, and the size at sexual maturity (the CL at which 50% of the ovaries are mature) was determined from the relationship between the percentage of mature ovaries and the CL. The number of mature ovaries by CL was fitted to a logistic equation by non-linear regression.

Ovigerous females from all size classes were used for the morphological study of the eggs and then to estimate brood size. Pleopods with attached eggs were removed from the females, and egg masses were then placed on a 100 µm mesh, washed and isolated from the pleopods and weighed. For each embryonic developmental stage identified from this research (see Results), a total of 12–15 females from each study area and size class was selected to estimate egg size. In each ovigerous female, the sizes of 65–75 randomly selected eggs were measured and then used to calculate the maximum diameter (Md in mm), minimum diameter (md in mm), mean diameter (xd in mm), and aspect ratio (Md/md) (Russ 1990).

The total number of Stage I embryos attached to the pleopods was directly counted in 60 females of all size classes under a binocular microscope for each study area. The brood size, defined as the egg production by batch, was estimated by the gravimetric method (Triay-Portella et al. 2014) and described by fitting a power function to the number of embryos and the CL data for each study area. Slopes of individual regressions were compared with the theoretical value 3 following Stechey & Somers (1995). The mass-specific gonad output or reproductive output (RO) (Havenhead & Todd 1989; Clarke et al. 1991) was estimated as follows: RO = total egg mass/total weight of female.

Results

The females examined in each area ($n = 320$) ranged in size from 16.24 to 28.25 mm CL (mean ± s.d.; 24.91 ± 1.91) from Madeira, from 16.08 to 27.10 mm CL (23.04 ± 2.05) from the Canaries and from 13.10 to 23.50 (20.32 ± 1.62) from the Cape Verde Islands.

Macroscopically, ovaries presented an inverted 'A' shape, and they were found developing in the cephalothoracic cavity and in some cases extended to the abdomen (Figure 1). The colour of the ovaries differed between the dorsal and ventral faces. At Stage 1, the gonads were macroscopically thin and generally translucent without visible oocytes, but histologically, gonads presented oogonia, early previtelogenic oocytes and some late previtelogenic oocytes. Oocytes were not surrounded by follicle cells, and the germinal zone was not totally apparent at this stage (Figure 1a). At Stage 2, ovaries became generally reddish-yellow on the dorsal face but were opaque white ventrally, and they filled less than half of the cephalothoracic cavity. Histologically, these ovaries appeared disorganized with abundant connective tissue while the germinal zone remained well defined. Oogonia, early previtellogenic oocytes and some late previtellogenic oocytes were present, and the follicle cells did not surround the oocytes (Figure 1b). At Stage 3, ovaries generally exhibited a reddish to bluish colour pattern on the dorsal face that became light blue on the ventral face. The ovaries filled more than half of the cephalothoracic cavity, and the oocytes became visible to the naked eye on the ventral face. Histologically, these ovaries presented two clear zones: the germinal zone in the centre of the ovary and the growth zone surrounding the germinal zone. The germinal zone was composed of oogonia, early previtellogenic oocytes, and late previtellogenic oocytes, while the growth zone contained late previtellogenic oocytes, early vitellogenic oocytes, and later vitellogenic oocytes surrounded by follicle cells (Figure 1c). At Stage 4, ovaries appeared compact and filled the entire cephalothoracic cavity with a dorsal bluish-green coloration that became bluish ventrally. Histologically, these ovaries presented a small, constrained germinal zone surrounded by later vitellogenic oocytes with vitelline membranes and advanced, later vitellogenic oocytes with a granular appearance due to a high concentration of yolk and nucleus migration. Oocytes reached their maximum size at this stage (Figure 1d). At Stage 5, ovaries were flaccid with a decreasing volume and a more yellowish aspect than at Stage 2, but with a similar size. Histologically, these ovaries were characterized by the presence of atretic oocytes undergoing reabsorption, abundant connective tissue and follicle cells (Figure 1e).

The physiological length at sexual maturity, which was based on the maturity of the ovaries, was estimated to be 19.73 mm CL in MA, 18.56 mm CL in CIS and 16.39 mm CL in CVS (Figure 2). The histological examination of the subsamples of 100 ovigerous females (larger than the size at sexual maturity) from each archipelago found females with ovaries at the resting stage (18–20%) bearing Stage I or II eggs, females with advanced ovaries (32–36%) bearing Stage II or III eggs, females with mature ovaries (30–36%) bearing Stage III or IV eggs and post-spawning females (10–16%) only bearing eggs at Stage I (Figure 3). No ovigerous females were observed with eggs at Stages III or IV or with ovaries at Stage 1. In the analysed ovigerous females, all of the maturity stages and all of the egg developmental stages were recorded in the four annual quarters. The histological examination of the subsample of 100 non-ovigerous females (larger than the size at sexual maturity) found females with ovaries in the resting (12–38%), advanced (30–36%) and mature stages (32–52%) (Figure 3). All maturity stages were recorded in each of the four annual quarters.

Eggs at Stage I were blue, with embryos lacking eye pigmentation and yolk filling most of the embryo volume (Figure 4a,b). At Stage II, eggs were pale blue, with eyespot pigmentation present in their embryos, appendage rudiments and with nerve ganglia appearing as a thickening of the blastoderm (Figure 4c). At Stage III, eggs were light brown, with visible eye pigmentation in their embryos, large cephalothoraces, extending abdomens and complete segmentation (Figure 4d). Finally, at Stage IV, embryos were completely developed and ready to be extruded (Figure 4e,f).

Eggs presented an ellipsoidal shape at all stages (Figure 4), and their development was not completely synchronous. Sometimes, two colour patterns were found simultaneously in the same egg mass. Mean egg size increased from Stage I to Stage III in all of the study areas (Table I). Increments were as follows: 24.5% (Madeira), 23.0% (Canaries) and 18.2% (Cape Verdes). ANOVA analysis of egg diameter by egg developmental stage (I–III) showed statistically significant

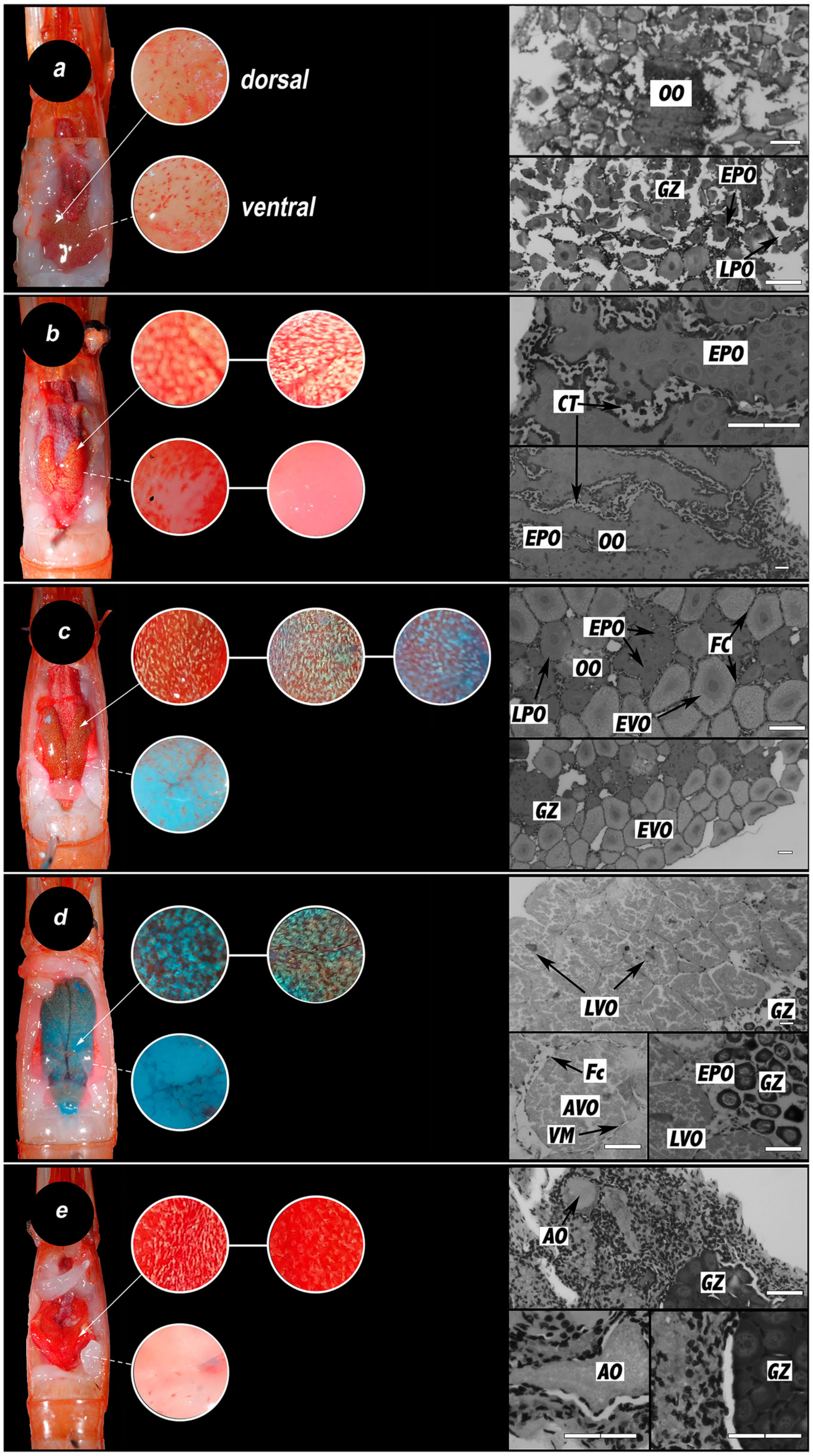

Figure 1. Macroscopic scale of the stages of sexual maturity in *Plesionika edwardsii* and histological sections. (a) Stage 1: gonads thin and translucent, without visible oocytes. Germinal zone not totally apparent. (b) Stage 2: gonads reddish-yellow and filling less than half of the cephalothoracic cavity. Ovaries disorganized, with abundant connective tissue and well-defined germinal zone. (c) Stage 3: ovaries from reddish to bluish and filling more than half of the cephalothoracic cavity. Oocytes and germinal and growth zones visible. (d) Stage 4: ovaries bluish-green with compact aspect and filling the entire cephalothoracic cavity. Ovaries with small, constrained germinal zone and advanced later vitellogenic oocytes. (e) Stage 5: ovaries flaccid, with atretic oocytes. OO, oogonia; EPO, early previtellogenic oocytes; LPO, late previtellogenic oocytes; EVO, early vitellogenic oocytes; LVO, later vitellogenic oocytes; AVO, advanced later vitellogenic oocytes; AO, atretic oocytes; FC, follicle cells; GZ, germinal zone; CT, connective tissue; VM, vitelline membrane.

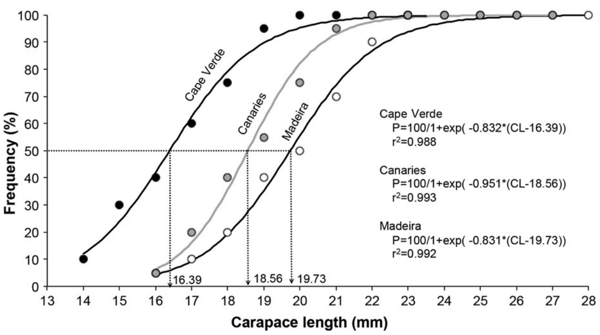

Figure 2. Maturity ogive estimated by means of the ovarian condition of *Plesionika edwardsii* females from Madeira, the Canaries and the Cape Verdes.

differences among the three areas (for all cases, $F = 6.11 > F_{0.05,2>1000} = 3.01$, $P < 0.011$).

The size of the eggs did not change with the size of the female for each stage of development in the three geographical areas (Figure 5). An ANOVA of egg size at each developmental stage by female carapace size indicated that the null hypothesis of no difference in egg size by female size was supported for each egg stage and the three study areas (for all cases, $F < 1.23 < F_{0.05,14>500} = 1.78$, $P > 0.122$). A two-way ANOVA analysis of egg diameter by egg developmental stage (I–III) among study areas revealed a statistically significant difference in egg diameter among egg stages and study areas ($F = 4.27 > F_{0.05,4>1000} = 2.38$, $P < 0.0019$).

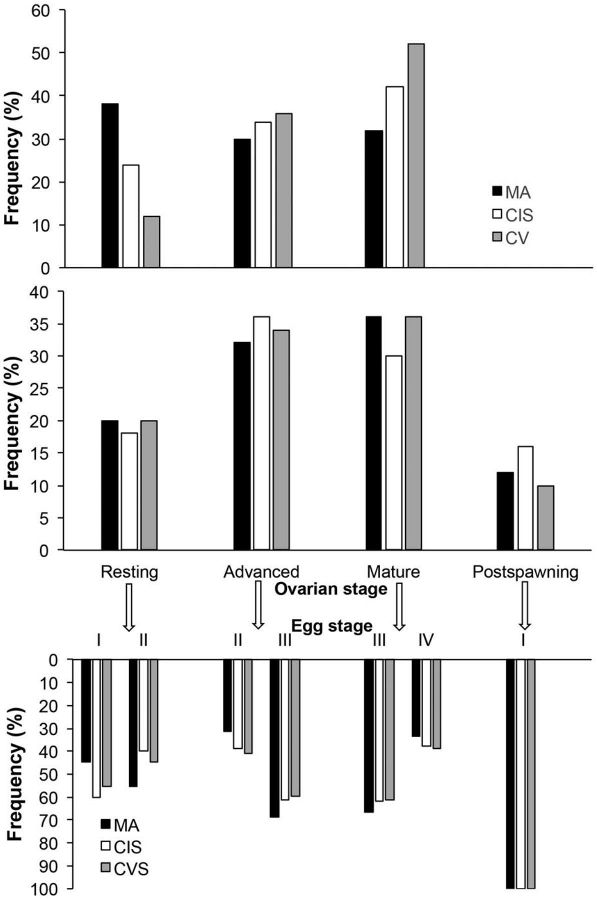

Figure 3. Ovarian maturity stage of ovigerous and non-ovigerous *Plesionika edwardsii* females from Madeira (MA), the Canaries (CIS) and the Cape Verdes (CV) with the egg stage of the bearing females.

The number of eggs increased significantly with female size in the three areas. The mean number of external eggs at Stage I produced by females was 7868.46 ± 2557.77, ranging from 2987 eggs (produced by one 19.5 mm CL/5.98 g TW female) to 13,177 eggs (produced by one 28.2 mm CL/14.61 g TW female) in MA; 6131.80 ± 2040.99, ranging from 2824 eggs (one 19.00 mm CL/5.56 g TW female) to 9789 eggs (one 26.30 mm CL/10.72 g TW female) in CIS; and 3781.37 ± 1258.50, ranging from 1879 eggs (one 18.2 mm CL/4.19 g TW female) to 6629 eggs (one 23.5 mm CL/7.19 g TW female) in CVS (Figure 6). The non-linear relationship between the brood size of the first egg developmental stage and CL was significant ($P < 0.0001$), and the relationship between brood size and female size was allometric and positive in all cases ($t \geq 2.44 > t_{0.05>60} = 2.00$, $P < 0.017$), implying that volumetric relationship was held, with smaller females carrying fewer eggs than larger females. An ANOVA of the number of eggs at Stage I showed significant differences among archipelagos ($F = 64.86 > F_{0.05,2>100} = 3.10$, $P < 0.0001$), and the three regression lines of the logarithmically transformed data of eggs at Stage I versus female size also revealed significant differences among study areas (ANCOVA, $F = 697.74$, $P < 0.0001$). For the common range of body sizes (19.6–24.20 mm CL) the number of eggs also showed significant differences among archipelagos (ANOVA, $F = 8.59 > F_{0.05,2>100} = 3.10$, $P < 0.0001$). The three regression lines of the logarithmically transformed data of eggs at Stage I versus female size for the common range of body sizes also indicated significant differences among areas (ANCOVA, $F = 121.24$, $P < 0.0001$).

The mean reproductive output increased significantly with latitude. Mean RO was 8.36 ± 2.41 (ranging from 4.27 to 15.85) in MA, 7.94 ± 2.49 (4.20–11.79) in CIS and 5.51 ± 1.83 (2.68–9.73) in CVS. An ANOVA of the RO showed significant differences among archipelagos ($F = 21.83 > F_{0.05,2>100} = 3.10$, $P < 0.0001$). RO did not show any relationship with CL or egg size.

Discussion

Many of the studies that have macroscopically assigned maturity stages to *Plesionika* species used maturity scales based on the size of the gonads and,

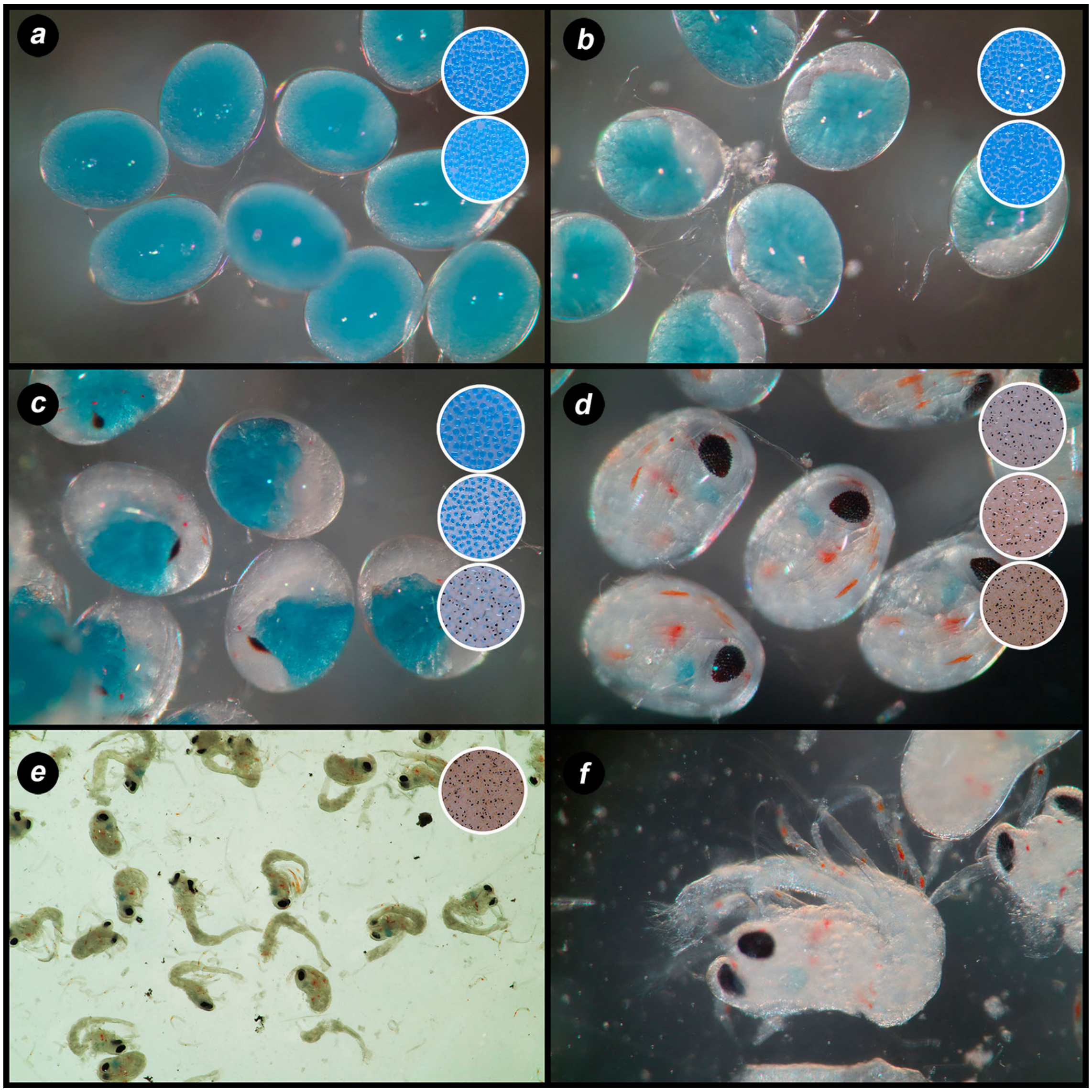

Figure 4. Macroscopic description of the egg developmental stages (I–V) of *Plesionika edwardsii* including egg mass colour. (a,b) Eggs in Stage I with yolk filling most of the embryo volume. (c) Eggs in Stage II with eyespot pigmentation present in their embryos and appendage rudiments. (d) Eggs in Stage III with embryos with highly visible eye pigmentation, large cephalothoraces, extended abdomens, and complete segmentation. (e,f) Eggs in Stage IV with well-formed embryos ready to be hatched.

Table I. Maximum (Md in mm), minimum (md in mm), and mean diameters (xd in mm) with standard deviations (± s.d.), number of eggs examined (*n*), and aspect ratios (Ar) by egg developmental stage (I–III) of *Plesionika edwardsii*.

Locality	Stage	Md (mm)	md (mm)	xd ± s.d. (mm)	*n*	Ar
Madeira	I	0.634	0.496	0.569 ± 0.039	875	1.25
	II	0.802	0.521	0.657 ± 0.061	864	1.36
	III	0.825	0.552	0.721 ± 0.062	954	1.38
Canaries	I	0.626	0.502	0.568 ± 0.033	813	1.22
	II	0.797	0.548	0.665 ± 0.056	817	1.45
	III	0.824	0.550	0.690 ± 0.045	979	1.46
Cape Verdes	I	0.604	0.489	0.546 ± 0.063	801	1.19
	II	0.678	0.513	0.585 ± 0.044	834	1.37
	III	0.744	0.507	0.623 ± 0.042	806	1.46

primarily, the colour pattern of the carapace (Ceccaldi 1968; Company 1995; Ohtomi & Hayashi 1995; Company & Sardà 1997; Ohtomi 1997; García-Rodríguez et al. 2000; Colloca 2002; Maiorano et al. 2002; Possenti et al. 2007; Ahamed & Ohtomi 2011). In some cases, the same maturity scale has been used for different *Plesionika* species, including *Plesionika edwardsii*, although the ovarian coloration pattern differs among species. Ahamed & Ohtomi (2011) described the mature ovary as dark yellow for *Plesionika izumiae* Omori, 1971; Colloca (2002) and Possenti et al. (2007) as dark blue for *P. edwardsii*; Ohtomi & Hayashi (1995) and Ohtomi (1997) as blue for

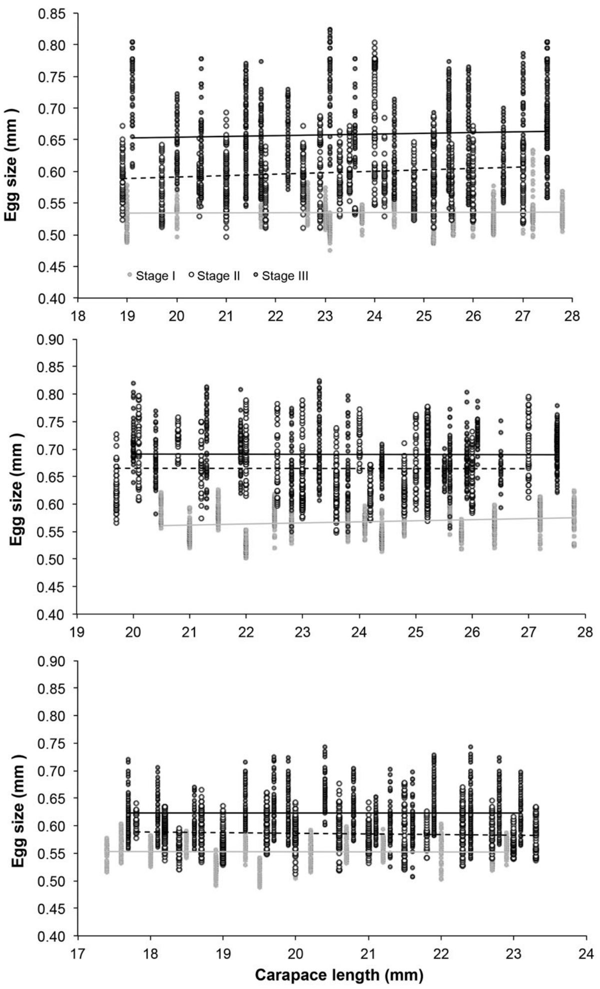

Figure 5. Egg size by egg developmental stage as a function of the carapace size of female *Plesionika edwardsii* from Madeira (top), the Canaries (middle) and the Cape Verdes (bottom).

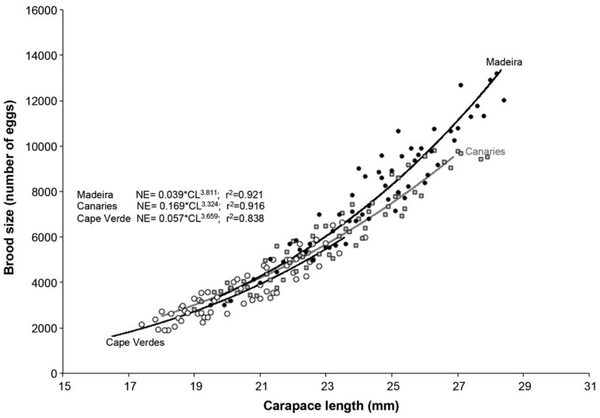

Figure 6. Relationship between brood size and the carapace length of female *Plesionika edwardsii* ($n = 60$) from Madeira, the Canaries and the Cape Verdes. NE, number of eggs; r^2, determination coefficient. Fitted lines correspond to each potential estimated model.

P. semilaevis Spence Bate, 1888; Maiorano et al. (2002) as dark green–blue and blue for *P. martia* (A. Milne-Edwards, 1883). Company (1995), Company & Sardà (1997) and García-Rodríguez et al. (2000) used the relative intensity of the colour to describe the mature ovary of *P. acanthonotus* (Smith, 1882), *P. edwardsii*, *P. gigliolii* (Senna, 1902), *P. heterocarpus* (A. Costa, 1871) and *P. martia*. In all cases, the number of stages used (3–8) and their description (without a descriptive picture or histological confirmation) varied greatly, making it impossible to compare results while the same, previously used scale was described or modified for the different ovarian stages (Company 1995; Company & Sardà 1997; García-Rodríguez et al. 2000; Colloca 2002; Maiorano et al. 2002; Possenti et al. 2007). A unification of terminology based on histological images is required to allow the correct and unambiguous application of scales, especially when the colour patterns can differ greatly among females at the same stage of maturity, as has been demonstrated in this study. The changes in the colour of decapod crustacean ovaries during the reproductive cycle (Adiyodi & Subramonian 1983; Arculeo et al. 1995; Triay-Portella et al. 2014; Biscoito et al. 2015) result from differences in the content of carotenoids during oogenesis (Goodwin 1951; Liñán-Cabello et al. 2002; Gregati et al. 2010) and therefore depend on the condition of the individual and the quantity and quality of food available, which can vary greatly within and among populations. In this study, histological analysis of the gonads did not validate the sexual maturity colour scale that has been extensively used because several colour patterns occurred simultaneously in several phases, proving the inadequacy of colour for use as a maturity scale. Similar results have not been described for other caridean shrimps; however, it has been found in other decapod crustaceans (Triay-Portella et al. 2014; Biscoito et al. 2015). The maturity scale based on the morphology of the gonads was confirmed histologically.

The estimation of size at sexual maturity based on ovarian maturation (physiological maturity) instead of ovigerous condition was more reliable because a high fraction of non-ovigerous females were mature but could be in the resting period, which could lead to an overestimation of the size at maturity. Differences in the size at sexual maturity of *P. edwardsii* in the same area (see Santana et al. 1997) can be more than 70 mm in carapace length, and the size at physiological maturity estimated in this study agrees with the sizes reported for *P. edwardsii* by Guennégan et al. (1992), Colloca (2002) and Possenti et al. (2007) of between 17.9 and 18.5 mm CL. Sexual maturity in the three analysed populations was reached at the same relative size, which corresponded to a specific percentage of the maximum body size described at each archipelago according to the Charnov (1990) rule. The relative size at sexual maturity varied slightly between 58% and 59%, and similar results have been observed for other pandalids with values oscillating between 53% and 58% in different localities regardless of species, sexual typology, latitude or reproductive strategy (Charnov 1990; Briones-Fourzán et al. 2010; Hirose et al. 2013). The absence of variation in the relative physiological size at sexual maturity among the studied populations reflects genotypic characteristics linked to a plasticity in the size of the species under different environmental conditions (Hirose et al. 2013).

In the three populations studied, ovigerous *P. edwardsii* females bearing early-stage embryos (I–II) had no mature ovaries, while ovigerous females with embryos near extrusion (Stage IV) exhibited mature ovaries. Furthermore, non-ovigerous females larger than the size at sexual maturity showed ovaries at all of the maturity stages. These results suggest that *P. edwardsii* produces embryos at least two or three times (as a function of the estimated three-month incubation period) (Colloca 2002) during one reproductive period, after which the reproductive process ends and a rest period begins, although the number of hatchings (three or more) throughout the year could not be determined. As no ovigerous females were observed with eggs at Stages III or IV and with ovaries at Stage 1, the resting period likely begins with a process that reabsorbs the energy invested in the ovaries. Multiple broods within a single reproductive period in *P. edwardsii* were also suggested by Colloca (2002). The resting period occurs asynchronously for the females in each of the studied populations, and this asynchronous break in the reproductive process may be due to a process of recovering the energy invested in prior reproduction and the previous moulting process. This break in the reproductive period involves a new process of ovarian maturation for an upcoming ecdysis and fecundation. The relationship between the reproductive receptivity of females and the moulting process is a common pattern in decapod shrimps, where the females are receptive for a short period after ecdysis (Ceccaldi (1968) and Possenti et al. (2007) for *P. edwardsii*; Correa & Thiel (2003) for carideans; Gregati et al. (2010) for stenopodideans; Salmon (1983) for decapods). This short time period suggests that the prior ovarian maturity process occurs to enable fecundation after moulting.

A seasonal synchronic reproductive pattern was described by Colloca (2002) for *P. edwardsii* from the Mediterranean. However, when those data are compared with the present study both patterns are very similar. Colloca (2002) described a developmental pattern between ovaries and embryos where females with immature ovaries carried early-stage embryos, whereas mature gonads were found in females carrying eggs near hatching, as observed in this study. However, Colloca (2002) pointed out that the development of ovaries is synchronous among all adult females and culminates in a period with quiescent gonads that indicates the end of the spawning season. This conclusion is contrary to the author's prior findings (Colloca 2002) and the presence of females carrying developed eggs on pleopods with gonads at an advanced stage of development as well as the occurrence of ovigerous and non-ovigerous adult females throughout the year. This result is consistent with García-Rodríguez et al. (2000) and Possenti et al. (2007), who described the presence of females with eggs at advanced developmental stages throughout the year. Colloca (2002) also described a period in which a high percentage of females without eggs presented ovaries at an advanced stage of maturity, as observed in this study, but Colloca (2002) attributed this observation to the beginning of the reproductive season, although such females and adult, non-ovigerous females at early stages of ovarian development can be observed throughout the year. The differences between both studies may be due to the ratio of females that reach the resting period. Thus, while the percentage of females reaching this stage in the Atlantic is distributed throughout the year, this stage is reached by a high percentage of females during the same period in the Mediterranean, although with low percentages during the rest of the year. A reproductive pattern consisting of continuous embryo hatching has also been described for *P. izumiae* (see Ahamed & Ohtomi 2011), *P. martia* (see Maiorano et al. 2002) and *P. semilaevis* (see Ohtomi 1997). Additionally, Company & Sardà (1997) and Campisi et al. (1998) suggested the existence of more than one spawning event during the same annual reproductive season for *P. acanthonotus*, *P. antigai* Zariquiey Álvarez, 1955, *P. edwardsii*, *P. gigliolii*, *P. heterocarpus* and *P. martia*, so this pattern seems to be a characteristic of the genus *Plesionika*.

The size of the embryos was independent of female size in the three regions studied, although embryo size increased with development, and this pattern has been described by Omori (1971) and Ahamed & Ohtomi (2011) for other *Plesionika* species. This incremental increase in embryo size during the incubation period is a general phenomenon in decapods due to changes in their biochemical composition and water content during embryonic development (Clarke et al. 1990; Clarke 1993a; Lardies & Wehrtmann 1996; Wehrtmann & Graeve 1998; Wehrtmann & Kattner 1998; Ahamed & Ohtomi 2011). During embryogenesis, the water content of the egg increases due to the water consumed by the embryo and the metabolic water resulting from respiration (Amsler & George 1984; Petersen & Anger 1997; Figueiredo et al. 2008).

When the sizes of the eggs are compared among the studied populations, it can be observed that less energy is invested in reproduction (in terms of number of eggs and size of the eggs) in the Cape Verdes than in the other regions. This pattern agrees with the general tendency of the production of larger eggs at higher latitudes (Thorson 1950; Clarke 1992; Wehrtmann & Lardies 1999). When egg sizes are compared among the studied populations and the Mediterranean population (Company & Sardà 1997), the eggs in the Atlantic are larger than in the Mediterranean populations (Stage I: 0.510 mm; Stage III: 0.590 mm) with sizes between 7% and 11% higher at Stage I and between 5% and 22% higher at Stage III. The Mediterranean area is located at a higher latitude than the populations studied, so larger eggs could be expected. However, the larger egg size found in the Atlantic could be explained because eggs in colder regions (such as the Atlantic) need to contain more yolk to provide sufficient internal energy for survival during longer incubation periods than in warmer areas (as in the Mediterranean) as an adaptation to protect the embryo against low temperatures (Thorson 1950; Wehrtmann & Kattner 1998; Lardies & Castilla 2001; Terossi et al. 2010a, 2010b; Viegas et al. 2012). Additionally, as *P. edwardsii* produces planktonic larvae that migrate to surface waters (Landeira et al. 2009), the isothermal conditions of the Mediterranean Sea produce larvae with a higher rate of survival because survival probability decreases with depth and with changes in water temperature (King 1987). However, in the Atlantic, the wide range of water temperatures experienced by the larvae during their vertical migration and the presence of different water masses (Pajuelo et al. 2015) reduce the probability of larval survival, which can be offset by the production of larger eggs, which produce larger larvae that have a higher survival rate than do smaller ones (King 1987; Company & Sardà 1997).

The size of Stage I embryos did not change with an increase in female size. Clarke (1993a) indicated that egg size is significantly correlated with nutrient content, so differences in egg size reflect a difference in energy investment per embryo (Wehrtmann & Lardies 1999). This implies that there are no female size-related differences in the energy allocated to each embryo, but differences in the size of Stage I embryos have been observed among study areas, implying the existence of a latitudinal effect in the quantity of energy allocated to each embryo, which increases northwards. This pattern indicates an intraspecific plasticity in egg size, which suggests that the variability in egg size observed among populations may be related to local environmental conditions (Clarke 1993b; Wehrtmann & Lardies 1999). This pattern of intraspecific differences in egg size along a latitudinal gradient has been observed in other decapod species (Clarke et al. 1991; Gorny et al. 1992; Clarke 1993b; Wehrtmann & Lardies 1999).

The results of the reproductive output also indicated that *P. edwardsii* invests more energy in the production of eggs in Madeira than in the Cape Verde Islands, with females in the latter locality producing smaller eggs. Values of the reproductive output also suggest that in *P. edwardsii* reproductive investment is predominantly governed by latitudinal factors such as temperature or food availability (Clarke et al. 1991). As has been observed in other caridean shrimps (Briones-Fourzán et al. 2010; Echeverría-Sáenz & Wehrtmann 2011), for *P. edwardsii* in the three studied areas a relationship between reproductive output and females' weight was not found. The production of thousands of small eggs, as well as the variability in the reproductive output among females of *P. edwardsii*, reflect a high and variable reproductive strategy to compensate high larval mortality (Briones-Fourzán et al. 2010).

Studies of the pattern of egg development in *Plesionika* species, including *P. edwardsii*, are based on two main scales proposed by Ceccaldi (1968) and Company (1995), which are included in two restricted pieces of grey literature that are used extensively, directly or in a modified form (Company & Sardà 1997; Campisi et al. 1998; García-Rodríguez et al. 2000; Colloca 2002; Chilari et al. 2005; Possenti et al. 2007; Arculeo & Lo Bruto 2011; Koçak et al. 2012), or on non-illustrated scales developed by different authors (Thessalou-Legaki 1992; Ohtomi 1997; Ahamed & Ohtomi 2011). In all cases, the number of stages used and their description (without a descriptive picture) vary greatly, making it difficult to compare results among studies. In some cases, authors have indicated the arbitrary nature of their scales (Ohtomi 1997) or their modifications (Campisi et al. 1998) that incorporate egg colour as a criterion (Ceccaldi 1968; Company 1995; Company & Sardà 1997; García-Rodríguez et al. 2000; Colloca 2002; Chilari et al. 2005; Possenti et al. 2007; Arculeo & Lo Bruto 2011; Koçak et al. 2012). This great variability can be observed in the

Table II. Brood size and carapace length (CL, mm) ranges from females of *Plesionika* species.

Species	Brood size	CL	Area	References
Plesionika acanthonotus (Smith, 1882)	800–3000	9.6–17.9	Catalan Sea	Company & Sardà (1997)
Plesionika edwardsii (Brandt, 1851)	3900–11,800	18.3–29.0	Catalan Sea	Company & Sardà (1997)
Plesionika edwardsii	847–13,721	No data	Fiji	King (1987)
Plesionika edwardsii	920–19,792	21.0–25.0	Tyrrhenian Sea	Possenti et al. (2007)
Plesionika gigliolii (Senna, 1902)	100–2700	9.3–18.6	Catalan Sea	Company & Sardà (1997)
Plesionika heterocarpus (A. Costa, 1871)	2200–6300	11.0–20.2	Catalan Sea	Company & Sardà (1997)
Plesionika heterocarpus	1446–3981	5.4–8.9	Aegean Sea	Bakir et al. (2009)
Plesionika izumiae Omori, 1971	479–4405	7.4–14.7	Japan	Ahamed & Ohtomi (2011)
Plesionika izumiae	184–1086	5.2–8.0	Japan	Omori (1971)
Plesionika martia (A. Milne-Edwards, 1883)	618–6244	11.8–22.9	Ionian Sea	Chilari et al. (2005)
Plesionika martia	1800–11,200	15.0–26.0	Ionian Sea	Maiorano et al. (2002)
Plesionika martia	1400–11,400	14.2–26.7	Catalan Sea	Company & Sardà (1997)
Plesionika martia	9345–13,750	16.3–20.1	Aegean Sea	Bakir et al. (2009)
Plesionika narval (Fabricius, 1787)	200–7500	7.9–18.7	Greece	Thessalou-Legaki (1992)
Plesionika quasigrandis Chace, 1985	1630–17,376	8.5–11.7	India	Chakraborty et al. (2014)
Plesionika semilaevis Spence Bate, 1888	1048–8221	10.4–18.0	Japan	Ohtomi (1997)
Plesionika serratifrons (Borradaile, 1900)	100–1344	No data	Fiji	King (1987)

description of the same non-eyed phases across studies as follows: non-segmented blastoderm and early segmentation of the body (Campisi et al. 1998); yolk fills most of the egg volume and the appearance of a ventral cleft (Ohtomi 1997; Ahamed & Ohtomi 2011); light blue eggs without embryo pigmentation (Possenti et al. 2007); egg with intense coloration (García-Rodríguez et al. 2000); embryos without eye pigmentation (Thessalou-Legaki 1992); blue eggs with embryos without eye pigmentation (Arculeo & Lo Bruto 2011); and recently spawned eggs with intense colour and no visible embryo pigmentation (Company 1995; Company & Sardà 1997; Chilari et al. 2005; Koçak et al. 2012). To clarify this variability, the unification of terminology based on images is necessary, allowing the correct and unambiguous application of scales, at least for *P. edwardsii*, where colour patterns, as has been demonstrated in this work, can be erroneous or differ among species.

Female body size is the principal factor determining brood size in decapods (Hines 1982, 1991; Corey & Reid 1991; Lardies & Wehrtmann 1996; Wehrtmann and Lardies 1999), and the reduction in the brood size and the higher maximum female body size from Madeira to the Cape Verdes supports this relationship.

Comparable information on brood size (which is related to female size) about *P. edwardsii* from different geographical regions as well as from other species of *Plesionika* are included in Table II. Brood size estimates in the three areas studied can be considered congruent with values obtained from other populations of *P. edwardsii* from the Mediterranean Sea (Company & Sardà 1997; Possenti et al. 2007) and Pacific Ocean (King 1987). Present brood size values are also similar with those reported for *P. narval* (Thessalou-Legaki 1992) and *P. martia* from the Mediterranean (Company & Sardà 1997; Maiorano et al. 2002; Chilari et al. 2005; Bakir et al. 2009) (Table II). The brood size of *P. edwardsii* differs from the values estimated for other *Plesionika* species of smaller size (Table II). A small brood size and a relatively large egg size is the general pattern found in deep-sea species (Thorson 1950; Omori 1975; Gage & Tyler 1991; Company & Sardà 1997). In addition, the high variability found in brood size is consistent with different lengths of the reproduction period, and this variability is common in *Plesionika* species (Company & Sardà 1997; Maiorano et al. 2002; Chilari et al. 2005).

Brood size during the incubation period suffers a significant embryo loss in several *Plesionika* species (Ohtomi 1997; Maiorano et al. 2002; Ahamed & Ohtomi 2011), including *P. edwardsii* (Guennégan et al. 1992; Possenti et al. 2007). This reduction in brood size has been estimated to be between 15% and 35% in *P. edwardsii* (Guennégan et al. 1992; Possenti et al. 2007). This loss during the incubation period is a common phenomenon that occurs due to mechanical stress, parasites and egg predators (Balasundaram & Pandian 1982; Kuris 1991; Figueiredo et al. 2008; Ahamed & Ohtomi 2011) as well as the increase of embryo volume during incubation, which results in a reduction of the space available to carry embryos below the pleon (Figueiredo et al. 2008; Ahamed & Ohtomi 2011). In the present study, no parasites or predators were observed to affect *P. edwardsii* in the studied area, as has been found for other *Plesionika* species (Ahamed & Ohtomi (2011) for *P. izumiae* and Chilari et al. (2005) *P. martia*). Therefore, the increase in egg size during development may be the main cause of embryo loss in *P. edwardsii* (Ahamed & Ohtomi 2011). Because the egg mass at Stage I completely fills the available brood space in *P. edwardsii*, the increase in egg size and egg mass during the incubation period increases the egg attachment area, which increases the mechanical abrasion of the outer embryos and, consequently, their loss (Kuris 1991; Wehrtmann & Lardies 1999; Figueiredo et al. 2008). The estimation of brood size from individuals caught in traps avoids the underestimation associated with trawl systems, in which egg loss is higher due to mechanical friction (Possenti et al. 2007).

Disclosure statement

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Latitudinal patterns in the life-history traits of three isolated Atlantic populations of the deep-water shrimp *Plesionika edwardsii* (Decapoda, Pandalidae)

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ABSTRACT

Patterns in the life-history traits of the pandalid shrimp *Plesionika edwardsii* are studied for the first time in three isolated Atlantic populations (Madeira, Canaries and Cape Verde Islands) to gain an understanding of their latitudinal variations. The maximum carapace size of the populations studied, as well as the maximum weight, showed clear latitudinal patterns. The patterns observed may be a consequence of the temperature experienced by shrimps during development, 1.37 °C higher in the Canaries and 5.96 °C higher in the Cape Verde Islands than in Madeira. These temperature differences among populations may have induced phenotypic plasticity because the observed final body size decreased as the temperature increased. A latitudinal north-south pattern was also observed in the maximum size of ovigerous females, with larger sizes found in the Madeira area and lower sizes observed in the Cape Verde Islands. A similar pattern was observed in the brood size and maximum egg size. Females of *P. edwardsii* produced smaller eggs in the Cape Verde Islands than did those at the higher latitude in Madeira. *P. edwardsii* was larger at sexual maturity in Madeira than in the Cape Verde Islands. The relative size at sexual maturity is not affected by latitude or environmental factors and is the same in the three areas studied, varying slightly between 0.568 and 0.585. *P. edwardsii* had a long reproductive season with ovigerous females observed all year round, although latitudinal variations were observed. Seasonally, there were more ovigerous females in spring and summer in Madeira and from winter to summer in the Cape Verde Islands. *P. edwardsii* showed a latitudinal pattern in size, with asymptotic size and growth rate showing a latitudinal compensation gradient as a result of an increased growth performance in the Madeira population compared to that of the Cape Verde Islands.

1. Introduction

A species can adjust its life-history traits to environmental conditions through plasticity or genetic variations, thereby giving the species the ability to have a wide geographical distribution (Cardoso and Defeo, 2004; Marshall et al., 2008). In this regard, the fitness of a species plays an important role in its distribution and abundance; the reproductive and growth components of fitness are two of the most important processes because they require the greatest energy inputs in the life cycle of an organism (Sastry, 1983; Sexton et al., 2009). Among the reproductive components, egg production is an important evolutionary and ecological trait that reflects the maternal energy investment and influences the offspring and maternal fitness (Briones-Fourzán et al., 2010). Other aspects, such as moult cycles, synchronization between reproduction and moulting, and size-related growth rate, are the main biological processes regulating growth in crustaceans. These biological processes are linked to external abiotic factors, such as temperature, hours of daylight, and food availability, which can stimulate or inhibit growth processes (Company and Sardà, 2000). All of these aspects are important because the accumulation of small fitness differences throughout the life cycle results in important differences in overall fitness, which affects the ability of distribution and abundance of the species (Sexton et al., 2009).

In species occurring along broad latitudinal gradients, such as the deep-water shrimp species of the genus *Plesionika* Bate, 1888,

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local phenotypic plasticity or genetic variations in environmental conditions may be observed as differences in growth and reproductive features among populations (Wehrtmann and Lardies, 1999; Marshall et al., 2008; Briones-Fourzán et al., 2010). Species of the genus *Plesionika* play an important ecological role in benthic ecosystems, and the life-history traits of species living in these habitats, such as *Plesionika edwardsii* (Brandt, 1851), may need to adapt to deep environmental features (Carbonell and Abelló, 1998; Vafidis et al., 2005).

P. edwardsii inhabits the eastern Atlantic, from the southwest of Spain to Angola, including Madeira, Canary and Cape Verde Islands (González et al., 2001). These three archipelagos are located in the Canary Current System, which is one of the Large Marine Ecosystems of the World and Linked Watersheds (LMEs) across global oceans (Sherman and Hempel, 2009). They are characterized by their singular bathymetry, hydrography and productivity, as well as their ability to support marine populations that have adapted their feeding, reproductive and growth strategies (Hernández-León et al., 2007). The region of Madeira is dominated by the Canary Current system, which induces a southward net transport (Caldeira and Sangrà, 2012). The presence of a seamount at the southeast end of Madeira produces a localized island upwelling of cold nutrient-rich waters around the coasts (Caldeira et al., 2002). The Canary Islands are characterized by the presence of the first 500 m of depth of Eastern North Atlantic Central Water (Hernández-Guerra et al., 2002). Meanwhile, the sea waters off the Cape Verde Islands are under the influence of the North Equatorial Counter-Current and the Canary Current. The seasonal circulation patterns of this Counter-Current mainly show their influence in the south-eastern part of the archipelago (Marques et al., 2009).

In this work, latitudinal variations in the life-history traits of *P. edwardsii*, including depth distributions and demography, are analysed as indicators of biogeographic trends along a latitudinal gradient in the three island regions. This comparison can reveal how this species responds to geographic environmental variations with regard to their life-history traits, providing more information for a better understanding of the relationship between variation in fitness and environment and between fitness and abundance (Sexton et al., 2009). A thorough understanding of their ecology, mainly the reproductive, growth and brood size strategies, and their latitudinal differences would be of great interest considering that deep-water species are especially vulnerable to exploitation (Polidoro et al., 2008).

2. Materials and methods

2.1. Sampling and data collection

Shrimp caught around the Madeira (MA), Canary (CIS) and Cape Verde (CVS) archipelagos (Fig. 1) during 22 research cruises conducted between 2006 and 2012 were studied. Shrimp were captured with multiple semi-floating shrimp traps deployed at approximately 2.5 m above the sea floor, with a 56 × 57 cm base length and a 57 cm height, covered with a 15 × 20-mm plastic mesh. Each trap had one troncoconical opening that had an inner diameter of 19 cm. The fishing gear consisted of 75 traps on a fishing rope separated from each other by 15 m. Atlantic chub mackerel (*Scomber colias*) was used as bait, and immersion times ranged from 20 to 24 h. For each cruise, salinity and temperature data were obtained along the water column using a CTD sensor..

The study areas were randomly sampled from a depth of 50–500 m. The sampled locations varied from trip to trip, and the sampling effort across the bathymetric range was equally distributed at 50 m intervals, with eight strata prospected: 100–149, 150–199, 200–249, 250–299, 300–349, 350–399, 400–449, and 450–500 m. During each cruise, an average of 225 traps for each depth stratum were deployed over the sea ground, covering sandy, muddy, and rocky bottoms, with a total of 1800 traps used. The standardized mean biomass (in weight per trap) of each stratum was analysed and tested for differences among the strata using ANOVA. Additionally, the standardized mean biomass (in weight per trap) of the strata of highest abundance were compared for differences among archipelagos using ANOVA.

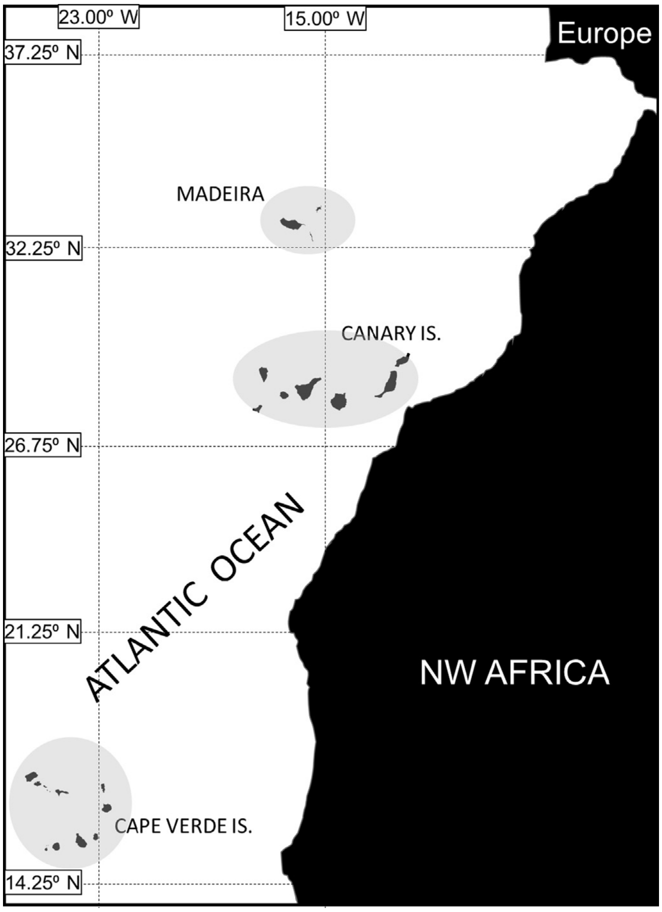

Fig. 1. Geographical location of the study areas of Madeira, Canaries, and Cape Verde Islands..

Five traits from each shrimp were measured: carapace length, weight, maturity stage, egg number, and egg volume. Further, five traits of each population were estimated, namely, length at maturity, fecundity, reproductive output, growth rate and maximum length.

Carapace length (CL, from the posterior edge of the eye socket to the mid-dorsal rear edge of the carapace) was measured with a digital calliper to the nearest 0.01 mm, and the total weight (TW) was measured to the nearest 0.01 g. Shrimp were sexed under a binocular microscope based on the presence or absence of the appendix masculina on the endopod of the second pleopod, together with the examination of the shape of the endopod of the first pleopod (King and Moffitt, 1984). The ovigerous condition of females was also recorded based on the presence of external or remaining eggs on the pleopods (King and Moffitt, 1984).

2.2. Relationships between main variables and sex ratio

The CL–TW relationship was estimated for males and females using a power equation. The equality of the two CL–TW regressions estimated by sexes was assessed using an *F*-test (Sachs, 1982). Differences between the expected value from the isometric growth ($b=3$) in the CL–TW relationship and values of the regression coefficient (*b)* were compared using a *t*-test (Sachs, 1982).

The sex ratio was estimated for the total sample and each size interval. The Pearson chi-square goodness-of-fit test was used to evaluate the equality of frequencies between sexes. The equality in CL and in TW between males and females among areas was analysed using two-way ANOVA. The equality in CL among depth strata was compared using ANOVA. Once the null hypothesis was rejected, Dunnett's *T3* post hoc test was applied to determine which strata differed. The post hoc test identified homogeneous subsets where means did not differ within each subset (Sokal and Rohlf, 2012). For all statistical tests, the significance level was $\alpha=0.05$.

2.3. Spawning period and maturity

To assess the reproductive period, the relative proportion of females of *P. edwardsii* in the ovigerous condition by season was determined. For seasonal analysis, winter includes samples from January to March, spring includes samples from April to June, summer includes samples from July to September, and autumn includes samples from October to December. The percentage of ovigerous females for each 1 mm CL class was examined using the samples collected during the main reproductive period ($>70\%$ of the females in ovigerous condition). Size at sexual maturity (CL_{50}) (the carapace length at which 50% of females are ovigerous) was determined from the relationship between the percentage of ovigerous females and the CL class. The percentage of ovigerous females (P) by size class was fitted to a logistic equation $P=100/(1+\exp(-c^*(CL–CL_{50})$ using non-linear regression, where c is the model parameter and CL_{50} is the size at sexual maturity.

The relative reproductive potential (RRP) was estimated for *P. edwardsii* according to Biscoito et al. (2015). The RRP estimates the size class of spawning females that makes the greatest contribution to egg production in a population.

The size of the appendix masculina was measured (Ahamedi and Ohtomi, 2014) and then estimated as a percentage of the size of the appendix interna (King and Moffitt, 1984) in a subsample of 150 males. This relative length of the appendix masculina with CL was estimated as an indicator of morphological maturity when increasing in size with shrimp growth, suggesting that male characteristics were developing and that those individuals with reduced appendix masculina were immature males (King and Moffitt, 1984). A power equation was fitted to the data using nonlinear regression for the values in which the data could be separated into two groups. The size at which allometric growth changed, as an indicator of morphometric maturity, was iteratively searched using increments of 0.1 mm CL (Ahamedi and Ohtomi, 2014). An *F*-test based on the difference between the residual sums of squares was estimated for assessing the equality of the sums of squares of the two subsets and of the simple model (Somerton, 1980). An *F*-test was also calculated to test differences between the two regressions, corresponding to the sexually immature and mature growth phases (Sachs, 1982). The relative growth patterns of the appendix masculina with the size of the second pleopods, in both sexually immature and mature growth phases, were analysed using a *t*-test for assessing the equality of the regression coefficient (Sachs, 1982).

To compare the results among the populations studied, the relative size at onset of maturity (R_{SOM}) was calculated using the equation $R_{SOM}=CL_{50}/CL_{\infty}$, where CL_{∞} is the asymptotic maximum size attained by shrimp (Charnov, 1990; Hirose et al., 2013).

2.4. Fecundity and egg morphology

For ovigerous females, egg morphology was classified in four stages as follows: Stage I, eggs are blue with their embryos lacking eye pigmentation and yolk filling most of the embryo volume; Stage II, eggs are pale blue with eyespot pigmentation present in the embryos and appendage rudiments, and the nerve ganglia appear as a thickening of the blastoderm; Stage III, eggs are light brown with eye pigmentation clearly visible in the embryos, and there is a large cephalothorax, extending abdomen, and complete segmentation; Stage IV, eggs are ready to hatch or the remains of hatched eggs are observed on female pleopods.

Ovigerous females from all size classes were used for the morphological study of eggs and then used to estimate fecundity. Pleopods with attached eggs were removed from females, and then egg masses were placed on a 100 μm mesh, washed and isolated from pleopods. For each developmental stage of embryos, 15 females of each size class were selected to estimate the egg volume (mm^3). From each ovigerous female, the maximum and minimum diameters of 30–35 randomly selected eggs were measured. Egg volume (mm^3) was calculated as $EV=(4/3\pi a2c)$, where "*a*" and "*c*" represent the maximum and minimum egg diameter, respectively. The equality in egg volume between males and females among areas was analysed using two-way ANOVA.

The total number of eggs in stage III attached to the pleopods was counted directly under a binocular microscope in 60 females from all size classes (Triay-Portella et al., 2014). A linear function was fitted to number of eggs versus CL.

2.5. Growth

The carapace length frequency distributions (in 0.5 mm intervals) were estimated seasonally for males and females. Growth was studied using seasonal length-frequency distributions by sex according to the Petersen method (Sparre et al., 1989). The CL-frequency distributions of each sex and season were separated using model progression analysis (Bhattacharya's method) with FiSAT II software (Gayanilo et al., 2005). Bhattacharya's method identifies normal distributions of the polymodal CL length-frequency distributions. Separation indices between different cohorts with values of less than 2 indicate a large overlap between cohorts and were considered statistically unacceptable (Sparre et al., 1989). The routine NORMSEP (normal distribution separator) in the FiSAT II software was used for the decomposition of mixtures of normal distributions on the basis of Hasselblad's maximum likelihood method (Hasselblad, 1966). The normal distribution of each component was assumed to represent an age group in the shrimp population. Growth was modeled using the von Bertalanffy growth function (VBGF). A preliminary estimation of L_{∞} was obtained separately for males and females using the Gulland and Holt (1959) method, and the k value was obtained by ELEFAN I using the FiSAT II software (Gayanilo et al., 2005). The growth parameters of the VBGF were estimated from the growth increment data, which were estimated from linking of the mean lengths. A routine analysis of length-at-age data were used for the non-linear estimation of the growth parameters. The growth performance index φ' ($\varphi'=2^*\log L_{\infty}+\log k$) was used to compare the growth rates between sexes and among areas (Pauly and Munro, 1984).

3. Results

3.1. Size structure

A total of 197,031 individuals of *P. edwardsii* were collected (30,458 in MA, 109,689 in CIS, and 56,884 in CVS) (Table 1). In all areas, females were larger and heavier than males (Table 1). In MA, differences between sexes were 2.43 mm (7.30%) in maximum size

Table 1
Carapace length (CL in mm) and total weight (TW in g) for males and females of *P. edwardsii*. *Min*, minimum; *Max*, maximum; *Mean*, mean value; s.d. standard deviation; *n*, number of specimens.

Area/Sex	CL			TW			
	Min	Max	Mean ± s.d.	Min	Max	Mean ± s.d.	n
Madeira							
Males	12.05	30.85	23.88 ± 2.62	1.07	19.22	9.60 ± 2.55	13879
Females	12.06	33.28	25.68 ± 2.88	1.06	24.21	12.96 ± 3.69	16582
Canaries							
Males	7.94	28.29	21.98 ± 2.66	0.71	15.20	7.57 ± 2.26	46622
Females	7.06	30.45	23.16 ± 2.93	0.55	20.60	9.47 ± 3.06	63067
Cape Verde Is.							
Males	10.95	26.86	18.20 ± 2.03	0.75	14.40	4.18 ± 1.31	24292
Females	10.60	29.10	18.98 ± 2.24	0.80	19.36	5.28 ± 1.87	32592

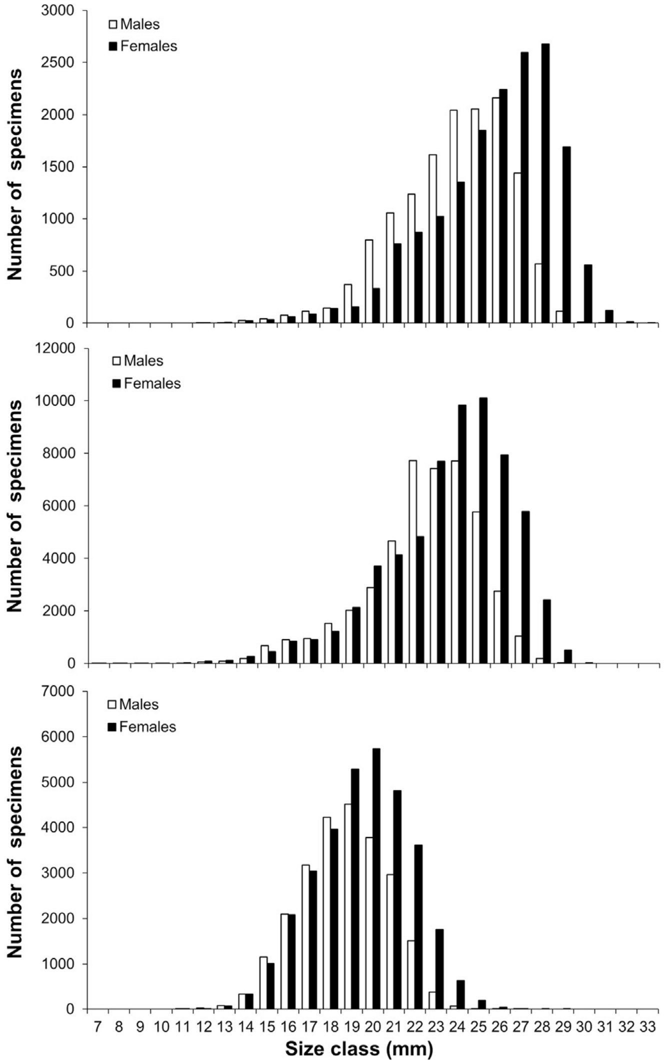

Fig. 2. Number of male and female specimens of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

(CL) and 4.99 g (20.61%) in weight (TW). In CIS, these differences were 2.16 mm (7.09%) in CL and 5.40 g (26.21%) in TW. In CVS, these differences were 2.24 mm (7.69%) in CL and 4.96 g (25.61%) in TW. The highest values of length and weight were recorded in MA, while the lowest were in CVS. (Fig. 2). Two-way ANOVA comparing the differences in CL and TW between males and females among areas showed significant differences for the factors of sex ($F_{1,>1000} > 6433$, $p < 0.0001$) and area ($F_{2,>1000} > 4191$, $p < 0.0001$), as well as for the interaction effect ($F_{2,>1000} > 290.17$, $p < 0.0001$)..

The *F*-test for the CL–TW relationship between sexes in all of the archipelagos showed statistically significant differences between the two regressions estimated (all areas: $F_{1,>1000} \geq 7.51$, $p = 0.0063$). The regression coefficient was highest in CVS and lowest in MA, and a *t*-test with the null hypothesis of equality in the regression coefficient (H_0: b=3) was rejected in all archipelagos for all groups (negative allometric growth) (Table 2). The *F*-test for the CL–TW relationship of males and females among areas showed significant differences between males and females for the three regions studied (males $F_{2,>1000} = 5.92$, $p = 0.0028$; females $F_{2,>1000} = 5.33$, $p = 0.0050$).

3.2. Sex ratio

The sex ratio showed a predominance of females in all areas (MA 1:1.20, CIS 1:1.35, CVS 1:1.34), and the Pearson chi-square goodness-of-fit test indicated that the null hypothesis of equality sex frequencies was rejected (all areas $\chi_1^2 \geq 240.4$, $p < 0.0001$). Males were significantly more abundant than females in the 17- to 25-mm CL size classes in MA ($\chi_1^2 \geq 4.0$, $p = 0.0455$) (Fig. 3). However, females were significantly more abundant in size classes larger than 25 mm CL ($\chi_1^2 = 119.03$, $p < 0.0001$). In CIS, females were dominant in the 23-mm CL size class ($\chi_1^2 = 5.11$, $p = 0.0238$),

Table 2
Parameters of CL–TW relationship ($TW = a^*CL^b$) for males, females and all shrimps of *P. edwardsii*. *a*, intercept; *b*, regression coefficient (allometric coefficient); s.d., standard deviation; r^2, determination coefficient; *n*, number of specimens; *t*, *t*-test value;

Sex	a	b	s.d. (b)	r^2	n	*t*
Madeira						
Males	0.005266	2.360	0.008785	0.869	13879	72.8[a]
Females	0.003494	2.525	0.009228	0.862	16582	51.4[a]
Ovigerous	0.005869	2.372	0.011431	0.804	12541	54.9[a]
Non ovigerous	0.001065	2.525	0.013429	0.921	4041	35.3[a]
All shrimps	0.001907	2.697	0.007076	0.860	30458	42.8[a]
Canaries						
Males	0.002442	2.592	0.003697	0.935	46622	110.3[a]
Females	0.001821	2.712	0.003789	0.919	63067	76.0[a]
Ovigerous	0.002301	2.651	0.003735	0.907	29420	93.4[a]
Non ovigerous	0.002158	2.643	0.003846	0.952	33647	92.8[a]
All shrimps	0.002796	2.590	0.005735	0.889	109689	71.4[a]
Cape Verde Is.						
Males	0.001373	2.754	0.008933	0.894	24292	27.5[a]
Females	0.000881	2.942	0.007070	0.922	32592	8.20[a]
Ovigerous	0.001146	2.858	0.008383	0.903	25732	16.9[a]
Non ovigerous	0.001065	2.854	0.013960	0.911	6860	10.4[a]
All shrimps	0.000751	2.981	0.006019	0.901	56884	2.5[a]

[a] null hypothesis of isometric growth rejected.

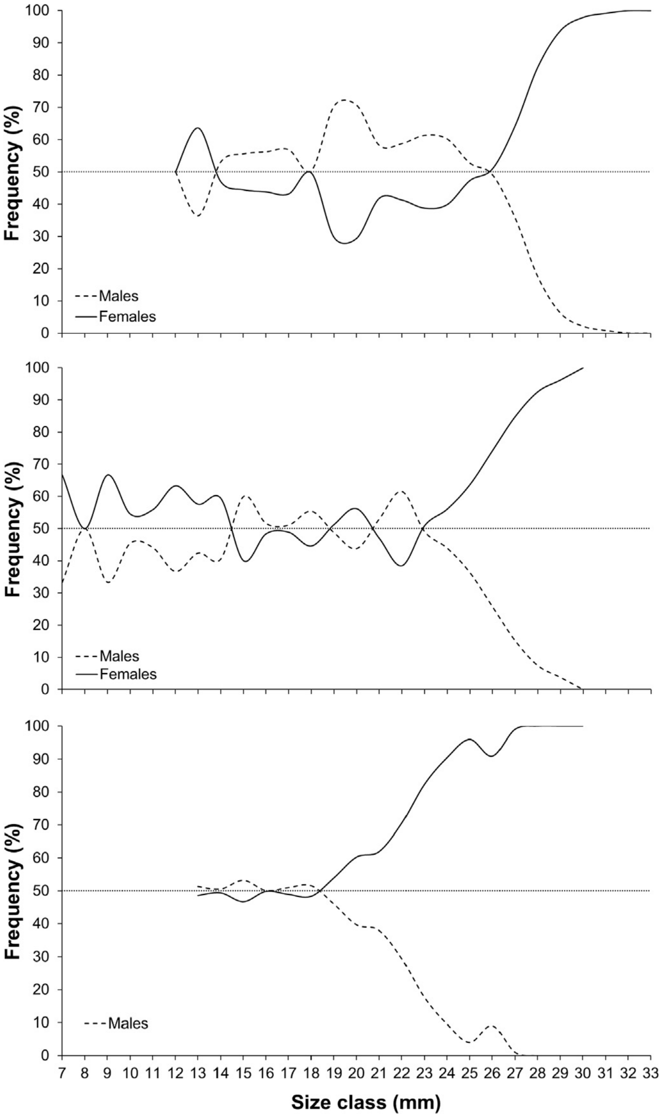

Fig. 3. Frequency of males and females by size classes of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

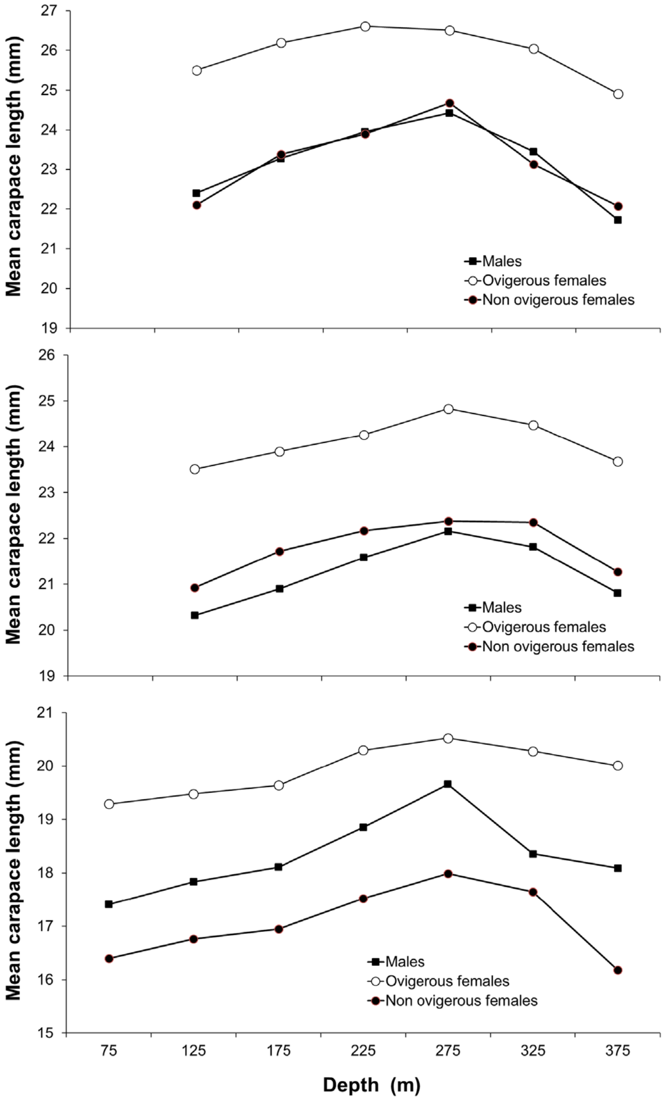

Fig. 4. Variation of the mean carapace length with depth for males, non-ovigerous and ovigerous females of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

and a similar pattern was observed in females in the 18-mm CL size class in CVS ($\chi^2_1 = 4.32$, $p = 0.0377$) (Fig. 3), indicating a north-south pattern. The relative magnitude of sex-ratio biases was different among areas, 69.29% in MA, 67.27% in CIS and 55.90% in CVS, with a maximum difference of 13.38% between areas, showing the highest relative difference in MA and the lowest in CVS..

3.3. Depth distribution

A similar pattern was observed for males and females in all areas, with the mean CL increasing until reaching the 225 to 275 m depth stratum (Fig. 4). However, the mean size observed in each stratum showed a north-south pattern, with the highest values in MA and the lowest in CVS. Student's *t*-test indicated that the null hypothesis for equality in the mean CL in each stratum between consecutive areas was rejected for males and females (in all cases: $t_{>1000} \geq 2.76$, $p = 0.0058$). ANOVA determining the differences between CL and sex among different depth strata showed significant differences in the three areas (all areas: males $F_{5,>1000} \geq 157.95$, $p < 0.0001$, females $F_{5,>1000} \geq 45.65$, $p < 0.0001$). Dunnett's *T3* post hoc test showed significant differences in CL among all strata in all areas ($p < 0.05$). The standardized biomass showed a decreasing pattern at depths below the thermocline in the three areas (Fig. 5). The maximum value of standardized biomass with depth was located immediately below the thermocline in the three areas and was found at depths of 100–150 m in CVS 17.01–22.30° C), 200–250 m in CIS 16.10–17.71° C) and 150–200 m in MA 15.48–16.34° C) (Fig. 5). Both temperature at the maximum abundance depth and at the depth range distribution showed a decreasing pattern with latitude. ANOVA of the standardized biomass among different depth strata showed significant differences in the three areas (MA $F_{6,>50} = 5.54$, $p = 0.0002$; CIS $F_{7,>200} = 4.62$, $p < 0.0001$; CVS $F_{7,>100} = 4.86$, $p < 0.0001$). ANOVA indicated significant differences in the standardized biomass at the maximum abundance stratum among areas ($F_{2,>120} = 9.95$, $p = 0.0001$). Dunnett's *T3* post hoc test showed significant differences in the mean standardized biomass among all areas ($p < 0.05$)...

3.4. Spawning period

Ovigerous females represented 75.63% of the total females in MA, 46.64% in CIS, and 79.58% in CVS. Ovigerous females were observed in all seasons in the three areas (Fig. 6). Of the total

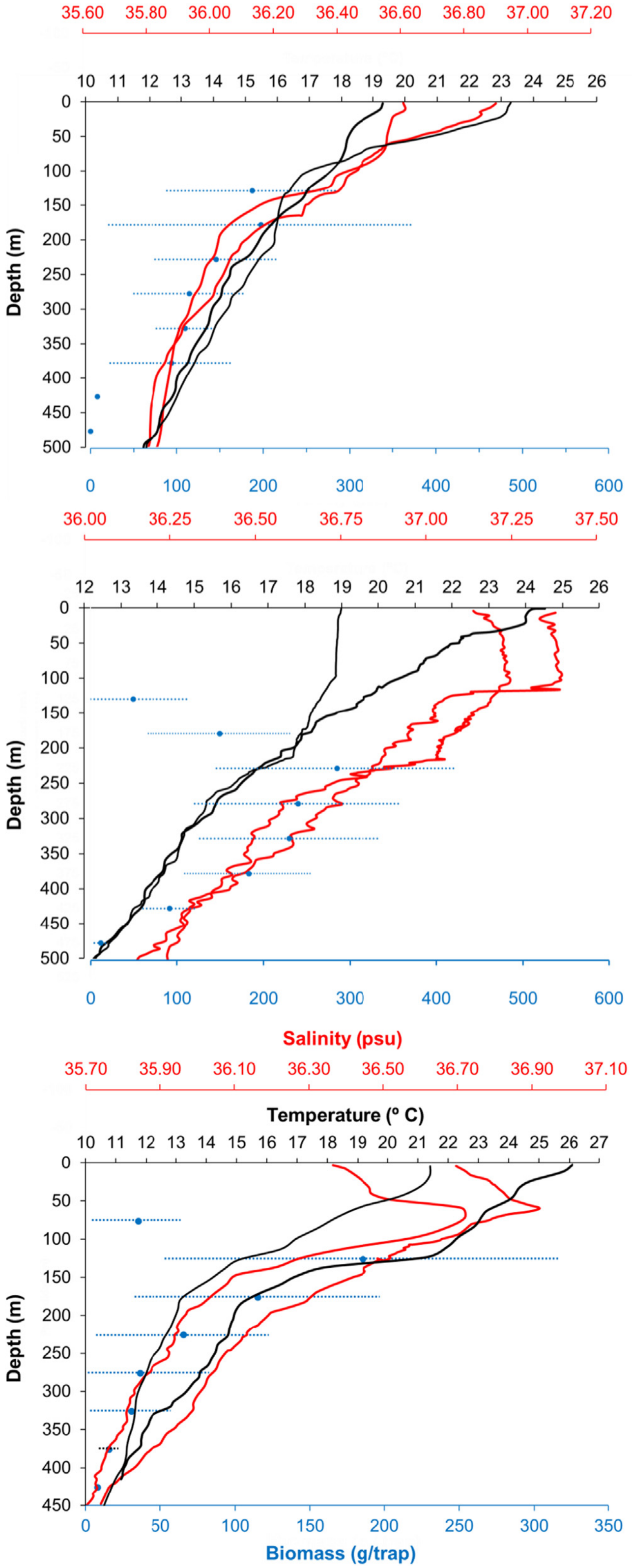

Fig. 5. Changes in both salinity and temperature with depth corresponding to the extreme values observed for seasons and areas and standardized *Plesionika edwardsii* biomass (horizontal lines mean ± sd) by depth stratum of 50 m in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

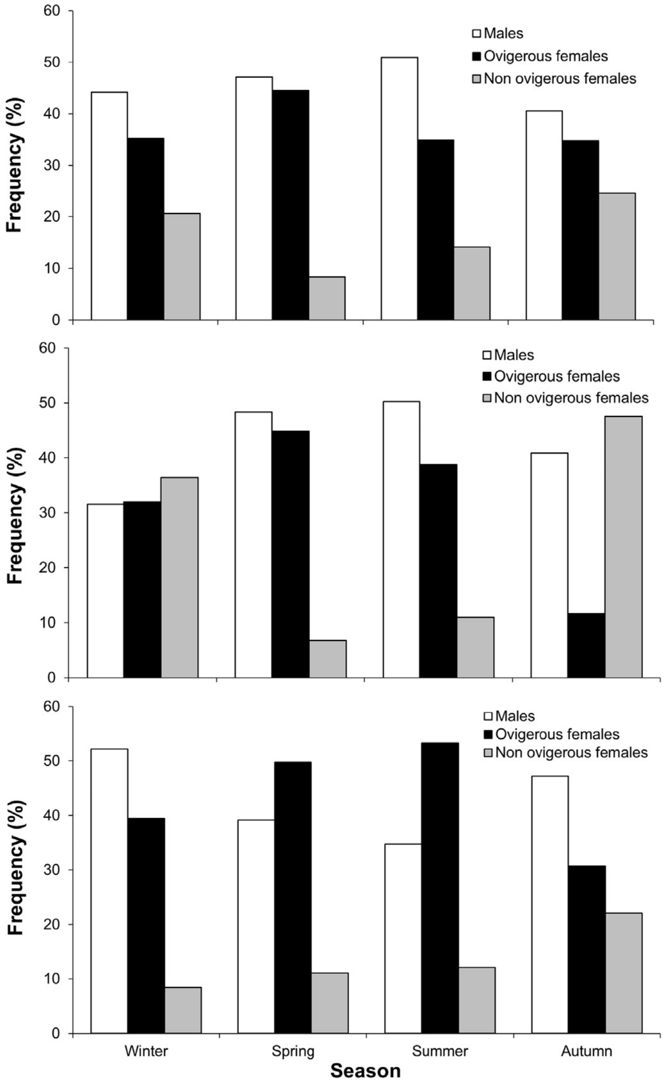

Fig. 6. Seasonal frequency of males, non-ovigerous and ovigerous females of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

females, the ovigerous ones were dominant (> 70% of females) in spring and summer in both MA and CIS and from winter to summer in CVS. Eggs in stage I were found in high proportions in females carrying eggs year-round in all areas and seasons (Fig. 7). Eggs in stages II and III were observed in proportions lower than 24.84% and 20.13% of females carrying eggs, respectively, in all areas and seasons (Fig. 7). Eggs in stage IV were found in proportions higher than 5% of berried females in spring and summer in MA, from spring to autumn in CIS, and in all seasons in CVS (Fig. 7)...

3.5. *Sexual maturity of females*

Student's *t*-test showed significant differences in mean CL between ovigerous and non-ovigerous females for the three areas (all cases, $t_{>1000} \geq 47.71$, $p < 0.0001$) (Table 3). Likewise, Student's *t*-test showed significant differences in the mean CL between ovigerous (all cases $t_{>1000} \geq 3.28$, $p = 0.0011$) and non-ovigerous females (all cases $t_{>1000} \geq 2.71$, $p = 0.0068$) of consecutive areas. The length at sexual maturity in ovigerous samples was estimated at 20.72 mm CL in MA, 19.65 mm CL in CIS, and 16.89 mm CL in CVS (Table 3), showing a north-south size pattern at sexual maturity.

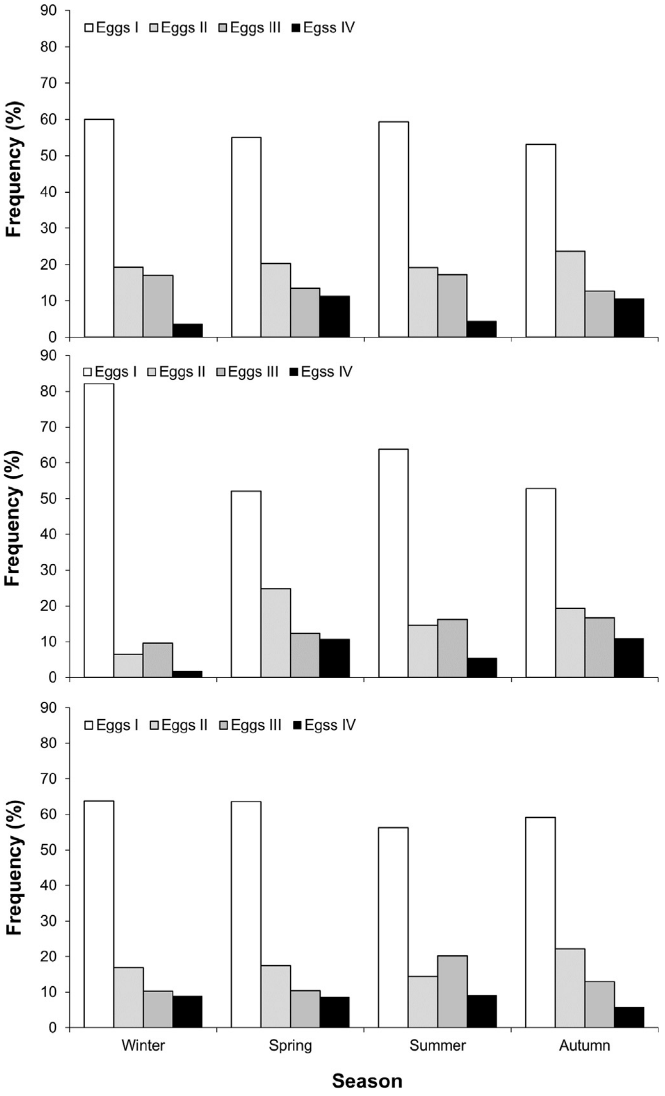

Fig. 7. Seasonal frequency of eggs developmental stage (I-IV) of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom)..

Table 3
Carapace length (CL in mm) for ovigerous and non-ovigerous females of *P. edwardsii. Min*, minimum; *Max*, maximum; *Mean*, mean value; s.d., standard deviation; *n*, number of specimens. c, parameter of the logistic equation of maturity; CL_{50}, size at sexual maturity; r^2 coefficient of determination..

Area/Sex	CL (mm)			c	CL_{50}	r^2	n
	Min	Max	Mean ± s.d.				
Madeira							
Ovigerous	12.45	33.28	26.36 ± 2.27	0.5194	20.72	0.982	13879
Non ovigerous	12.06	33.28	23.58 ± 3.58				16582
Canaries							
Ovigerous	12.01	30.45	24.18 ± 2.05	0.7357	19.65	0.966	46622
Non ovigerous	7.06	30.45	22.26 ± 3.27				63067
Cape Verde Is.							
Ovigerous	10.63	29.60	21.57 ± 1.90	0.7449	18.29	0.984	24292
Non ovigerous	10.60	29.10	19.84 ± 2.11				32592

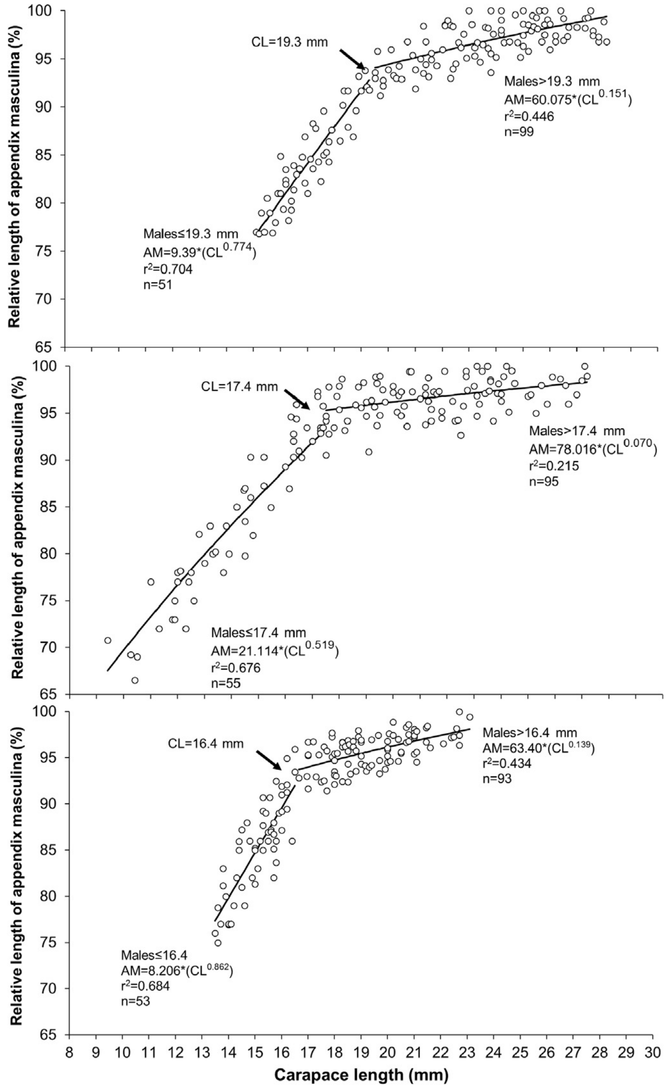

Fig. 8. Relative length of the appendix masculina by carapace length for males of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom), where n is the number of shrimp and r^2 is the determination coefficient. Fitted lines correspond to each potential model estimate. Arrows indicate the size at which allometric growth changes, as an indicator of morphological maturity.

3.6. Sexual maturity of males

The ratio of the appendix masculina was plotted against CL, revealing changes in relative growth associated with maturity (Fig. 8). The relative growth of the appendix masculina showed changes related to ontogeny. Allometric growth changes occurred at a size of 19.3 mm CL in Madeira, 17.4 mm CL in the Canaries, and 16.4 mm CL in the Cape Verde Islands ($F_{2,>50} \geq 5.01$, $p = 0.0104$), showing the largest size in MA and the smallest in CVS. An *F*-test showed significant differences between the two regressions (the pre- and post-maturity growth phases) in all cases ($F_{1,>40} \geq 8.56$, $p = 0.0056$). A *t*-test on the growth of the appendix masculina showed significant differences in the regression coefficient between the subsets considered ($t_{>50} = 3.95$, $p = 0.0003$). Allometry in the growth of the appendix masculina was always observed irrespective of subset (pre- or post-maturity phase) or area..

R_{SOM} was very similar for males and females from Madeira (0.582 and 0.573 for males and females, respectively), with a difference of 1.42% between sexes. In the Canaries, the difference in R_{SOM} between sexes was 0.71% (0.578 males, 0.574 females). In the Cape Verde Islands, R_{SOM} was very similar (0.585 males, 0.568 females), with a difference of 2.98% between sexes. Differences were smaller than 1.13% in males and 1.16% in females when comparing each sex among populations.

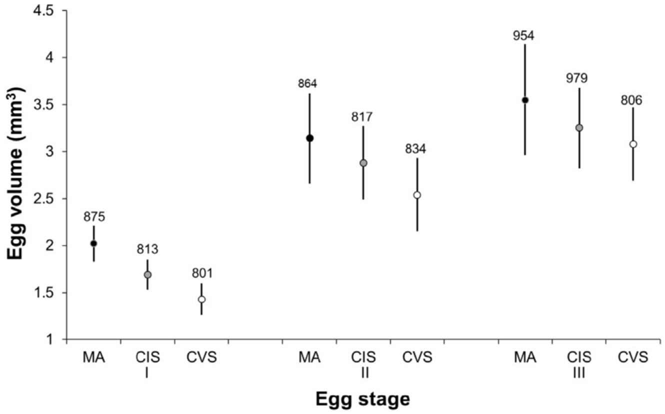

Fig. 9. Mean egg volume (mm^3) and standard deviation of *Plesionika edwardsii* by area and egg development stage. The number indicates the number of eggs counted.

3.7. *Egg volume and number of eggs*

The mean egg volume increased from stage I to stage III in all areas (Fig. 9), showing the highest volume in MA and the lowest in CVS. A two-way ANOVA on egg volume by egg developmental stage among areas showed significant differences for factors stage and area (stage, $F_{4,>1000}=1567.4$, $p<0.0001$; area, $F_{4,>1000}=340.9$, $p<0.0001$), as well as for the interaction effect ($F_{4,>1000}=48.75$, $p<0.0001$)..

The number of eggs increased significantly with female size in the three areas, showing a north-south pattern. The linear equations of the three regression were significantly different (ANCOVA, $F_{2,177}=17.13$, $p<0.0001$) (Fig. 10). The number of external eggs carried by females in stage III ranged from 2382 to 10859 eggs in MA (Table 4), from 1856 to 8032 eggs in CIS, and from 1278 to 7094 eggs in CVS, with females having the lowest limits of this range (Table 4). The number of eggs among archipelagos for the whole body size ranges of each area showed significant differences (ANOVA, $F_{2,177}=57.21$, $p<0.0001$). For the common range of body size of the three archipelagos (19.4–23.5 mm) the number of eggs among areas also showed significant differences (ANOVA, $F_{2,88}=5.43$, $p<0.006$), with mean number of eggs of 3616 in CVS, 4059 in CIS, and 4407 in MA..

The modal size class of egg production showed the largest size in MA and the smallest in CVS, with a north-south pattern. The modal size class of egg production in Madeira was 24–29 mm CL (74.78% of females), which yielded 83.75% of the population egg production (Fig. 11); females smaller than 24 mm CL comprised 21.02% of the population and produced only 8.66% of the eggs. In the Canaries, the modal size class was 23-27 mm CL (60.55% of females), which yielded 66.07% of total egg production; females smaller than 23 mm CL comprised 25.34% of the population and produced only 9.45% of the eggs (Fig. 11). Finally, in the Cape Verde Islands the modal size class of egg production was 19–22 mm CL (59.68% of females), which yielded 70.71% of the population egg production (Fig. 11); females smaller than 19 mm CL comprised 32.23% of the population and produced only 9.65% of the eggs..

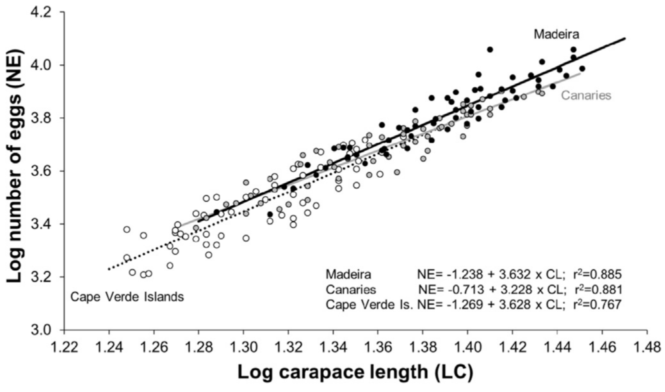

Fig. 10. Brood size estimates in logarithmic number of eggs (NE) by logarithmic carapace length (CL) for *Plesionika edwardsii* females in Madeira, Canaries and Cape Verde Islands, where n is the number of females and r^2 is the determination coefficient. Fitted lines correspond to each logarithmically transformed linear model estimate.

3.8. *Growth*

The analysis of modal progression showed that males attained a smaller asymptotic length and growth rate than females in the three archipelagos (Table 5). The asymptotic length and the growth rate for males and females increased according to a south-north pattern from the Cape Verde to Madeira Islands. The growth performance index (φ') was highest in MA and lowest in CVS, varying between 2.60 and 2.77 for males and from 2.73 to 2.88 for females. The highest relative age estimated by means of the growth increment data converted in length at relative age was 3.81 years in MA, 3.85 years in CIS, and 3.88 years in CVS.

4. Discussion

In the studied areas, the populations of *P. edwardsii* showed clear variations in their life-history traits. These changes could be due to variations linked to changes in environmental factors along latitudinal gradients, as in the case of temperature, or could occur as a consequence of the species being distributed among geographic breaks in the form of isolated islands with different environmental conditions (Barria et al., 2014). In the present study, latitude could be more important than breaks in the phenotypic variations for the majority of these fitness-related traits because the influence of geographic breaks depends on the larval dispersal ability of each species; species with low dispersal ability and short larval stages are highly affected by breaks (Barria et al., 2014). In this regard, Landeira et al. (2009) described a series of long larval stages for *P. edwardsii* that increases their potential for dispersal ability and reduces the influence of geographic breaks in the form of isolated islands. In any case, *P. edwardsii*, as an ectotherm species, has minimized the fitness costs associated with exposure to variations in temperature in the studied areas through local phenotypic plasticity or genetic variations. Both mechanisms could be evolving together, and it is difficult to determine the contribution of each (Yampolsky et al., 2014).

The maximum carapace size of the populations studied, as well as the maximum weight showed a clear latitudinal pattern, with larger shrimps observed at higher latitudes (Madeira) and smaller shrimps at lower latitudes (Cape Verde Islands). This increase in body size with latitude is known as Bergmann's rule and has been described in other decapod crustaceans (Hirose et al., 2013). The mechanisms underlying Bergmann's rule are related to different thermal exposures that could result in different physiological costs at the cellular level (Stillman and Somero, 2000; Hirose et al., 2013). This agrees with the range of temperatures of the maximum abundance of the species, which is 1.37° C higher in the Canaries and 5.96° C in the Cape Verde Islands than in Madeira. The clear latitudinal gradients found in body size are consistent with the trends observed in morphological characteristics, showing higher asymptotic size, physiological and morphometric length at maturity, modal class size egg production, and growth rate in Madeira compared to the Cape Verde Islands.

The size at sexual maturity also showed a correlated increase

Table 4
Maximum, minimum and mean number of eggs, with standard deviation (±sd), and the corresponding carapace length (CL), total weight (TW) and CL range analysed of females of *P. edwardsii*. n, number of specimens. *Min*, minimum; *Max*, maximum; *Mean*, mean value; s.d., standard deviation; *n*, number of specimens.

Area	Eggs number			CL (mm)		TW (g)		CL range (mm)		n
	Min	Max	Mean ± s.d.	Min	Max	Min	Max	Min	Max	
Madeira	2739	11455	5998 ± 1823	20.5	28.00	6.15	14.43	19.4	28.3	60
Canaries	2436	7998	4482 ± 1947	19.1	25.10	5.48	10.54	19.0	27.1	60
Cape Verde Is.	1621	6183	3209 ± 1495	17.7	22.30	3.94	6.91	17.7	23.5	60

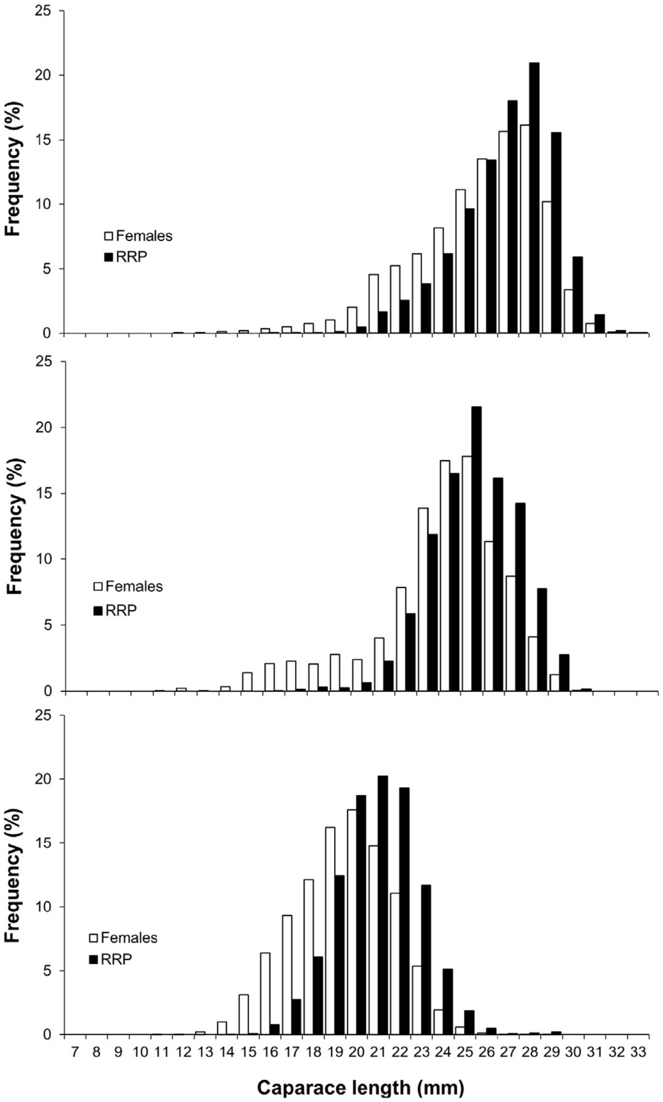

Fig. 11. Frequency-size distribution of *Plesionika edwardsii* females in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom) and its relative reproductive potential (RRP).

Table 5
von Bertalanffy growth parameters (±standard deviation) of *P. edwardsii* and growth performance index (φ') (φ'=2*log L_∞+log k), where L_∞, is the asymptotic length; k, the growth rate; t_0, the relative age at 0 length.

Area/Sex	L_∞ (mm)	k ($year^{-1}$)	t_0 (year)	φ'
Madeira				
Males	33.13 ± 1.335	0.54 ± 0.052	0.12 ± 0.070	2.77
Females	36.08 ± 1.608	0.59 ± 0.060	0.03 ± 0.058	2.88
Canaries				
Males	30.06 ± 0.511	0.52 ± 0.028	0.03 ± 0.044	2.67
Females	34.19 ± 1.871	0.57 ± 0.078	−0.18 ± 0.073	2.82
Cape Verdes Is.				
Males	28.01 ± 1.390	0.51 ± 0.090	0.09 ± 0.143	2.60
Females	32.20 ± 0.165	0.53 ± 0.009	−0.01 ± 0.010	2.73

with latitude. This may be because as the latitude increases, selection should favor an increase in size at maturity to maximize adult fitness (Fischer and Fiedler, 2002). This pattern of maturity, beginning at smaller sizes in the Cape Verdean population with warmer habitats, compared to those in colder habitats and in higher latitudes, such as Madeira, has been described in other decapods (Hines, 1989; Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001; Terossi et al., 2010a, b). The relative morphometric and physiological size at sexual maturity is not affected by latitude or environmental factors and occurs at the same size in the three areas studied, varying only slightly between 0.568 and 0.585. Similar results have been observed for other pandalids, with values oscillating between 0.53 and 0.58 in different localities irrespective of species, sexual typology, latitude or strategy of reproduction (Charnov, 1990; Briones-Fourzán et al., 2010; Hirose et al., 2013). The absence of intraspecific variation in the relative size at sexual maturity can reflect a genotypic character that is linked to the large plasticity in size of *P. edwardsii* under different environmental conditions.

The sex ratio as a function of size showed that females reached a larger size than males. This pattern is common when males do not show a defensive behavior towards females or do not exhibit aggressive male-male competition for copulation (Briones-Fourzán et al., 2010). The sex ratio, as a function of relative size, showed that the size at which sex-ratios diverged is strongly affected by latitude or environmental factors.

P. edwardsii, similar to other deep-water pandalids, usually had long reproductive seasons (Ohtomi, 1997; Company and Sardá, 1997), with ovigerous females observed year-round, although with latitudinal variations. Seasonally, there were more ovigerous females in spring and summer at higher latitudes, but more in winter to summer at lower latitudes. These changes in spawning activity may reflect differences in the local availability of food or the optimal thermal environmental conditions, which are limiting factors for reproductive activity (Tyler, 1988; Barradas-Ortiz et al., 2003). A latitudinal north-south pattern was also observed in fecundity and maximum egg size. In the Cape Verde Islands, the developed strategy involves a lower production of embryos and a smaller size of eggs than those at the higher latitude in Madeira. These results are in agreement with the latitudinal differences in egg production and size observed for other decapods (Lonsdale and Levinton, 1985a; Wehrtmann and Kattner, 1998; Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001; Terossi et al., 2010a, b). This pattern may be explained by the necessity of a higher yolk content in eggs in colder regions to provide sufficient internal energy provisions for survival during longer periods of incubation than in warmer areas as an adaptation to protect the embryo against low temperatures (Wehrtmann and Kattner, 1998; Lardies and Castilla, 2001; Terossi et al., 2010a, 2010b; Viegas et al., 2012).

The latitudinal egg size increment observed was likely related to the maternal body size (Rollinson and Hutchings, 2011). Females with larger embryos have less available space for egg attachment on pleopods and lower fecundity than females of the same size from different populations with small eggs (Terossi et al., 2010a, b). Therefore, the higher maximum size reached for females in Madeira compensates for the reduction in the available space for egg attachment on pleopods with the higher eggs size, which is advantageous for more offspring production (Briones-Fourzán et al., 2010; Terossi et al., 2010a, b).

The asymptotic size and growth rate, like other components of the life-history traits studied, showed a latitudinal pattern in *P. edwardsii*. Theoretically, a latitudinal increment in temperature and growing season generate a latitudinal increment of the growth rate and asymptotic size in the populations at lower latitudes. This was observed in the Cape Verde Islands, with individuals experiencing a higher temperature during longer seasons than those of higher latitudes, such as Madeira, where environments would theoretically reduce growth (Yamahira et al., 2007; Chavarie et al., 2010). To avoid this reduction of the growth rate body size in Madeira, latitudinal compensatory growth has been observed in the present study. Adaptations to higher latitudes through latitudinal compensation in growth is common among ectotherms (Yamahira et al., 2007; Yamahira and Takeshi, 2008). This compensation mechanism may be due to a maximization of growth rate, named thermal adaptation, suggesting that individuals from Madeira have a thermal reaction norm for better growth rates at lower temperatures than individuals from the Cape Verde Islands (Levinton, 1983; Lonsdale and Levinton, 1985b; Chavarie et al., 2010). In this case, populations differ in the temperatures at which lesser and maximal growth are possible and not in temperatures the maximal growth rate that can be reached, meaning that the growth rate can be maximized in each environmental condition (Yamahira and Conover, 2002).

Latitudinal compensation in growth could also be a consequence of latitudinal differences in the length of the growing season as indicated by Conover and Present (1990) and Yamahira et al. (2007). The annual temperature cycle in Madeira involves favorable periods that permit growth, and periods when growth ceases, and energy reserves are utilized for metabolism. As the length of the growing season declines with the increase of latitude, the Madeiran population may compensate for the shorter growing season by evolving a higher overall capacity for growth through temperature adaptation. In this situation, the growth of individuals may occur over the same temperature range in all areas, but the reaction norms of growth with temperature, named countergradient variation, may differ in intensity (Conover and Present, 1990; Conover, 1992; Yamahira and Conover, 2002; Chavarie et al., 2010). Although a local temperature adaptation has been described for crustaceans (Lonsdale and Levinton, 1985b; Yamahira and Conover, 2002), the growth strategy of *P. edwardsii* may be the result of a mixture of both forms of latitudinal compensation by adapting to differences in the temperature and length of growing season.

Acknowledgments

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Sex with the lights off: Can a morphological structure reveal the sex and functional sexual maturity in the genus *Plesionika*?

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ABSTRACT

The present work describes a taxonomic trait able to determine sex in pandalid shrimps of the genus *Plesionika* and an indicator of functional maturity in females. This structure is described as formed by two teeth with abundant setae present in all males of the nine *Plesionika* species examined. This morphological trait has been ignored across the taxonomy in pandalids. Thoracic teeth were located on the 7th thoracic sternite. Each species presents a characteristic trait of this structure, although *P. williamsi* has a particular pair of thoracic teeth compared with their congeners. This structure could be used as a tool in the systematics of this genus. Sex determination through thoracic teeth shall represent a faster alternative to the classical appendix masculina sexing method. Functional maturity of females is linked to the fading of immature thoracic teeth. The observation of living specimens in tanks has allowed for the finding that males of *P. narval* and *P. edwardsii* actively seek (search for) females and use their third pair of multi-articulate legs to locate the teeth of the thoracic region, which implicates these structures in the activity of "pure searchers" to locate mature females. Thoracic teeth open a new window to different fields of research, such as taxonomy, systematics, and sexual behaviour, and are a tool to determine the first maturity of the *Plesionika* species.

1. Introduction

Since the pioneering research of King and Moffitt (1984), sex determination in deep-sea pandalids has been based on two types of taxonomic evidence: i) the morphology of the first and second pleopods (with endopods modified according to sex), and ii) the presence of male gonopores located on the coxa of the 5th pereiopod. The transition of individuals from juveniles to adults is a crucial phase of the reproductive process in decapod species, and many of them show morphological changes when reaching sexual maturity (Petriella and Boschi, 1997). Changes in the relative growth of some morphological structures with body growth when the animal reaches the pubertal moult are often used as a tool for estimating sexual maturity in decapods (Hartnoll, 1974). The growth of a morphological structure, such as the appendix masculina, in relation to the appendix interna located on the 2nd pair of pleopods has often been used as a proxy for first maturity in pandalid males (King and Moffitt, 1984; Thessalou-Legaki, 1989). On the other hand, the change in relative growth between carapace length and the width of the abdomen is used as a proxy for morphological maturity in *Plesionika* females (Ahamed and Ohtomi, 2014).

Sexual interactions among shrimps may be mediated by combinations of several signals or a single signal (Hughes, 1996). Among caridean shrimps, at least 4 of 11 known species showing a pure-searching mating pattern belong to the family Pandalidae (Correa and Thiel, 2003). In these species, the use of contact pheromones may play a crucial role in mate recognition (Bauer, 2010). The individuals of *Plesionika* species generally live aggregated in groups formed by small males and large females, with a high frequency of contact among them (King and Moffitt, 1984). Females of pure-searching mating patterns "hide" their reproductive condition as much as possible until the moult, perhaps to prevent male harassment before they are receptive (Bauer and Abdalla, 2001; Díaz and Thiel, 2004). In pure-searching mating species, there are no complex behaviours, such as the courtship of receptive females or the presence of aggressive encounters between males (see Correa and Thiel, 2003 and papers cited therein). Therefore, in this context of an aggregated species with a pure-searching male mating strategy, the receptive sexual condition of the female is perceived by

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males by sex pheromones (Caskey and Bauer, 2005). The real mechanism of reproductive appendages is still poorly known in crustaceans and remains a fertile topic for study (Bauer, 2013). The exact receptor involved and contact pheromone associated with the social recognition still remains unidentified in caridean shrimps (Chak et al., 2015).

Plesionika Spence Bate, 1888 is the most taxonomic speciose genus within the family Pandalidae, containing 93 species (Cardoso, 2011; De Grave and Fransen, 2011; Li and Chan, 2013; Ahamed et al., 2017). This genus has a widespread distribution around the world in subtropical, tropical and in some temperate waters (Holthuis, 1980; Chace, 1985). The misidentification of *Plesionika* species may occur sometimes (Shanis et al., 2014) due to scarce differences in the current diagnostic morphological characteristics among similar species (Crosnier and Forest, 1973; Chan and Yu, 1990, 2000; Chan and Crosnier, 1997; Li and Chan, 2013). Moreover, molecular systematics of the genus *Plesionika* indicate that although it is genetically distinct, this genus is not monophyletic as it currently is defined, highlighting some discrepancies between their current taxonomy and systematics (da Silva et al., 2013; Chakraborty et al., 2015). In addition, from the point of view of systematic use, the morphology of the pleopods and pereiopods in *Plesionika* species is a useful tool to determine sex and maturity (King and Moffitt, 1984; Thessalou-Legaki, 1989; Ahamed and Ohtomi, 2014).

The aim of this study is to describe a morphological structure present in *Plesionika* species that can be used in several ways: i) for sexual assignment in both juveniles and adults, ii) to estimate sexual maturity conditions of females at any time of the year, iii) to estimate the mean size at sexual maturity for females, according to the receptive sexual condition and developmental stage of the ovaries, iv) to contribute in new taxonomic tools to clarify possible future discrepancies between taxonomy and molecular systematics, and v) to study mating interactions and reproductive strategies in aquarium. These goals are relevant because this structure can contribute to improve the biological knowledge of these species, helping to obtain better biological parameters for *Plesionika* shrimps, which constitute a valuable fishing resource on continental/insular shelves and slopes of tropical and subtropical areas (Cartes et al., 1994; Vafidis et al., 2008; Pajuelo et al., 2015; González et al., 2016).

2. Materials and methods

Nine of the thirteen *Plesionika* species occurring in the north-eastern Atlantic waters, i.e., *Plesionika antigai* (Zariquiey Álvarez, 1955), *Plesionika edwardsii* (Brandt, 1851), *Plesionika ensis* (A. Milne-Edwards, 1881), *Plesionika gigliolii* (Senna, 1902), *Plesionika heterocarpus* (A. Costa, 1871), *Plesionika longicauda* (Rathbun, 1901), *Plesionika martia* (A. Milne-Edwards, 1883), *Plesionika narval* (Fabricius, 1787), and *Plesionika williamsi* (Forest, 1964), were examined. *Plesionika* species occurring in the North Atlantic but not available in the present study are *P. acanthonotus* (Smith, 1882), *P. geniculatus* (Milne-Edwards, 1883), *P. holthuisi* Crosnier & Forest, 1968, and *P. rossignoli* Crosnier & Forest, 1968. The individuals studied came from decapod collections of the University of Las Palmas de Gran Canaria (namely, the ICCM study collection) and of the Funchal Natural History Museum (MMF). The number and geographical sampling location of individuals examined were as follows: *P. antigai* (n = 46; Madeira), *P. edwardsii* (n = 129; Cape Verde and Canary Islands, Mediterranean Sea, Madeira, Azores, Agadir), *P. ensis* (n = 53; Agadir, Cape Verde and Canary Islands, Madeira), *P. gigliolii* (n = 64; Mediterranean Sea), *P. heterocarpus* (n = 45; Agadir, Mediterranean Sea), *P. longicauda* (n = 20; Cape Verde Islands), *P. martia* (n = 23; Canary Islands, Madeira, Mediterranean Sea), *P. narval* (n = 60; Cape Verde and Canary Islands, Madeira) and *P. williamsi* (n = 83; Cape Verde and Canary Islands, Madeira). The carapace length (CL) was measured with digital callipers (0.01 mm). Individuals were sexed under a binocular microscope based on the presence or absence of the appendix masculina on the endopod of the 2nd pair of pleopods and on the examination of the endopod shape of the 1st pair of pleopods (King and Moffitt, 1984).

Shape and position of thoracic teeth for each *Plesionika* species have been described for the first time based on a combination of features, which include the form of the outer and inner sides of teeth, the shape of the tip, the separation between both teeth and its height referred to the male gonopore.

The time consumed by using the 2nd pair of pleopods sexing technique was measured in a sample of 50 non-ovigerous specimens of *P. edwardsii*. Individuals of *P. edwardsii* were randomly selected in 10 successive samplings by two trained samplers. Then, following the same procedure, specimens were sexed based on the presence or absence of the teeth structure on the 7th thoracic sternite, between the 5th pair of pereiopods. Pearson's correlation was used to establish the degree of success between techniques. An analysis of variance (ANOVA) was also applied to test differences in the samplers and sex determination methods (Underwood, 1997).

Females of *P. edwardsii* from the Canary Islands (n = 150, 10 for each 1-mm CL) between 10 and 25 mm CL were dissected, and the maturity stage was histologically assessed following Triay-Portella et al., (2014, 2017). The histological morphology of the ovary stages and the oocytes were described following the scale proposed by ICES (2010) and adapted for *P. edwardsii* in Triay-Portella et al. (2017).

The teeth structures of the 7th thoracic sternite of 10 males and females for each 1-mm CL between 10 and 25 mm in CL were recorded and photographed. The percentage of females without thoracic teeth for each 1-mm CL class was calculated for *P. edwardsii, P. narval, P. gigliolii* and *P. williamsi*. In these species, all sizes between the transitional point were represented, particularly in sizes in which the degeneration of the thoracic teeth occurs in the females. Size at sexual maturity ($CL_{m50\%}$; the carapace length at which 50% of females have no thoracic teeth) was estimated by fitting data to the logistic equation $P = 100/1 + \exp(r(CL\text{-}CL_{m50\%}))$ by a non-linear regression, where $CL_{m50\%}$ is the size at 50% maturity, P the proportion of individuals without thoracic teeth in each size class, and r is the parameter of the model (González et al., 2016).

Other samples of 45 individuals of *P. edwardsii* and 45 individuals of *P. narval* were kept alive for one month in two tanks of 1000 l and two observation tanks of 500 l in dark conditions with a water temperature of 14 °C and salinity of 35.8 ppt, following the recommendations of Landeira et al. (2009). Males and females (with and without the teeth structures of the 7th thoracic sternite) were marked with fluorescent paint to be identified. These conditions were the same as those recorded with a XR-420-CTD sensor at the capture area at 300 m in depth. Living individuals (n = 15) were filmed using an HD camera with red light during the night when the shrimps showed increased activity. A total of 381 interactions were recorded (n = 129, male-male; n = 135 male-female; n = 117, male-immature females). An analysis of variance (ANOVA) was also applied to test differences in the contact time and interaction groups (Underwood, 1997).

3. Results

3.1. New secondary sexual characters

A new distinguishing feature located on the 7th thoracic sternite between the 5th pair of pereiopods was observed (Figs. 1a, b). This structure showed a clear morphological difference between males and females from all *Plesionika* species examined. In males and immature females, this morphological structure consists of two teeth located on the 7th thoracic sternite, specifically placed between the 5th pereiopods (Figs. 1b, c). Thoracic teeth from immature females (incisor shape) can be differentiated from thoracic teeth from males by a more pointed shape and the absence of male gonopores in immature females (Fig. 2).

However, this structure was absent in mature females in all *Plesionika* species studied. Indeed, females presented short denticles on

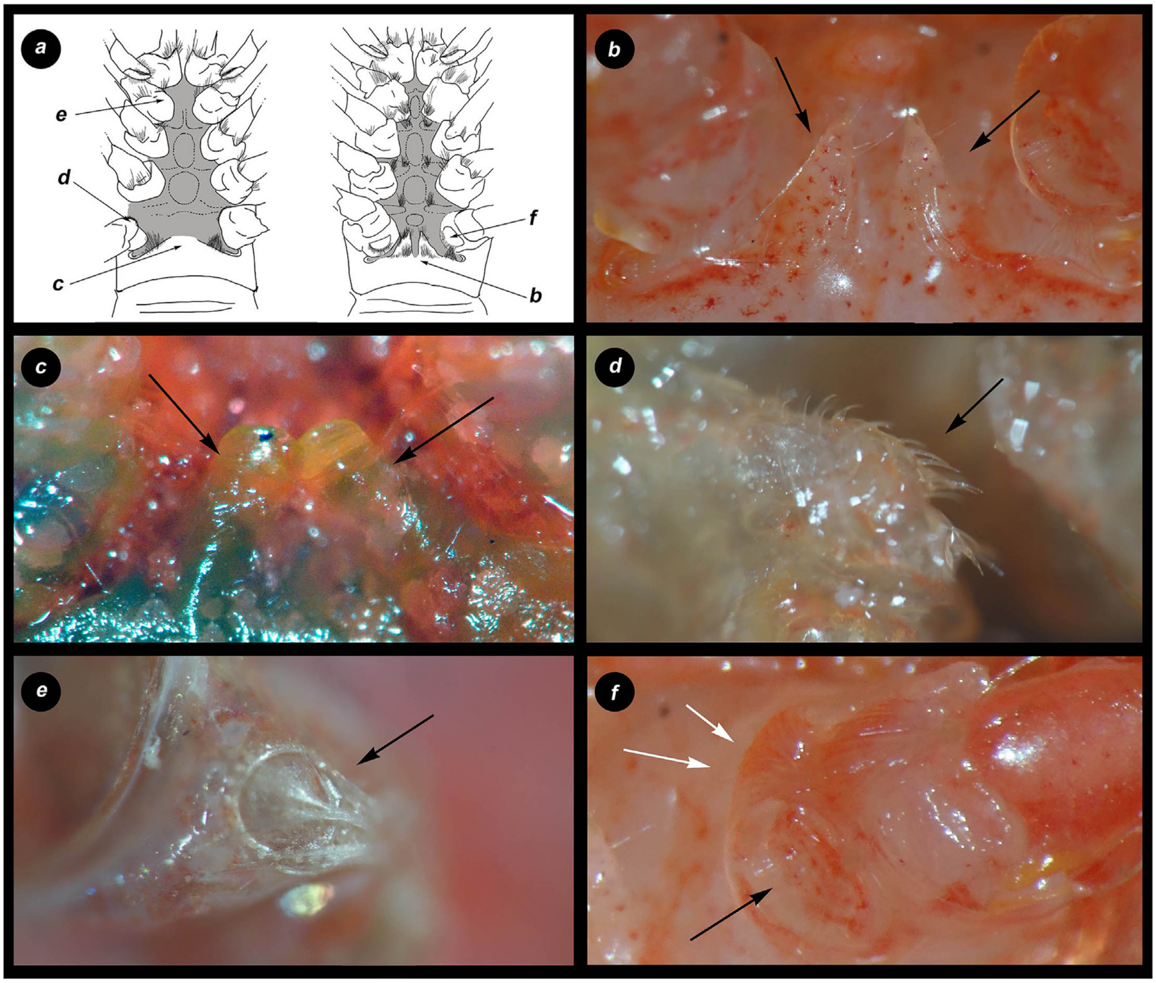

Fig. 1. Location of secondary sexual characters in *Plesionika edwadsii* as a model of genus *Plesionika* (a). Thoracic teeth in males (b) and immature females (c), short denticles on coxa of mature females (d), female gonopore (e), male gonopore (f) and devoid coxa denticles (f). Black arrow indicates the presence of the character; white arrow indicates the absence of the character.

the coxa of 5th pereiopods (Fig. 1d). In addition, the gonopores of both sexes were photographed; female gonopores were on the 3rd pair of pereiopods (Fig. 1e), and male gonopores were on the coxa of 5th pereiopod and devoid of denticles on coxa (Fig. 1f). In males, teeth on the 7th thoracic sternite were always present in the entire size range in all species of *Plesionika* examined in the present study.

Differences between the thoracic teeth for each species can be observed (Fig. 3a-c). Teeth descriptions are as follows: *P. antigai*: Both sides of teeth symmetrical, with a slight inclination to the inside. Teeth obovate with a constriction in the middle, well separated, its height clearly exceeding the male gonopores (constriction coincides with the top of the gonopore) (Fig. 3a3). *P. edwardsii*: Both sides of teeth symmetrical, appearing as a triangle with a slight inclination to the inside. Tip pointed (the most pointed within the studied *Plesionika* species). Inner side slightly concaved near top. Teeth clear and progressively more separated from the base to the top, its height slightly exceeding the male gonopores (Fig. 3b3). *P. ensis*: Outer side of teeth draws an irregular and pronounced slope. Tip small and rounded. Inner side of teeth with overhanging slope. Both teeth joined at the top and appearing progressively separated to the base, its height barely reaching the male gonopores (Fig. 3c3). *P. gigliolii*: Both sides of teeth symmetrical. Tip squared-off in the outer side. Inner side of teeth with a less pronounced tip and ending in flat back. Teeth clearly separated, its height barely exceeding the male gonopores (Fig. 3d3). *P. heterocarpus*: Outer side of teeth draws a gentle slope to its end, where the slope is more pronounced. Tip rounded. Inner side of teeth flat back. Teeth clearly separated, its height not reaching half of the male gonopores (Fig. 3e3). *P. longicauda*: Outer side of teeth has a pronounced concave slope ending in a rounded tip. Inner side draws a complex slope: a rounded convex slope from the top to the middle followed by an overhanging slope to the base. Teeth separated by a narrow space, its height clearly exceeding the male gonopores (Fig. 3f3). *P. martia*: Outer side of teeth draws a curving slope, with rounded tip. Inner side has a flat back or a slightly overhanging slope. Teeth clearly separated, its height nearly reaching the top of male gonopores (Fig. 3g3). *P. narval*: Outer side of teeth with steep slope. Tip squared-off in the outer side. Inner side of teeth with a less pronounced tip and ending in flat back. Teeth separated by a narrow space, its height clearly reaching male gonopores (Fig. 3h3). *P. williamsi*: Outer side of teeth with smooth slope until the tip. Inner side with rounded tip and pronounced slope. Teeth joined at level of the base, its height not reaching half of the male gonopores (Fig. 3i3).

3.2. *Time consumption in sex determination related to sampling strategies*

The percentage of males and females correctly identified using the teeth located on the 7th thoracic sternite was 100% correlated with the sex assigned by using traditional secondary sexual characteristics, such as female gonopores on the 3rd pair of pereiopods, differences in the morphology of endopods on the 1st pair of pleopods, and the presence of appendix masculina on the endopod of the 2nd pleopod in males but the absence on the endopod in females.

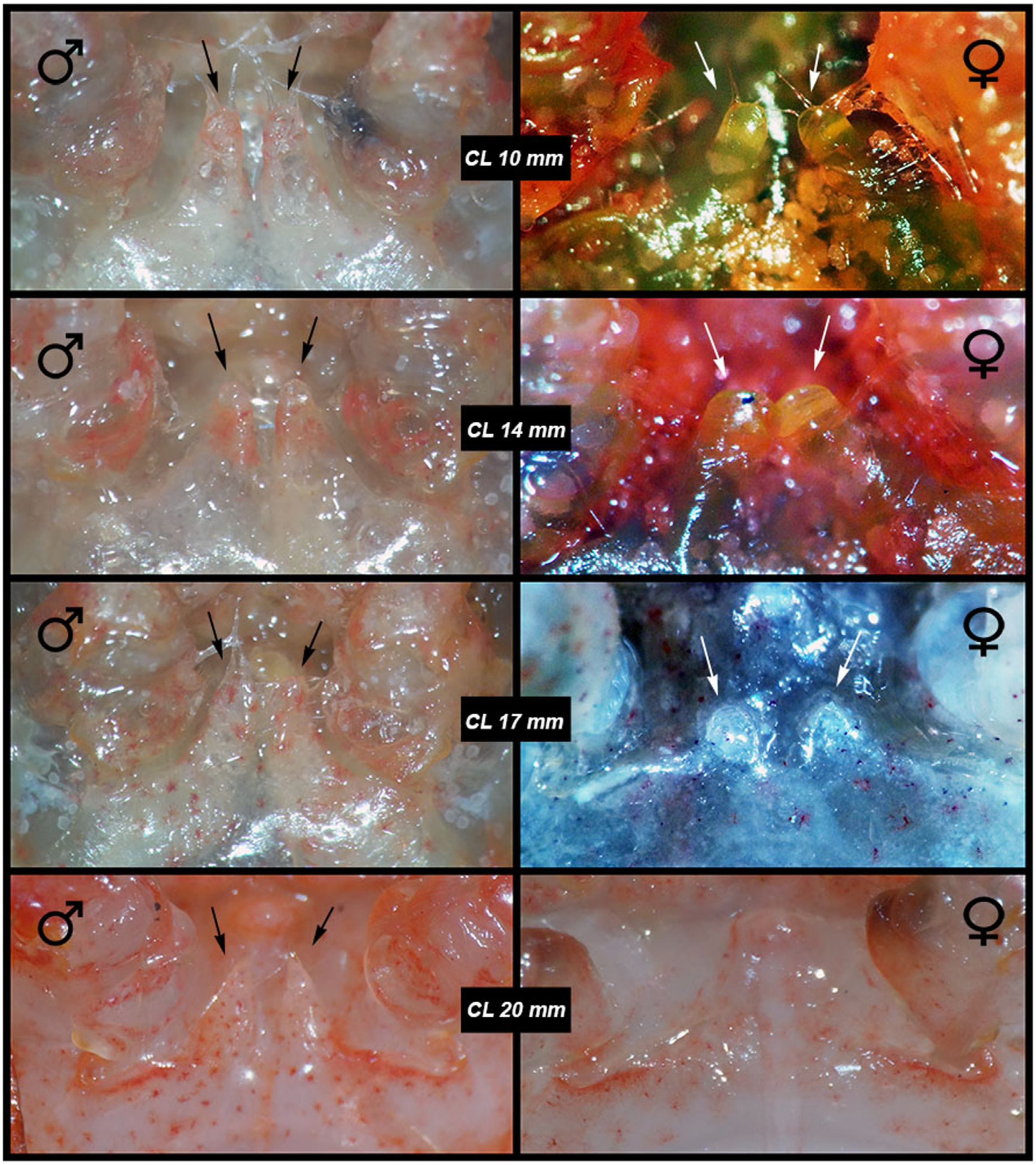

Fig. 2. Progressive degeneration of immature thoracic teeth in *Plesionika edwardsii* females until pubertal moult (right), and the prevalence of thoracic teeth in males (left). From top to bottom, there is an increase in carapace size.

The mean time consumed in the sexing technique based on 2nd pair of pleopods was 6.28 ± 0.76 min/50 shrimps. On the other hand, the mean time consumed in sex determination based on thoracic teeth was 2.21 ± 0.08 min/50 shrimps. The sexing technique based on teeth was faster than the 2nd pleopod technique (Table A.1; F = 674.305, $p < 0.001$); in fact, there was a reduction in time consumed of more than 60% ($t = 25.12$, $p < 0.001$, Fig. A.1).

3.3. Changes in the thoracic teeth and functional maturity in females

The "disappearance" (degeneration) of thoracic teeth in females of all *Plesionika* species examined does not occur abruptly. Some morphological changes occur in the thoracic teeth prior to pubertal moult, in which they degenerate progressively until their disappearance (Fig. 2). However, males always present thoracic teeth without the changes associated with moult. The fading in the teeth prior to pubertal moult is linked to the functional ovarian maturation of females. Prior to pubertal moult, during the period in which teeth are degenerating progressively until their disappearance, *P. edwardsii*, *P. narval* and *P. williamsi* showed histologically in all cases that females with thoracic teeth always had immature ovaries in which the germinal zone was not totally apparent (Stage I). Macroscopically, at this stage, gonads were characterized for their thin and translucent aspect (Fig. 4). However, females without thoracic teeth always had mature ovaries. Although, macroscopically, the resting phase (Stage II) could be confused with immature ovaries, there are some characteristics that can differentiate them. At Stage II, gonads were reddish-yellow and filled less than half of the cephalothoracic cavity. Histologically, ovaries were disorganized, with abundant connective tissue and a well-defined germinal zone (Fig. 4). The length at sexual maturity, which was based on the fading

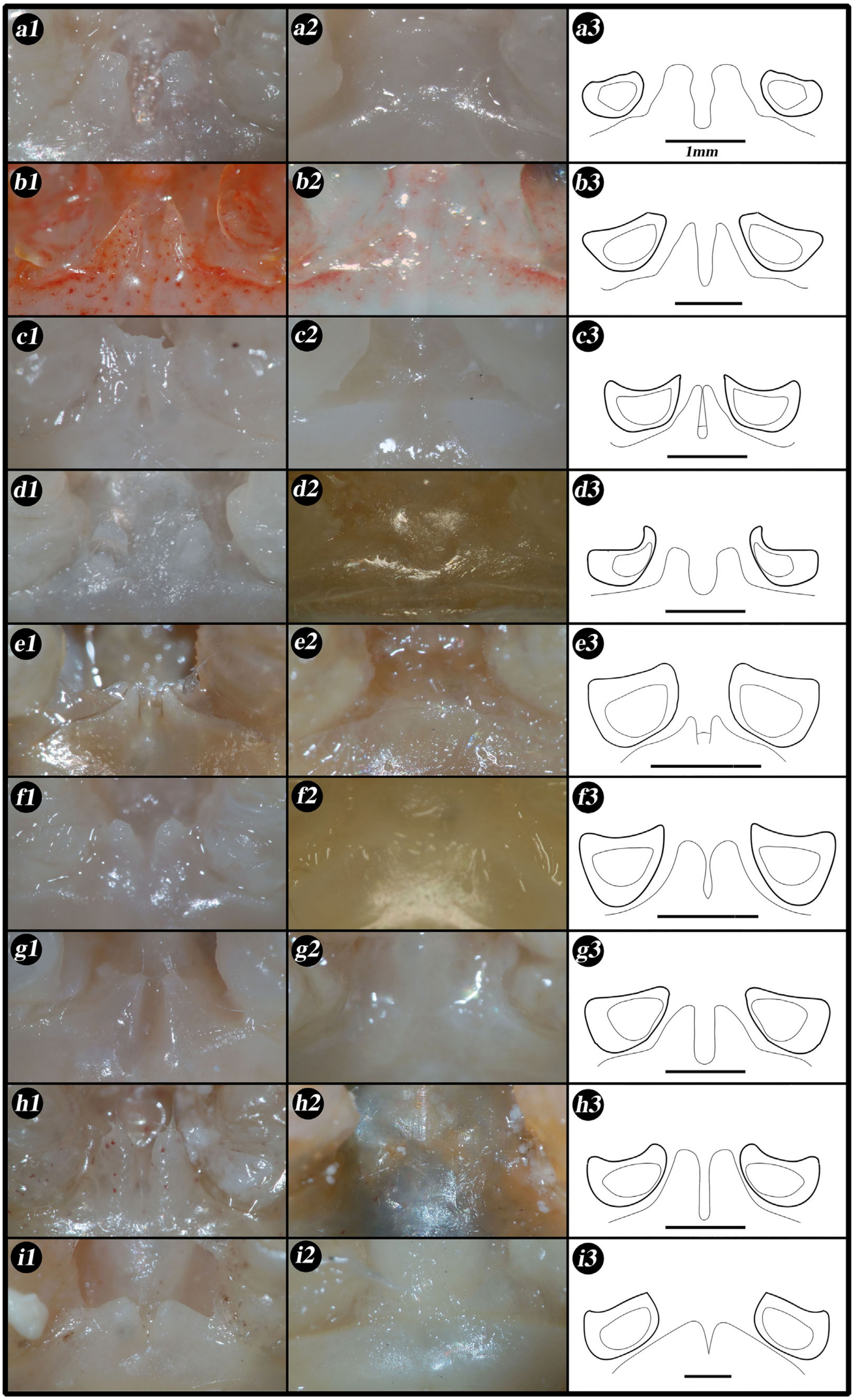

Fig. 3. Thoracic teeth present in males (1,3), absent in females (2) for Plesionika antigai (a), Plesionika edwardsii (b), Plesionika ensis (c), Plesionika gigliolii (d), Plesionika heterocarpus (e), Plesionika longicauda (f), Plesionika martia (g), Plesionika narval (h) and Plesionika williamsi (i).

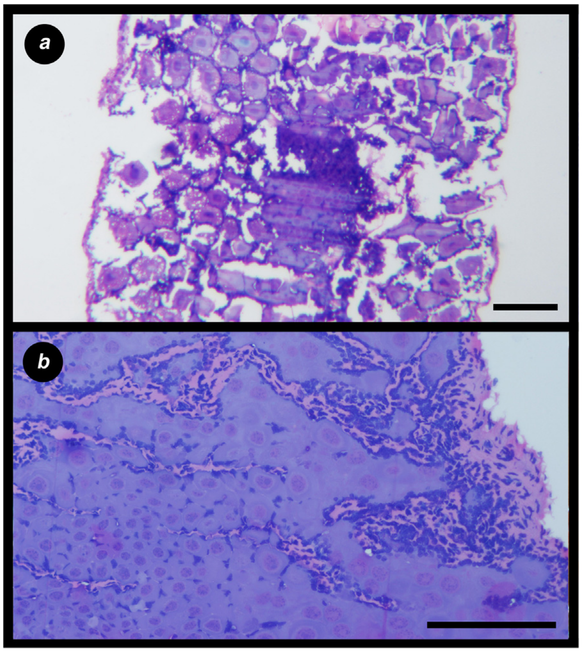

Fig. 4. Histological sections of immature *Plesionika edwadsii* with thoracic immature teeth present, while immature ovaries (a) and mature *P. edwardsii* without teeth present while resting ovaries (b).

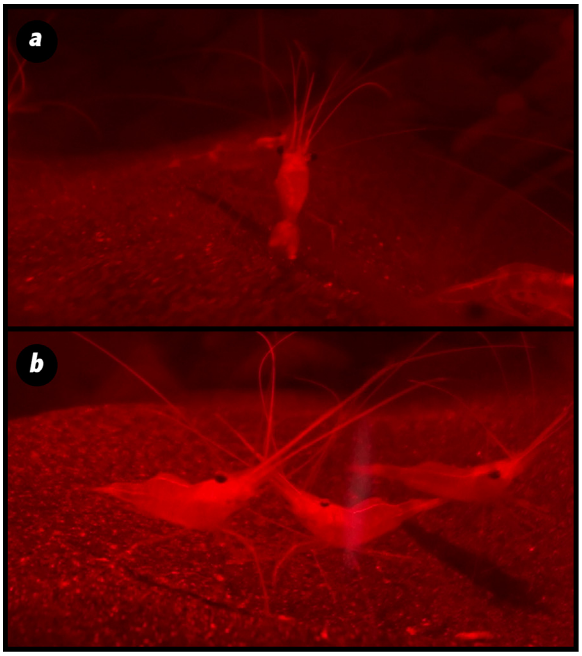

Fig. 6. Social interactions related to thoracic teeth in observation tanks between male-female *Plesionika edwardsii* (a) and *Plesionika narval* (b).

of thoracic teeth in females, was estimated to be 18.11 mm CL in *P. edwardsii* (Canary Islands population) (18.56), 12.01 mm CL in *P. gigliolii* (Mediterranean population), 13.85 mm CL in *P. narval* (Canary population), and 18.70 mm CL in *P. williamsi* (Canary population) (Fig. 5). The similar sizes at maturity were obtained when estimated by using the histological stage of ovaries.

3.4. Role of thoracic teeth in the pure-searcher reproductive strategy

It was not possible to make quantitative observations regarding the reproductive behaviour between specimens of *P. edwardsii* and *P. narval* because all females died during the ecdysis process, as they were unable to harden the exoskeleton. However, observations of contacts between males and females were recorded. The contacts were made at the thoracic region where thoracic teeth are located. Contact between males (2.63 ± 0.57 s) or between males and immature females was abruptly interrupted (2.59 ± 0.46 s). Contact between males and mature females (170.18 ± 0.93 s) was more prolonged (ANOVA test F = 6.04, p = 0.0026), since males were more active and conducted several contacts, always at the thoracic zone of females, where the 3rd pair of pereiopods are located (Fig. 6).

4. Discussion

The correct identification of some species of the genus *Plesionika* remains difficult using the current taxonomic traits due to their similarity (Chace, 1985; Chan and Crosnier, 1991, 1997; Chan and Yu, 2000; Shanis et al., 2014; Ahamed et al., 2017). Current works on genetics indicate that the genus *Plesionika* is not monophyletic as currently defined (da Silva et al., 2013, Chakraborty et al., 2015), highlighting some discrepancies between the current taxonomy and molecular systematics. In females of *Plesionika*, thoracic teeth constitute a taxonomic trait that could be used to separate groups according to the morphology or shape of teeth. Systematics in *Plesionika* reveals the existence of morphological variations among specimens from different

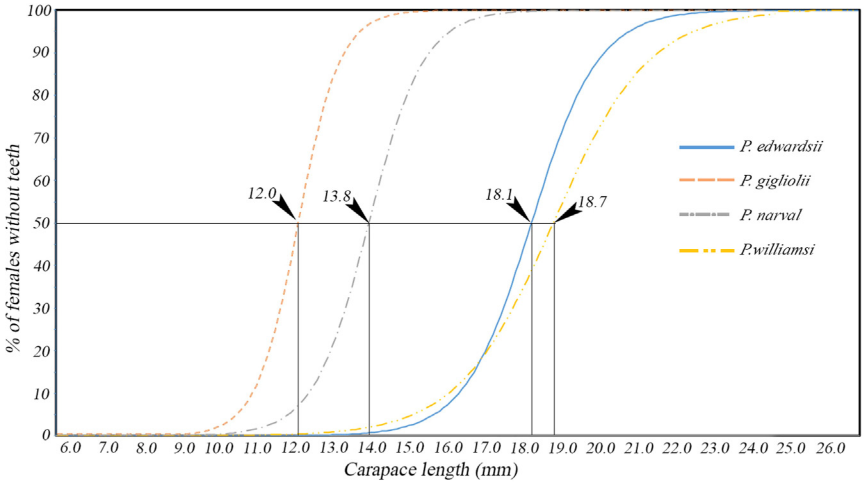

Fig. 5. Maturity ogive estimated by $CL_{m50\%}$ (the CL at which 50% of females without thoracic teeth). Fitted to a logistic equation of *Plesionika edwardsii*, *Plesionika gigliolii*, *Plesionik anarval* and *Plesionika williamsi*.

localities (Shanis et al., 2014; Centelles et al., 2016). A first preliminary morphological analysis showed clear differences in the shape of thoracic teeth in *P. williamsi* in comparison with the other species examined. Both taxonomy and molecular systematics stress the importance of the accumulation of new data on morphology and colouration of *Plesionika* shrimps to clarify the taxonomy of some species of this genus (da Silva et al., 2013; Centelles et al., 2016; Ahamed et al., 2017).

Since the publication by King and Moffitt (1984), the direct sex determination of deep-sea pandalids has consisted of three types of taxonomic evidence: i) the shape of the endopod of the first pair of pleopods, ii) the coxa of the fifth pair of pereiopods (male gonopores located on the coxal segments of the 5th pair of pereiopods), and iii) the appendix masculina on the endopod of the second pair of pleopods in males. The present results showed that the examination of thoracic teeth can advantageously replace two methods regularly used in the field of reproductive biology in *Plesionika* species, such as the examination of traditional secondary sexual characteristics (female gonopore, morphology of endopods or presence/absence of appendix masculina) and the histological examination of ovaries (Fanelli and Bellucio, 2003; Consoli et al., 2004; Triay-Portella et al., 2017). The gradual disappearance of thoracic teeth is linked to the functional maturity and development of the female ovaries and the time of reaching maturity, indicating their complete disappearance. Additionally, sex assignment by the presence/absence of thoracic teeth is an enhanced method because its application is faster than the aforementioned techniques (saving more than 60% of the time). Indeed, sex assignment by the thoracic teeth method does not require the use of a magnifying glass for sex classification of individuals with sizes above average at sexual maturity, which is indispensable when sex determination is conducted by the presence/absence of appendix masculina on a second pair of pleopods, as it is usually done. The absence of male gonopores in the 5th pereiopods, together with the presence of teeth is an unequivocal combination for the female's immature determination. The combination of both methods, i.e. the presence of immature teeth and the absence of male gonopores on the 5th pair of pereiopods, is a robust technique and it does not lead to error. Time consumption in case of mature size is more valuable than sex determination, based on the fact that gonadal histology techniques are not necessary to estimate the size of first functional maturity in these species.

The ratio between appendix masculina and appendix interna is used as a proxy of morphological maturity in mid- and deepwater pandalids. Similarly, changes in the relative growth of the abdomen with body size in *Plesionika* species were used as a proxy of size morphological maturity in females (Ahamed and Ohtomi, 2014). However, this relative growth has been rarely verified with ovarian development (Triay-Portella et al., 2017). Reviewing the literature, the most extended method to obtain size at physiological maturity in females of *Plesionika* is based on the ovigerous condition of females (Table A.2). This method, which is based on the percentage of females carrying eggs by size during the breading season, is strongly biased because it is not able to differentiate mature females without eggs from immature females, yielding an overestimated size at maturity. The use of thoracic teeth gives a new way to estimate maturity in females based on percentages of individuals with or without thoracic teeth by size. The advantages of this method seem to be considerable, since the identification of the maturity condition is not linked to the ovigerous condition or breeding season, and it is correlated with the ovarian maturation and development, which does not need the use of histological techniques to verify the physiological maturity condition in species of *Plesionika*.

Recent research reveals that some of the pereiopodal setae in pandalids present differences between sexes, while some specific setae only present in male pereiopods (Wortham et al., 2014). In this sense, female cuticle setae on the coxa of the 5th pair of pereiopods could be related to the spermatophore fixation on the ventral thoracic area (Bauer, 1976). Setae structure attached to pereiopods and antenna in decapods are vital in overall mechanical, sensory reception, feeding and morphological functions, including sensory mating and grooming activities (Bauer, 2013). In terrestrial arthropods such as Trichoptera, the 5th sternite is related to the occurrence of a female sex and aggregation pheromones (Löfstedt et al., 1994). Observations done in tanks with living individuals under dark conditions have allowed for the finding that males of *P. narval* and *P. edwardsii* actively seek females and use the third pair of their multi-articulate legs for it, making contact mainly at the thoracic region where teeth are located. When a male detects the presence of thoracic teeth during interactions between male and male or between male and immature female, the contact was abruptly interrupted. However, when thoracic teeth were not detected during male-female interaction, the interaction was more prolonged. This suggests that these thoracic teeth play a role in the recognition of sex and the sexual condition of *Plesionika* in deep dark environments. The role of thoracic teeth and their importance in the reproductive biology of these species promise to be an interesting field of study. Additionally, the presence of thoracic teeth in close relatives and closely related taxa remains unknown.

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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.dsr.2018.10.005.

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Chapter 4

Codlings from the eastern-central Atlantic

(Article 5). A new species of *Physiculus* (Teleostei: Moridae) from the Cape Verde Islands (Eastern Central Atlantic).

(Article 6). Morphology data update, otolith description and occurrence of tail regeneration for the *Physiculus cyanostrophus* (Osteichthyes: Moridae), with some notes on the Atlantic species of *Physiculus.*

(Article 7). Caudal region regeneration in a natural population of the morid fish *Physiculus cyanostrophus* in the tropical eastern Atlantic Ocean.

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A new species of *Physiculus* (Teleostei: Moridae) from the Cape Verde Islands (Eastern Central Atlantic)

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Abstract

A new species of *Physiculus*, *P. caboverdensis* **n. sp.**, is described from the outer shelf and upper slope of the Cape Verde Islands. This species differs from all other congeners from the Atlantic Ocean by its peculiar dentition, composed of large fang-like teeth in both jaws, interspaced with smaller canine-like teeth, arranged in two series on upper jaw and one on lower. This is the tenth species of the genus to occur in the Atlantic Ocean and the third to be recorded from the Cape Verde Islands.

Key words: Moridae, *Physiculus caboverdensis*, new species, Cape Verde Islands, Eastern Central Atlantic

Resumo

No presente trabalho é descrita uma nova espécie de abrótea do género *Physiculus*, *P. caboverdensis* **n. sp.** Esta espécie difere de todas as suas congéneres do Oceano Atlântico pela sua dentição, composta de dentes caninos grandes intercalados por outros mais pequenos, em duas séries no premaxilar e numa só fiada na mandíbula. Esta é a 10ª espécie deste género que ocorre no Oceano Atlântico e a 3ª a ocorrer em Cabo Verde.

Introduction

The genus *Physiculus* is represented by 42 valid species (Froese & Pauly 2017), 41 according to Biscoito & González (2018) distributed worldwide, nine of which occur in the Atlantic Ocean. Of these, seven occur in the eastern Atlantic Ocean: *P. cyanostrophus* Anderson & Tweddle, 2002, *P. dalwigki* Kaup, 1858, *P. helenaensis* Paulin, 1989, *P. huloti* Poll, 1953, *P. karrerae* Paulin, 1989, *P. maslowskii* Trunov, 1991, and *P. microbarbata* Paulin & Matallanas, 1990 (Biscoito & González 2018).

Following six fish-trapping surveys off the Cape Verde Islands (2003–2012), three *Physiculus* species were collected, *P. cyanostrophus* and *Physiculus* spp., including two different species (González *et al.* 2014). One of which turned out to be *P. dalwigki,* which had already been recorded from these islands (Cadenat 1950; Menezes *et al.* 2004) and the other has proved to be a new species to science, that is described herein.

Material and methods

Specimens of the new species were collected in 2011 off the island of Santiago, Cabo Verde, at depths of 108–270 m. Meristic and morphometric measurements were made following Hubbs & Lagler (1958) and Paulin (1989). Light organ measurements follow Shcherbachev (1993). SL—standard length; InV-af—distance between interventral line and origin of anal fin; InV-Lo—distance between interventral line and anterior margin of light

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organ; Lo-An—distance between posterior margin of light organ and anus; LoD—light organ diameter. Otolith shape terminology and indices follow Tuset *et al.* (2008). Institutional abbreviations follow Fricke & Eschmeyer (2017).

Physiculus caboverdensis n. sp.

(Capeverdean codling; *PT*, Abrótea de Cabo Verde)
Tables 1–2, Figs. 1–4

Material examined (10 specimens, SL 83–168 mm, Cruise "Camarão 1", R/V Prof. Ignacio Lozano, semi-floating shrimp traps, rocky bottom). Holotype: MMF 42537, SL 167 mm, East of Cidade Velha, 15° 14'N, 23° 34'W, St. 14D2, 108–111 m, 25 Nov. 2011. Paratypes: BMNH 2013.5.10.1, SL 142 mm, same collection data as holotype; MMF 43122, SL 165 mm, Ponta Covinha, 15° 09.6'N, 23° 43.8'W, St. 10, 260–270 m, 21 Nov. 2011; MMF 43123, SL 153 mm, MMF 43124, SL 168 mm, TFMCBMVP/01955, SL 154 mm, MNHN 2013-0648, SL 150 mm, Ponta Água Doce, 15° 09'N, 23° 47' W, St. 4, 220–258 m, 19 Nov. 2011; MMF 43127, SL 83 mm, MMF 43128, SL 132 mm, USNM 440407, SL 144 mm, Ribeira da Barca, 15° 07'N, 23°47' W, St. 9, 225–238 m, 20 Nov. 2011. Additional 67 specimens, not included in the type series, were caught and are being studied for its biology.

Diagnosis. A species of *Physiculus,* as defined by Paulin (1989) and Shcherbachev (1993), with the following combination of characters: teeth in upper jaw in two series, the outer one with large inward-curved canine teeth interspaced with small canine-like teeth, and the inner one a narrow band with small canine-like teeth identical to the smaller teeth on outer row, irregularly distributed; teeth in lower jaw in one series, with large straight canine teeth, interspaced with small canine-like teeth; scales in longitudinal series ca. 111–128; scale rows between base of first dorsal fin and lateral line 8–9; D 11–12, 57–67; A 63–69; P 26–28; V 7; C 25–28; vertebrae: 52–55 (Tab. 1).

FIGURE 1. *Physiculus caboverdensis* **n. sp.**, holotype, MMF 42537, SL 167 mm, East of Cidade Velha, 108–111 m of depth. Scale bar 10 mm.

Description. Body moderately elongate, laterally compressed posteriorly; greatest body depth at level of the origin of first dorsal fin, slightly less than four times into SL (17.3%–24.3%); head moderately conical; eye large (21.7%–28.9% HL); snout short (24.1%–28.5% HL), blunt at tip; mouth terminal, slightly oblique, upper jaw reaching to vertical from posterior rim of orbit; jaw teeth unequal (Fig. 2), distributed as above; upper jaw symphyseal separation wide; chin barbel very small (7.0%–9.6% HL); outer gill rakers on first gill arch small, varying from spinous tubercles to small clubs, spinous initially at tips and progressively more spinous towards the angle on lower branch and spinous at tips on upper branch (Fig. 3); abdominal cavity reaching the 15th pterygiophore of anal fin.

TABLE 1. Morphometry, meristics and light organ size and position of the type series of *Physiculus caboverdensis* n. sp.

	Holotype	Paratypes									
	MMF 42537	MMF 43127	MMF 43128	BMNH 2013.5.10.1	USNM 440407	MNHN 2013-0648	MMF 43123	TFMCBMVP 01955	MMF 43122	MMF 43124	Range
Standard length (mm)	167	83	132	142	144	150	153	154	165	168	83-168
(%SL)											
Head length	27.5	27.1	27.5	28.2	26.7	26.7	29.6	27.9	27.9	26.8	26.7-29.6
Pre-dorsal 1 length	31.1	31.3	30.6	32.4	29.3	29.7	31.5	30.5	29.7	29.5	29.3-32.4
Pre-dorsal 2 length	41.6	41.0	40.5	40.8	40.3	39.7	40.8	39.6	40.0	39.9	39.6-41.6
Pre-pectoral length	29.9	29.5	29.5	29.6	28.5	29.3	30.7	29.9	29.1	28.9	28.5-30.7
Pre-pelvic	26.9	24.7	28.0	27.1	26.7	26.0	30.1	26.0	27.9	23.2	23.2-30.1
Pre-anal length	38.9	33.6	37.9	36.6	38.2	37.0	41.2	36.4	37.6	34.5	33.6-41.2
Pre-anus length	34.7	32.5	34.8	33.1	35.4	32.3	35.9	32.5	33.3	33.9	32.3-35.9
First dorsal fin base length	9.6	8.6	9.2	9.5	9.4	9.3	9.9	9.1	9.4	9.0	8.6-9.9
Second dorsal fin base length	56.9	55.3	53.5	57.0	54.8	54.6	53.5	55.2	52.1	53.6	52.1-57.0
Anal fin base length	59.0	59.7	60.3	61.6	63.9	64.7	63.4	62.3	61.3	58.9	58.9-64.7
Pectoral fin length	16.8	21.7	19.6	15.5	17.0	18.0	19.0	16.2	16.8	15.9	15.5-21.7
Caudal peduncle length	5.1	4.8	3.8	4.8	3.5	4.7	3.9	4.5	4.2	3.9	3.5-5.1
Least depth of caudal peduncle	2.4	2.4	2.3	2.3	2.1	2.1	2.1	2.3	2.1	2.4	2.1-2.4
Maximum body depth	23.4	21.9	21.6	23.2	24.3	20.7	20.8	17.5	21.4	17.3	17.3-24.3
(%HL)											
Snout length	26.1	26.7	28.5	27.5	25.2	26.7	24.3	26.7	25.3	24.1	24.1-28.5
Post-orbital length	54.3	48.1	52.3	50.0	52.2	52.3	50.8	50.0	52.2	53.3	48.1-54.3
Eye diameter	21.7	28.9	28.2	27.3	26.0	26.4	22.6	25.6	24.8	24.4	21.7-28.9
Inter-orbital width	20.7	22.3	20.4	20.8	19.4	19.1	17.7	20.9	20.7	22.2	17.7-22.3
Preopercular length	82.6	80.1	79.8	80.0	77.9	79.8	77.3	76.7	79.3	81.1	76.7-82.6
Upper jaw length	52.2	53.8	53.7	51.3	48.4	50.8	50.8	46.5	49.5	53.3	46.5-53.8
Gape length	37.0	33.4	34.4	40.0	35.1	38.6	34.3	27.9	37.0	35.6	27.9-40.0
Chin barbel length	8.0	-	9.6	7.5	8.6	7.8	7.0	8.1	9.6	7.1	7.0-9.6
Head height at posterior border of orbit	63.0	57.9	55.0	55.0	57.2	67.3	57.5	55.8	56.5	55.6	55.0-67.3

……continued on the next page

TABLE 1. (Continued)

	Holotype	**Paratypes**									
	MMF 42537	MMF 43127	MMF 43128	BMNH 2013.5.10.1	USNM 440407	MNHN 2013-0648	MMF 43123	TFMCBMVP 01955	MMF 43122	MMF 43124	Range
Pelvic fin reaching anal fin ray no.	1	5	2	1	2	5	3	2	3	1	1-5
Pectoral fin reaching second dorsal fin ray no.	4	6	5	5	4	4	5	5	4	4	4-6
Meristics											
First dorsal fin rays	12	11	12	12	12	12	11	12	11	12	11-12
Second dorsal fin rays	58	60	67	57	58	59	59	60	57	57	57-67
Anal fin rays	63	69	68	66	65	68	68	67	67	67	63-69
Pectoral fin rays	27	28	27	27	27	28	27	26	27	28	26-28
Pelvic fins rays	7	7	7	7	7	7	7	7	7	7	7
Caudal fin rays	27	28	27	27	28	27	25	25	25	28	25-28
Branchiostegal rays	7	7	7	7	7	7	7	7	7	7	7
Gill rakers (1st arch)	5+10+1r	5+10	5+10+1r	5+10+1r	4+10+1r	5+10	5+10	5+10+1r	5+10	5+10+1r	4-5+10=14-15
Scale rows between base of first dorsal fin and lateral line	8	9	9	8	9	9	9	9	9	9	8-9
Scales in longitudinal series	123	-	117-118	128	117	117	117	113	111-113	113	111-128
Vertebrae	15+40=55	14+38=52	15+40=55	14+38=52	14+40=54	16+38=54	14+40=54	14+40=54	14+40=54	13+40=53	13-16+38-40=52-55
Light organ size and position	in% InV-af										
Light organ diameter (LoD)	11.1	8.3	9.3	13.3	9.5	13.2	6.8	10.5	9.5	10.0	6.8-13.3
Distance between interventral line and anterior margin of light organ (InV-Lo)	25.0	20.8	23.3	20.0	26.2	26.3	25.0	23.7	23.8	25.0	20.0-26.3
Distance between posterior margin of light organ and anus (Lo-An)	27.8	20.8	23.3	26.7	23.8	21.1	18.2	18.4	26.2	20.0	18.2-27.8

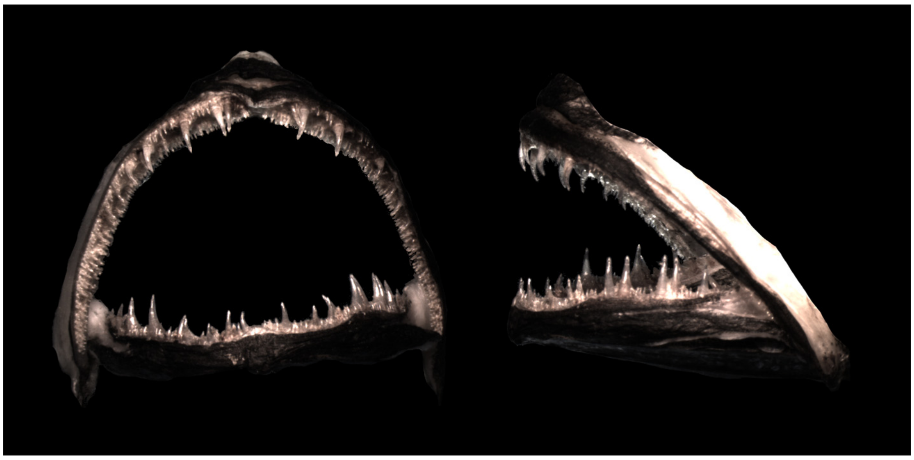

FIGURE 2. Upper and lower jaws of *Physiculus caboverdensis* **n.sp.**, showing distinct unequal teeth.

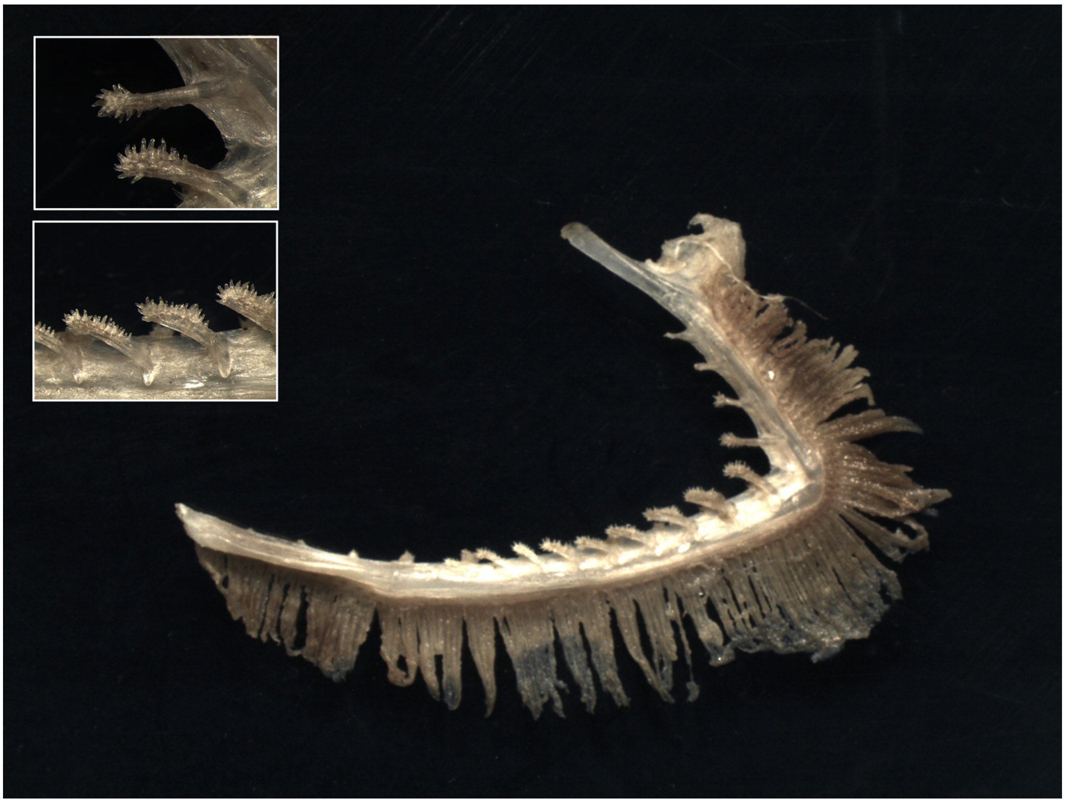

FIGURE 3. Gill rakers on first gill arch of *Physiculus caboverdensis* **n. sp.** Upper insert showing rakers near angle. Lower insert showing rakers 2–4 on lower branch.

Scales moderately large, ca. 111–128 in longitudinal series; 8–9 scale rows between base of first dorsal fin and lateral line; scales present on head and gular region; no scales penetrating into vertical fin membranes; lateral line starting above upper angle of opercle; continuous tube of lateral line reaching at least to mid second dorsal fin; discontinuous tubes of lateral line reaching caudal peduncle.

First dorsal fin higher than second, 5th ray longest, a very small gap separating first from second dorsal fins; second dorsal fin origin at level of vertical through 6th anal-fin ray; anal fin base slightly larger than second dorsal fin base, both fins not indented, their rear tips rounded; pectoral fins symmetrical, their origin almost at level of vertical through origin of first dorsal fin and extending to below 4th to 6th second-dorsal fin rays; pelvic fins small, the first two rays elongate, reaching at least the 5th anal-fin ray; caudal peduncle narrow (2.1–2.4% SL), caudal fin rounded and well separated from second dorsal and anal fins.

Light organ small, its diameter ranging from 6.8% to 13.3% InV-af and behind interventral line (20.0–26.3% InV-af), distance from posterior margin of light organ to anterior margin of anus 18.2% to 27.8% InV-af.

Otoliths sagitiform. Sulcus acusticus heterosacoidal positioned in the longitudinal line of the otolith with well differentiated tail and ostium. Ostium smaller than the tail, long and elliptical, ending close to the anterior margin. Tail funnel-shaped and slightly convex. Anterior region slightly pointed. Posterior region very sharp, with postrostrum long, narrow and pointed and antipostrostrum short, narrow and pointed. Excisura caudalis with a deep and sharp notch (Fig. 4, Table 2).

TABLE 2. *Physiculus caboverdensis* **n. sp.** otolith shape indices taken from 11 specimens (TL 133–170 mm) not belonging to the type series (OL=otolith length; OH=otolith height; OT=otolith thickness; TL=total length of the fish).

Shape indices	n	Mean ± sd	Minimum	Maximum
OL/TL (%)	11	5.29 ± 0.32	4.52	5.71
OH/OL (%)	11	34.46 ± 2.93	30.52	39.54
OT/OL (%)	11	32.14 ± 2.01	29.31	34.31
OT/OH (%)	11	93.60 ± 6.28	86.13	101.75
Circularity	11	27.17 ± 1.77	24.34	29.98
Rectangularity	11	0.59 ± 0.02	0.56	0.61

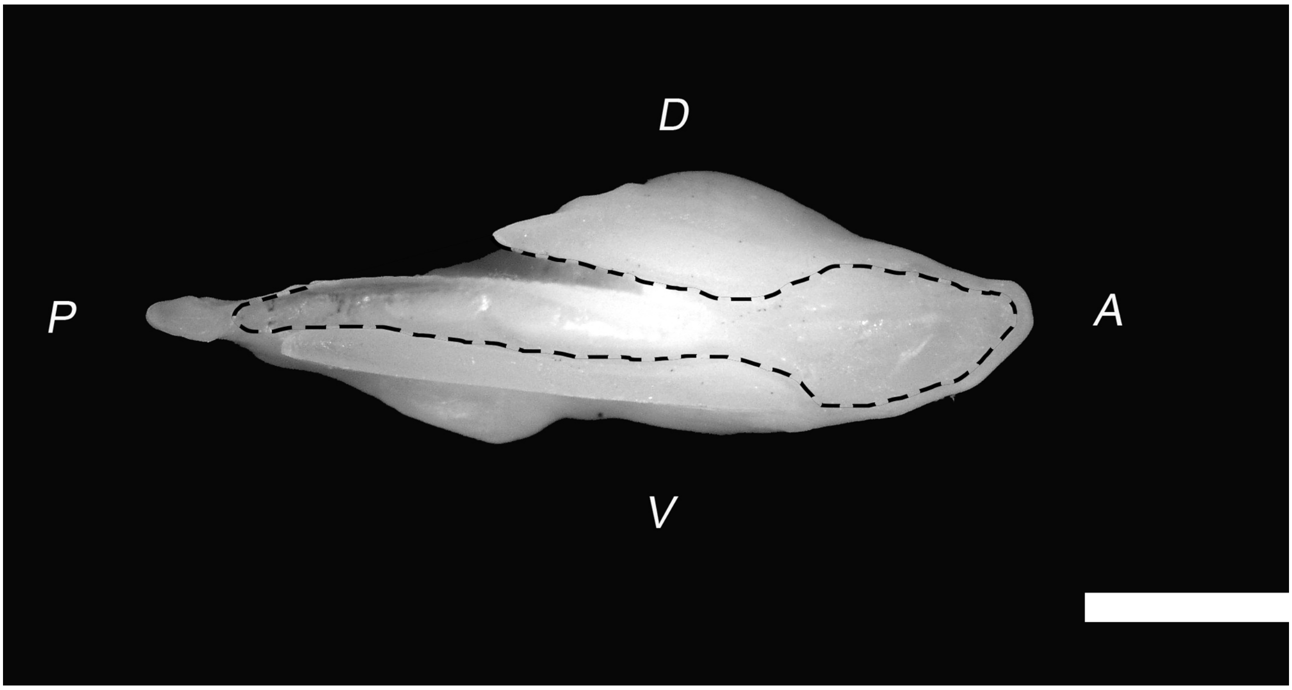

FIGURE 4. Inner side of right sagittal otolith of *Physiculus caboverdensis* **n. sp.**, showing the major anatomical features (D = dorsal margin; P = posterior margin; A = anterior margin; V = ventral margin; sulcus acusticus limited by a discontinuous line). Scale bar 2 mm.

Vertebrae: 13–16+38–40=52–55.

Colouration. In recently caught specimens, overall body reddish-brown, bluish silvery on belly and golden reflections on cheeks, opercles, and dorsum above lateral line. Fins reddish. Pectorals with dark bluish mark at base, first dorsal fin ray with a dark mark distally, second dorsal and anal fins with dark bluish margins. Interior of mouth pale.

Comparative remarks. Taking into account that *Physiculus* species have fairly restricted geographical distributions (Paulin 1989) and that up to the present there are no known species occurring in more than one ocean basin (Froese & Pauly 2017), *P. caboverdensis* is only compared with their Atlantic Ocean congeners.

P. caboverdensis can be distinguished from all other nine Atlantic *Physiculus* species by the dentition, being the only one to have large fang-like teeth, interspaced with smaller canine teeth in both jaws.

In comparison with the other 33 or 32 species from the Indian and Pacific oceans, only *Physiculus cynodon* Sazonov, 1986 from the Emperor Seamount chain, in the North Pacific, has a similar dentition. However, it differs from this species by several characters, namely, the number of fin rays in first dorsal fin (11–12 *vs* 9–10), second dorsal fin (57–67 *vs* 72–79), anal fin (63–69 *vs* 78–85), pectoral fin (26–28 *vs* 24–25), the number of scales in longitudinal series (111–128 *vs* ca. 200) and number of vertebrae (52–55 *vs* 54–59) (Sazonov 1986). Moreover, the present species has a shorter abdominal cavity than *P. cynodon* (extending to the 15th pterygiophore of the anal fin *vs* 24th to 26th) (Sazonov 1986).

Distribution. At present, *P. caboverdensis* is only known from the Cape Verde archipelago, where it has been found off the islands of Santa Luzia, São Vicente, Santiago and Sal, at depths between 104 m and 339 m, over rocky bottoms. Its collection in semi-floating traps, and not on benthic ones, seems to indicate that it is epibenthic.

Etymology. *P. caboverdensis* is named for the Cape Verde Islands, the type locality of the species.

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Morphology data update, otolith description and occurrence of tail regeneration for *Physiculus cyanostrophus* (Osteichthyes: Moridae), with some notes on the Atlantic species of *Physiculus*

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Summary*:* Among of 917 individuals of *Physiculus cyanostrophus* caught from the outer shelf and upper slope of the Cape Verde Islands, a total of 258 specimens (28.1%) showed caudal region regeneration. Within whole body individuals, 200 fish were selected for morphological and meristic purpose. This subsample covered a size range between 139 and 348 mm of total length (which is maximum length observed in this species to date), and between 125 and 317 mm of standard length. Morphometric and meristic data obtained have significantly broadened the known ranges of these morphology variables for *P. cyanostrophus*. Description of sagitta otolith of this species is provided for the first time. An updated table comparing the relative position and size of the light organ among Atlantic species of *Physiculus* is given, representing a taxonomic tool for species identification. Importance of regeneration phenomenon in genus *Physiculus* is discussed herein

Key words: caudal region regeneration; morphology; otolith; *Physiculus*; *P. cyanostrophus*; Cabo Verde Islands; eastern Atlantic.

INTRODUCTION

The genus *Physiculus* Kaup, 1858 currently comprises 42 valid species (González et al. 2018, Eschmeyer et al. 2019, Froese and Pauly 2019), exhibiting the highest degree of diversity within the family Moridae (Paulin 1989). *Physiculus* species have fairly restricted geographical distributions (Paulin, 1989) and up to the present there are no known species occurring in more than one ocean basin (Froese and Pauly 2019). Ten species occur in the Atlantic Ocean: *P. caboverdensis* González, Triay-Portella & Biscoito, 2018, *P. capensis* Gilchrist, 1922, *P. cyanostrophus* Anderson & Tweddle, 2002, *P. dalwigki* Kaup, 1858, *P. fulvus* Bean, 1884, *P. helenaensis* Paulin, 1989, *P. huloti* Poll, 1953, *P. karrerae* Paulin, 1989, *P. maslowskii* Trunov, 1991, and *P. microbarbata* Paulin & Matallanas, 1990.

These species are distributed in all tropical, subtropical, and warm-temperate seas of the world at depths of 100–600 m (Paulin 1989). They are mainly known from a taxonomic perspective, but few data concerning their ecology and population structure are available (Triay-Portella et al. submitted). Most species are very similar externally and none are easily identified. For these reasons, in general they are poorly known (Paulin 1989, Prokofiev 2006). Sagittal otolith morphology and size and dermal fossa position of the light organ are important features for distinguishing species of *Physiculus*, and most sympatric populations can be separated based on these characters (Paulin 1989).

In recent years new morphology data on *Physiculus* species have been published, including synonymyzation and redescription of species (Biscoito and González 2018) and description of new species (González et al. 2018). For *P. cyanostrophus*, apart from its original description based on 12 individuals and its first record for Cape Verde Islands based on 3 individuals (González et al. 2010), no more data are available in the literature.

Present work provides (i) morphometric and meristic data of *Physiculus cyanostrophus* based on a wide sample of individuals, including some comments on its caudal region regeneration, (ii) the first description of its sagittal otolith, and (iii) an updated comparative table on size and position of the light organ of *Physiculus* species occurring in the Atlantic Ocean.

MATERIAL AND METHODS

Seven expeditions took place to investigate the marine epi- and benthic macrofauna of the Cape Verde archipelago (2003-2017). During each expedition, macrofauna were sampled using bottom traps and semi-floating shrimp traps (operating approximately at 2.4 m above the seafloor) at depths ranging from 100 to 390 m (e.g. González et al. 2018). Specimens of *Physiculus cyanostrophus* (Fig. 1) were collected around the islands of Boa Vista, Santiago including Bancona Bank, São Vicente, Santa Luzia, Sal and São Nicolau (González et al. 2010, 2014, Pajuelo et al. 2018).

Meristic and morphometric measurements were made following Hubbs and Lagler (1958) and Paulin (1989). Light organ measurements follow Shcherbachev (1993). TL—total length; SL—standard length; InV-af—distance between interventral line and origin of anal fin; InV-Lo—distance between interventral line and anterior margin of light organ; Lo-An—distance between posterior margin of light organ and anus; Lo—light organ diameter; An—anus diameter. Fin-ray and vertebral counts were obtained from radiographs. Otolith shape terminology follows Tuset et al. (2008).

RESULTS

Of a total of 917 individuals of *Physiculus cyanostrophus* caught, 258 (28.1%) had a regenerated caudal region. From the lot with intact bodies, 200 individuals were selected for the aims of the present study covering a size range between 139 and 348 mm TL (which is the maximum length observed to date for the species), and between 125 and 317 mm of SL.

Morphometric measurements are listed below. Expressed as a percentage of SL: head length (HL, 19.6-25.1%), snout length (4.6-6.0%), eye diameter (4.2-6.7%), pectoral fin length (15.3-21.6%), body height at level of the 1st dorsal fin (16.2-22.8%), and interorbital distance (4.5-6.0%). Expressed as a percentage of HL: snout length (16.4-28.7%), horizontal diameter of orbit (18.8-25.8%), interorbital width (21.0-25.4%), and chin barbel length (3.2-7.4%). Expressed as a percentage of InV-af: InV-Lo (30.0-43.7%), Lo-An (13.1-23.9%) (Table 1). Light organ data include a revised light organ size and position of the *Physiculus* species occurring in the Atlantic Ocean (Table 2).

The meristic study on *P. cyanostrophus* has significantly broadened the ranges of the variables considered by Anderson and Tweedle (2002) and González et al. (2010). Radial formulae: first dorsal fin, 7-9; second dorsal fin, 64-73; anal fin, 65-82; pectoral fin, 19-26; pelvic fin, 5-7; caudal fin, 22-28. Gillrakers on the first branchial arch: 3-4 upper, 9-11 lower, 12-15 total. Branchiostegal rays, 7. Scales: in longitudinal series, 121-134; in oblique series (between base of the first dorsal fin and lateral line), 8. Number of pyloric caeca, 11. Vertebrae, 13+44–45=57–58. Other morphometric and meristic characteristics are also given in Table 1.

Otoliths sagitiform. Sulcus acusticus heterosacoidal positioned in the longitudinal line of the otolith with well-differentiated tail and ostium. Ostium smaller than the tail, long and elliptical, ending close to the anterior margin. Tail funnel-shaped and slightly convex. Anterior region slightly pointed. Posterior region very sharp, with postrostrum long, narrow and pointed and antipostrostrum short, narrow and pointed. Excisura caudalis with a deep and sharp notch (Fig. 2).

DISCUSSION

Although the existence of fishes with a pseudo-hypural plate (or false tail) is still poorly investigated in the deep-sea, the occurrence of individuals with regenerated caudal region is a characteristic trait in some species of *Physiculus*. Brüss (1986) described it for the first time in *P. marisrubri* Brüss, 1986, and estimated a c. 10% of regenerated individuals as a high proportion. Later, some authors described this phenomenon in other *Physiculus* species (Paulin 1989, Paulin and Matallanas 1990, Prokofiev 2006). Present work reveals c. 28% of regenerated individuals, suggesting that the importance of this trait in natural populations of *Physiculus* species could be higher; however most of the available data are based on a small number of specimens. However, the recently described *Physiculus caboverdensis* (González et al. 2018) does not present this trait or at least no regenerated specimens were found in the sample caught (75 individuals) together with *P. cyanostrophus* (RT-P observations). Although *Physiculus* species are morphologically similar to those of *Gadella* and *Salilota*, the examination of 114 specimens of these genera (Paulin 1989) did not reveal individuals with missing caudal fins, and the loss and regeneration of a caudal fin in any other morid genera is extremely rare (Paulin and Matallanas 1990). The factors making *Physiculus* species particularly susceptible to this type of injury are unknown. It should be noted that, although some species of *Physiculus* are common, the vast majority of them have been described based on very few individuals (Prokofiev 2006), and the magnitude of regeneration ability at population level in natural populations of these species has been recently described (Triay-Portella et al. submitted). In this sense, a greater effort should be made to explore this capacity in other *Physiculus* species, especially with those that can be kept in aquariums, such as the Japanese codling *P. japonicus* Hilgendorf, 1879.

Anderson and Tweedle (2002) noted that, within all known species of *Physiculus*, *P. cyanostrophus* appears to be close to *P. nigripinnis* Okamura, 1982 from the north-western Pacific. Both species have similar small light organs, meristic values and the blue band around their body, but *P. cyanostrophus* differs from *P. nigripinnis* in seven characters (Anderson and Tweedle 2002). Even though the present study has significantly broadened the ranges of the meristic variables considered, none of the seven characters that differentiate it from *P. nigripinnis* comes into conflict or became invalid. Regarding the original description of *P. cyanostrophus*, one specimen (paratype RUSI 64639) presents a significant lower number of vertebrae 13+36=49, and Anderson and Tweedle (2002) attributed this to the normal intraspecific variability. Based on the high number of individuals X-radiographed and the high percentage of specimens with false tail found in the present work, the most probable explanation for the vertebral formula of paratype RUSI 64639 is that it has a false tail.

Haneda (1953) first observed a functional light organ of one species of *Physiculus*, specifically in *P. japonicus* in aquarium tank, at the Asamushi Marine Biological Station in 1936. To date, the real function of the light organ in *Physiculus* remains unknown. From a taxonomic point of view, size and position of the dermal fossa of the light organ are the most important characters in distinguishing species of *Physiculus* (Paulin 1989). Present work provides an update for size and position of dermal fossa of *Physiculus* species occurring in the Atlantic Ocean (Fig. 3).

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FIGURE CAPTIONS

Figure 1. *Physiculus cyanostrophus* from the Cape Verde Islands (218 mm TL, São Vicente, 220-228 m depth).

Figure 2. Inner side of right sagittal otolith of *Physiculus cyanostrophus*, showing the major anatomical features (sulcus acusticus limited by a discontinuous line). Scale bar 2 mm.

Figure 3. Size and position of dermal fossae of light organ of *Physiculus* species occurring in the Atlantic Ocean (as percent of InV-af). Updated and enlarged from Paulin (1989).

TABLE CAPTIONS

Table 1. Morphometric and meristic data from *Physiculus cyanostrophus.* * Indicates a new range for the morphology variable of the species.

Table 2. Comparison of relative position and size of the light organ in % InV-af among Atlantic species of *Physiculus*.

Figure 1

Figure 2

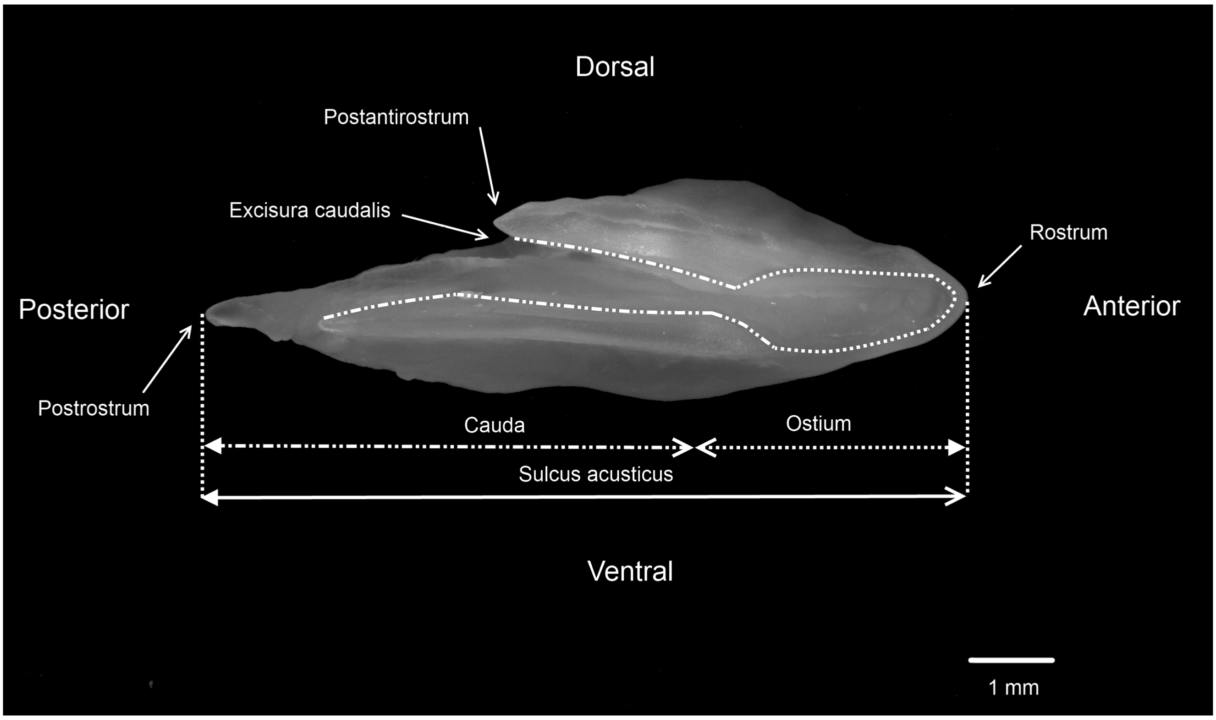
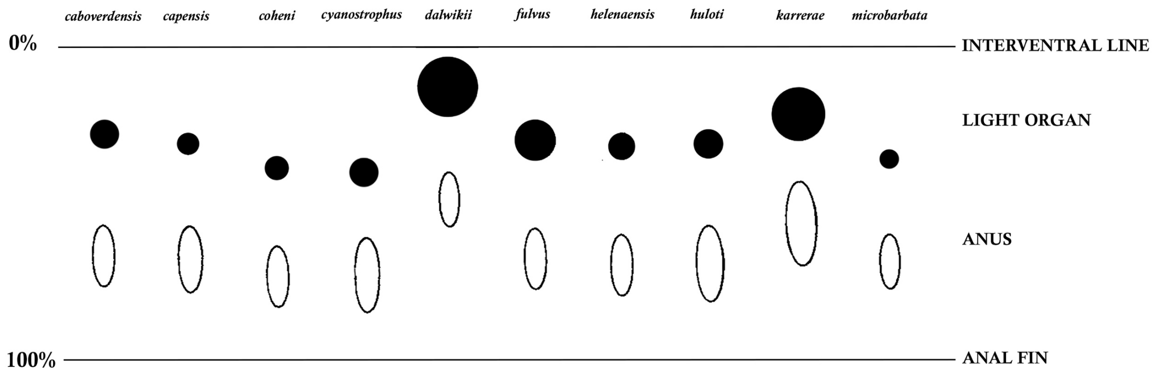

Dorsal
Postantirostrum
Excisura caudalis
Rostrum
Posterior
Anterior
Postrostrum
Cauda
Ostium
Sulcus acusticus
Ventral
1 mm

Figure 3


caboverdensis
capensis
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cyanostrophus
dalwikii
fulvus
helenaensis
huloti
karrerae
microbarbata
0%
INTERVENTRAL LINE
LIGHT ORGAN
ANUS
100%
ANAL FIN

Meristic counts and morphometric measurements	200 specimens	3 specimens	12 specimens	215 specimens
	125-317 mm SL	206-295 mm SL	115-278 mm SL	115-317 mm SL*
	(present study)	(González et al. 2009)	(Anderson and Tweddle 2002)	available information
First dorsal-fin rays	7-9	8	8-9	7-9*
Second dorsal-fin rays	64-73	69-72	65-70	64-73*
Anal-fin rays	69-82	68-74	71-76	65-82*
Pectoral-fin rays	21-23	19-26	22-23	19-26
Pelvic-fin rays	5-7	7	5-6	5-7
Filamentous pelvic rays extending to	8-13th anal ray	8-9th anal ray	-	8-13th anal ray*
caudal-fin rays	24-28	22-27	25-28	22-28
Scales in longitudinal series	ca. 121-134	+105	ca. 126-130	ca. 121-134*
Scales between first dorsal fin base and lateral line	8	9-10	8	8-10
Gillrakers on upper limb	3-4	4	3-5	3-5
Gillrakers on lower limb	9-11	10	9-11	9-11
Total gillrakers	13-15	14	13-16	13-16
Branchiostegal rays	7	7	7	7
Teeth (villiform)	equal-sized	equal-sized	equal-sized	equal-sized
Vomerine and palatine teeth	absent	absent	absent	absent
Vertebrae	13+44-45= 57-58	-	49-59	57-59*
IN PERCENT OF SL				
Head length	19.6-25.1	22.7-23.1	21.7-24.4	19.6-25.1*
Interorbital width	4.5-6.0	4.9-5.1	4.1-4.8	4.1-6.0*
Pectoral fin length	15.3-21.6	15.4-18.0	15.4-17.9	15.4-21.6*
Greatest body depth	16.2-22.8	17.2-20.3	17.6-20.2	16.2-22.8*
Snout length	4.6-6.0	4.4-5.0	3.6-4.8	3.6-6.0*
Eye diameter	4.2-6.7	4.1-5.6	4.9-6.4	4.2-6.7*
IN PERCENT OF HL				
Snout length	16.4-28.7	19.4-21.7	15.6-20.6	16.4-28.7*
Eye diameter	18.8-25.8	16.7-24.6	22.2-27.8	18.8-27.8*
Interorbital width	21.0-25.4	21.3-22.4	18.8-21.4	21.0-25.4*
Chin barbel length	3.2-7.4	3.9-4.5	4.2-9.2	3.2-9.2*
IN PERCENT OF InV-af				
Distance between interventral line and anterior margin of light organ	30.0-43.7	37.1-38.5	31.0-39.7	30.0-43.7*
Distance from posterior margin of light organ to anterior margin of anus	13.1-23.9	23.8-25.8	23.6-28.5	13.1-28.5*
Light organ diameter	6.8-12.4	-	-	6.8-12.4*
Anus diameter	19.4-28.6	-	-	19.4-28.6*

	InV-Lo	Lo-An	LoD	Size	References
P. caboverdensis	0.0 - 5.7	15.8 - 20.0	12.8 - 15.8	large	González et al. (2018)
P. cyanostrophus	30.0 - 43.7	13.1 - 28.5	6.8 - 12.4	moderately large	Anderson and Tweddle (2002), present work
P. dalwigki	0.0 - 2.4	16.8 - 23.1	17.5 - 20.0	very large	Paulin (1989)
P. fulvus	17.6 - 25.6	21.1 - 24.5	7.5 - 13.2	moderately large	Paulin (1989)
P. helenaensis	27.5	25.0	8.8	moderately large	Paulin (1989), Shcherbachev (1993)
P. huloti	22.8 - 27.9	21.6 - 23.9	7.0 - 12.5	moderately large	Poll (1953), Paulin (1989)
P. karrerae	8.2 - 16.8	13.3 - 27.4	14.8 - 21.3	large	Paulin (1989), Trunov (1991), Shcherbachev (1993)
P. kaupi	19.5 - 22.2	26.4 - 28.8	8.8 - 11.1	moderately large	Paulin (1989)
P. maslowskii	23.8 - 37.5	20.5 - 27.7	8.0 - 12.5	moderately large	Trunov (1991)
P. microbarbata	34.3 - 36.0	18.0 - 19.7	5.2 - 6.3	small	Paulin and Matallanas (1990)

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Caudal region regeneration in a natural population of the morid fish *Physiculus cyanostrophus* in the tropical eastern Atlantic ocean.

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ABSTRACT

The present study describes a remarkable caudal regeneration capacity of *Physiculus cyanostrophus*, a benthopelagic fish from the twilight zone. This trait reveals the ability of this particular morid to survive attacks that would be lethal in other species. In teleosts, the most widespread sublethal predation is confined to scale-eating and fin-nipping by specialized predators. In *P. cyanosytrophus* the larger sized individuals the greatest amount of tissue loss occurred in the caudal region (maximum 28 vertebrae, corresponding to 45% lost body length). The amount of regenerated tissue was independent of body losses and ranged between 5 and 19% of total length for the entire range of sizes. The frequency of regenerated individuals in the population increases with ontogeny (16.8–67.5%). Tissue losses represent a significant allocation of costs in terms of growth and offspring production. Nevertheless, regeneration capability decreases mortality in the large breeding females of a population, maximizing maternal fitness.

1. Introduction

In marine ecosystems, fishes are subject to injuries due to aggressive behaviour, predation and diseases (Winemiller, 1990; Ziskowski et al., 2008; Sinclair et al., 2011). From a trophic viewpoint, some predators in aquatic ecosystems have specialized in sublethal attack mechanisms (Farmer and Beamish, 1973; Papastamatiou et al., 2010).

Among fishes (as prey), the most widespread sublethal predation, in both fresh and marine waters, is due to specialized scale-eating (lepidophagous) and fin-nipping predators (e.g., Sazima, 1983; Winemiller, 1990; Nakae and Sasaki, 2002). Additionally, in marine ecosystems, some prey species have developed mechanisms to revert potential lethal attacks into sublethal injuries. This sublethal predation in marine ecosystems occurs among prey species with regenerative abilities and autotomy (Bely and Nyberg, 2010), such as, crustaceans, polychaetes and echinoderms. In animals, sublethal predation is the predominant mechanism of tissue loss (Bely and Nyberg, 2010). Nevertheless, it is widely accepted that sublethal predation may influence prey dynamics. The degree and consequences of these predatory effects depend on the amount of lost biomass or the loss of function resulting from sublethal attacks (Maginnis, 2006).

Research studies on regeneration, based on the ability of fish to regenerate lost tissues, has largely focused on zebrafish and electric fishes (Unguez, 2013). However, in nature, evidence of tissue regeneration is quite rare. From an ecological perspective, the population-level consequences of the regeneration of body parts are poorly understood in fishes (Maginnis, 2006; Unguez, 2013). Studies that incorporate the costs associated with the regeneration process into understanding population dynamics are necessary.

The genus *Physiculus* Kaup, 1858 currently comprises 41 valid species (see Gonzalez et al., 2018) exhibiting the highest degree of diversity within the family Moridae (Paulin, 1989). The *Physiculus* species are mainly known from a taxonomic perspective, but few data are available concerning their ecology and population structure. The *Physiculus* species are distributed in all tropical, subtropical, and warm-temperate seas of the world at depths of 100–600 m (Paulin, 1989). Some *Physiculus* species has the ability to regenerate the caudal fin. This newly regenerated fin develops a replacement skeletal structure known as the “pseudo-hypural plate” (Brüss, 1986; Paulin and Matallanas, 1990). Sublethal injuries (or regenerated caudal fin) frequently occur in Macrouridae and other Moridae genera to such an extent that total length has been replaced by preanal fin length in taxonomic and ecological studies (Atkinson, 1991). Within benthopelagic species belonging to these groups (e.g., grenadiers, rattail fishes and deep-sea cods), a high percentage of individuals with sublethal injuries or regenerated caudal fins have been found (e.g., Paulin and Matallanas, 1990; Massutí et al., 1995; Andrews et al., 1999). Nevertheless, sublethal predation in the deep-sea has not yet been explored, probably

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because ecological knowledge of these species is lacking and because most sublethal injuries are often attributed to the trawl net effect (Massutí et al., 1995). Regeneration of caudal fins has been described in macrourids and morids (Brüss, 1986; Atkinson, 1991) and tail loss occurs frequently in deep-sea gadiformes e.g *Bathysaurus mollis* specialises in biting tails off marcrourids and hence avoids parasitic infections (Campbell et al., 1980). Our study describes and evaluates the importance of caudal region regeneration in *Physiculus cyanostrophus*, including consequences in their population dynamics, growth and fitness.

2. Materials and methods

2.1. Biological data collection

Seven expeditions were undertaken to investigate the marine epi- and benthic macrofauna of the Cape Verde archipelago. Sampling was carried out off the islands of Boa Vista, Santiago, including the Bancona Bank, São Vicente, Santa Luzia, Sal, and São Nicolau in order to search for new living resources, between 2010 and 2012 and 2017, at depths of 66 m and 458 m. Expeditions were conducted in the spring (April and March), summer (June and July), autumn (November) and winter (January and February). In all cruises bottom traps and semi-floating traps (operated around 2.4 m above the seafloor) (see González et al., 2014 for trap design) were used as sampling system.

2.2. Morphology measures

Each fish was sampled (n = 917) following standard measurements for family Moridae (Paulin, 1989; Trunov 1989). The total length (TL), head length (HL) and regenerated total length (regTL) were measured to the nearest 0.01 mm. The theoretical total length (tTL) was obtained from the linear regression between HL and TL from the non-regenerated (NR) specimens to estimate the corresponding TL of regenerated individuals (R). Body lost length was estimated as the difference between tTL and the length after injury. Other measurements are explained in Fig. S1. Gutted mass and gonad mass were recorded to the nearest 0.001 g. Sex determination was assessed according to macroscopic differences in gonads. Otoliths (n = 767) were extracted, and otolith mass was recorded to the nearest 0.0001 g. Based on current ontogenetic data (maturity and fecundity), three ontogenetic groups were defined for both sexes: juveniles (females TL $<$ 210 mm; males TL $<$ 190 mm), young-adults (females 210 mm $>$ TL $<$ 300 mm; males 190 mm $>$ TL $<$ 240 mm) and old-adults (females TL $>$ 300 mm; males TL $>$ 240 mm). The specimens (n = 120) were prepared with their fins fully extended and were then photographed with a digital camera for further image analysis to obtain fin surface estimates (mm^2). Similarly, specimens with a “pseudo-hypural plate”, considered regenerated individuals (R), were photographed (n = 73) to estimate their regenerated fin surface (body area from the beginning of the length regenerated to the end of the body, including fin surface; mm^2). Vertebral counts on a subsample of specimens (n = 30) were obtained from radiographs by means of an X-ray machine and were then processed with eFilm Lite™ software. The percentage of body lost length was calculated along with the number of lost vertebrae (Fig. S4).

2.3. Growth

Otolith mass versus TL and tTL of R (n = 215) and NR (n = 562) females within the same size range were compared. Otolith sections from R (n = 72) and NR (n = 159) females were prepared according to protocols described by McCurdy et al. (2002). Age was estimated twice, with two researchers reading the otolith sections according to Wright et al. (2002). Observed length-at-age was described by the *von Bertalanffy growth model* using a non-linear least square procedure of a *Gauss-Newton algorithm* for R and NR females.

2.4. Fecundity outputs

The ovaries (n = 764) were fixed and preserved in 4% buffered formaldehyde and were subsequently processed for histological analyses to verify the macroscopic maturity stage using H&E staining, following standard procedures for fish biology studies. Following the terminology of Brown-Peterson et al. (2011), spawning capable fish were selected from R (n = 42) and NR (n = 58), covering the entire range of sizes (Murua et al., 2003), to estimate the total fecundity (TF) and batch fecundity (BF) (Hunter et al., 1985). TF and BF were estimated using gravimetric methods (Murua et al., 2003). Each subsample was weighted to the nearest 0.0001 g and was then filtered via 100 μm mesh to exclude previtellogenic oocytes for the estimation of TF. The mesh size was estimated by calculating the diameter of previtellogenic oocytes with image analysis (Thorsen and Kjesbu, 2001) from early-developed subphase ovaries, following the methods of Brown-Peterson et al. (2011).

2.5. Data analysis

Differences in the HL–TL relationship between the sexes were evaluated by an *F-test*, and differences between *b* values and the expected value from isometric growth ($b = 1$) were evaluated by a *t-test* (Sachs, 1982).

Differences in mean TL and TM between sexes were analysed using *Student's t-test*. The *Kolmogorov–Smirnov non-parametric Z-test* was used to analyse differences in TL and TM distributions between groups male-female and R-NR (each sex).

The regeneration-ratio (R:NR) and the sex-ratio (male:female) were estimated for the whole population and for each of the three ontogenetic groups. A *Pearson Chi-square test* was conducted to test the null hypothesis of equality of frequencies between R and NR and by sexes (H_0 = 1:1 ratio) with a significance level of $\alpha = 0.05$ (Sachs, 1982; Sokal and Rohlf, 2012).

The bias and precision of annuli counts in otoliths were compared between readers, using paired *t-tests* (Campana, 2001). Estimates of ageing precision were determined using the coefficient of variation (Chang, 1982). The multivariate *Hotelling's* T^2*-test* was used to compare growth parameters between R and NR females (Bernard, 1981).

Otolith mass, TF and BF for R and NR females were represented as a function of tTL and TL, respectively. Potential regressions for different groups were statistically compared with slope homogeneity and covariance of linearized potential regression applying an *F-test* (Sachs, 1982). These tests evaluated the null hypothesis of equality of two regressions estimated by sexes with a significance level of $\alpha = 0.05$. The same procedure was conducted to compare TF and BF within R and NR against age.

3. Results

3.1. Regeneration pattern

A total of 917 individuals classified into two groups were sampled: non-regenerated (NR, n = 659) and regenerated (R, n = 258). R individuals had fewer vertebrae than NR individuals as a consequence of sublethal attacks, causing body loss in the caudal region. Most R individuals had a thicker caudal peduncle, produced by the regeneration process. By means of X-ray, the absence of a caudal skeleton, as well as the transformation of the last present vertebra after injury into a “pseudo-hypural plate” for insertion of new C-rays, was observed (Fig. 1).

3.2. Prevalence of tail regeneration in a natural population

The NR females reached a mean size and a mean mass larger than males (TL, $t = 8.86$ $p < 0.05$; TM, $t = 7.92$, $p < 0.05$) (Table S1). R

Fig. 1. (a) *Physiculus cyanostrophus* with intact and regenerated tails. (b) Radiographs of three regenerated individuals (R) within 10 and 35% of body losses in total length (blTL). Examples of a regenerated caudal region "pseudo-hypural plate" with regenerated new c-rays.

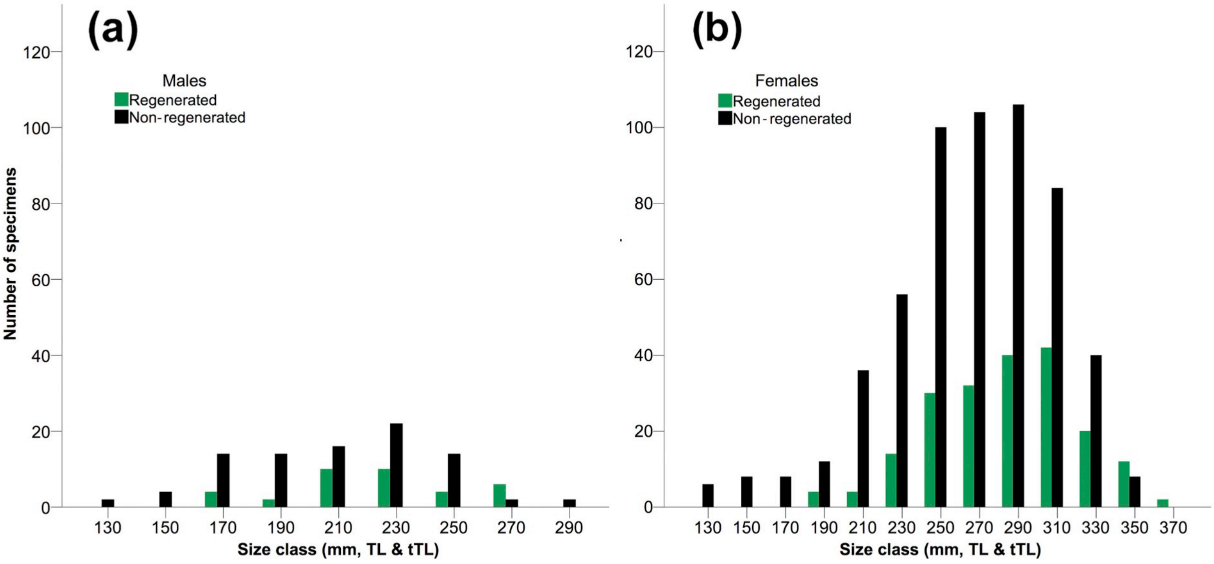

Fig. 2. Size distribution of males (a) and females (b) population of *Physiculus cyanostrophus*. Bars correspond to individuals for each size class of 10 mm TL. Green bars are regenerated individuals (R), and black bars non-regenerated ones (NR). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

females presented a mean size and mean mass greater than R males (tTL, $t = 6.62$ $p < 0.05$; TM, $t = 6.36$, $p < 0.05$). The TL and TM distributions of NR and R also differed significantly between females and males (Fig. S4b; TL, $Z = 3.93$ $p < 0.05$; TM, $Z = 3.72$, $p < 0.05$). The distribution of tTL and TM of R individuals also differed significantly between females and males (tTL, $Z = 2.61$, $p < 0.05$; TM, $Z = 2.62$, $p < 0.05$). For R females, the mean size was larger than NR ($t = 3.30$, $p < 0.05$). Conversely, a similar mean size between R and NR males was found ($t = 0.799$, $p > 0.05$) (Fig. 2a). The size distribution of R and NR groups was different, with NR females being present in the small classes, but the R group was absent in these classes ($Z = 1.47$, $p < 0.05$). Male size distributions were similar in both groups ($Z = 0.80$, $p > 0.05$) (Fig. 2b).

NR females were more abundant than NR males (1:6.3, $\chi^2 = 348.17$, $p < 0.05$). Size classes less than or equal to 180–200 mm TL showed similar numbers of NR males and NR females (1:1, $\chi^2 = 0.923$, $p > 0.05$). However, NR females were more abundant in size classes larger than 200 mm TL ($\chi^2 > 7.14$, $p < 0.05$), mainly over 300 mm TL, where only females were observed. R Females were also more abundant than R males (1:5.14, $\chi^2 = 117.35$, $p < 0.05$). With size classes, R females and R males followed the same pattern as that observed for NR individuals. Female regeneration-ratio (R:NR) was 1:2.6 ($\chi^2 = 79.02$, $p < 0.05$). Statistical differences were found among ontogenetic groups, where dominance of NR females

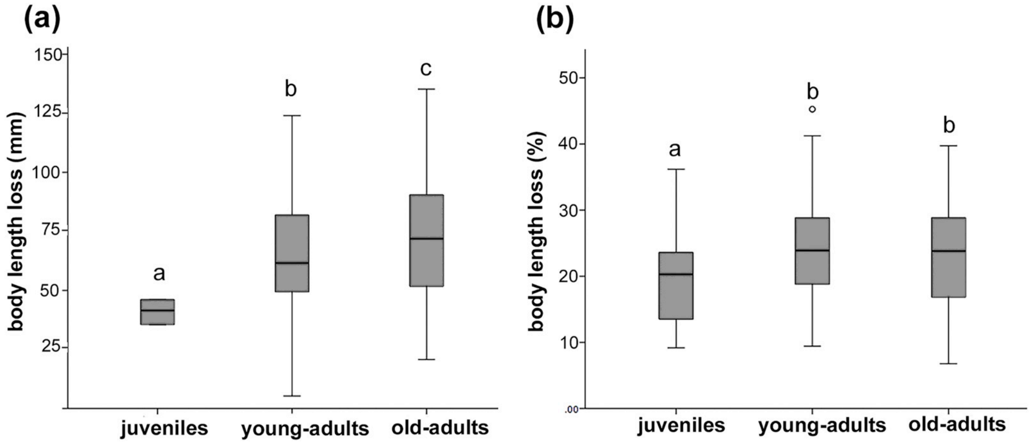

Fig. 3. Box-plot showing ranges of body lost length (a) and in % of theoretical total length (tTL) (b) for juveniles, young-adults and old-adults in regenerated individuals of *Physiculus cyanostrophus*. Different letters above bars denote statistically significant differences ($p < 0.05$) between ontogenetic groups. The line within each box is the median value, box ends represent the inner and outer quartiles, and whiskers are the inner and outer tenths.

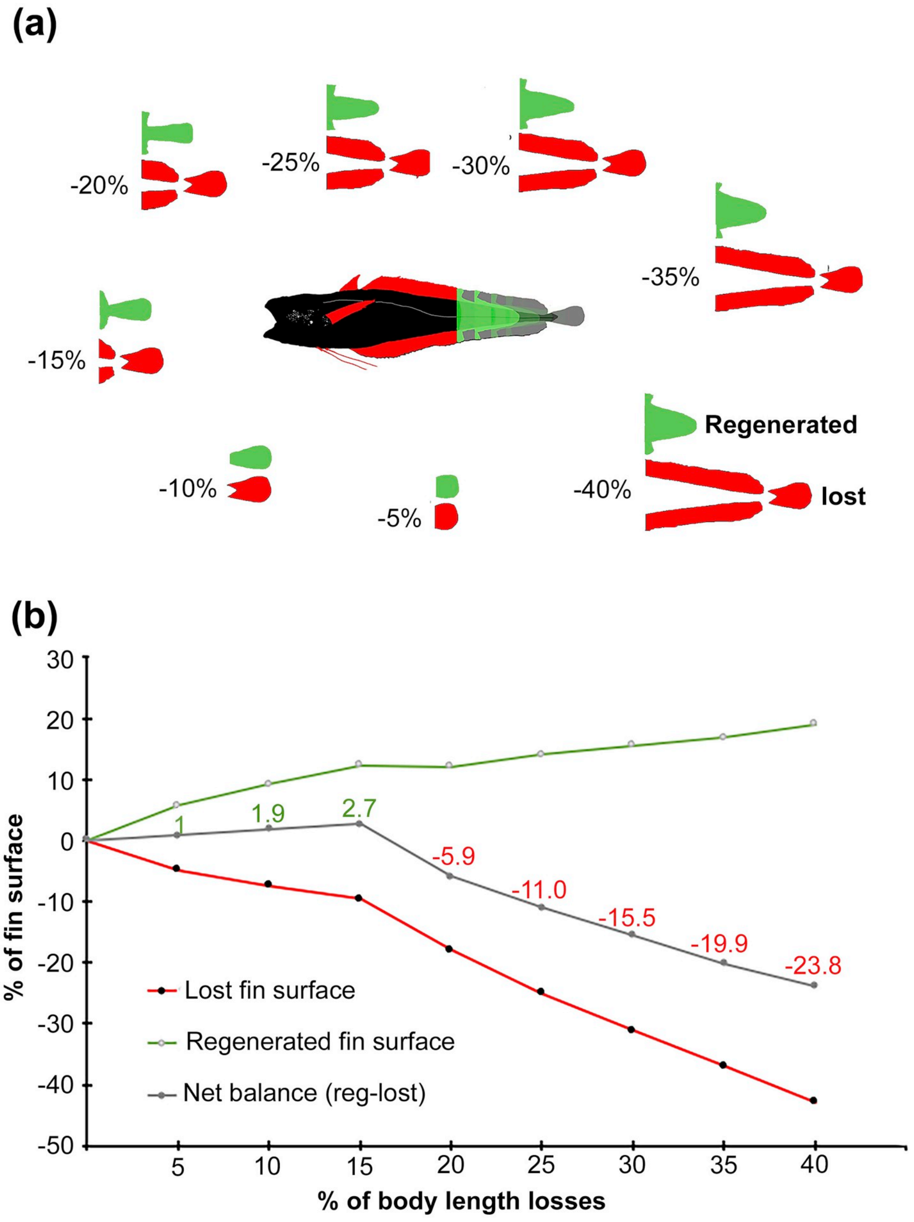

Fig. 4. (a) Schematic representation of *Physiculus cyanostrophus* lost fin surface (red) and regenerated fin surface (green) for each % in total body lost length. (b) Net balance in fin surface for each % of body lost length of *P. cyanostrophus*. The green line denotes regenerated fin surface, the red line represents lost fin surface, and the grey line represents the balance between both measurements. Net balance means values for each interval of body lost length have been indicated. Net balance was completely offset up to losses of 15% of the total length. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

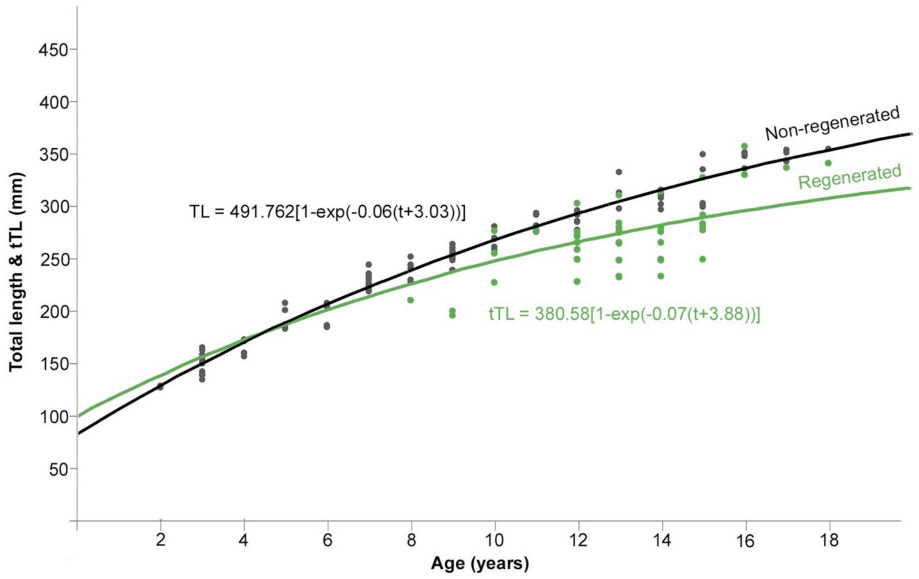

Fig. 5. Length-at-age data for regenerated (R) and non-regenerated (NR) females of *Physiculus cyanostrophus* with fitted von Bertalanffy growth curves: $LT = L_\infty\ [1 - \exp\ (-k\ (t - t_0))]$, where LT is the length of fish at age t, L_∞ is the estimated asymptotic length, k is a constant that determines the rate at which TL approaches L_∞, and t_0 is the hypothetical age at zero length. Age-range for regenerated individuals was 8–18. No individuals younger than 2 years were located in the studied population. Percentage agreement between otolith readings of Reader 1 and Reader 2 (83.6–86.2%) was similar. Moreover, the exact match of the average readings between both readers was high (85.3%) with a quite low variability of IAPE ($t = 1.654$ $p < 0.001$) and CV indices (3.9% and 3.4%, respectively).

decreased from juveniles (1:5.6, $\chi^2 = 16.03$, $p < 0.05$) and young-adults (1:3.1, $\chi^2 = 65.05$ $p < 0.05$) to old-adults (1:1.6, $\chi^2 = 5.84$ $p < 0.05$). Moreover, NR males were more abundant than R males in the ratio 1:2.1 ($\chi^2 = 11.57$, $p < 0.05$). This ratio was similar through the ontogeny of males (1:2.6, 1:2.1 and 1:1.8; $\chi^2 = 0.297$, $p > 0.05$).

3.2.1. *Tail loss*

Estimations of tTL based on the HL–TL relationship of NR individuals yielded significant differences between sexes ($F = 29.1403$, $p < 0.05$), being isometric in females and males ($t > 7.69$, $p < 0.05$). The body lost length increased with ontogeny ($F > 18.154$, $p < 0.05$): being 43.21 ± 18.37 mm (mean ± s.d) for juveniles, 61.90 ± 25.29 mm for young-adults and 77.33 ± 28.36 mm for old-adults, with the last group exhibiting the highest losses (Fig. 3a). Young-adults showed the widest range of body lost length (0–45%), (Fig. 3b). A *post hoc test* showed differences in body lost length between young-adults and old-adults ($p < 0.05$). Indeed, these groups showed differences within juveniles ($p < 0.05$). The relationship between tTL and the number of vertebrae in regenerated specimens is shown in Figs. S2 and S3. The highest vertebrae loss was 28, corresponding with a specimen of 45% body lost length. We also measured the net balance between lost fin surface and regenerated fin surface, and our results indicate that they were completely offset until losses reached 15% of tTL (Fig. 4).

The regenerated length (regL) is independent of body lost length and of total length regenerated in % of theoretical total length (tTL). Values of regL showed a mean increase of 13 ± 3.31 mm (mean ± standard deviation, in %) and ranged between 5 and 19% of tTL for the entire range of sizes (Fig. S4).

3.3. *Growth*

Statistical differences between NR and R females were found in the otolith mass–TL power function relationship ($F = 180.58$, $p < 0.05$). Indeed, mean otolith mass of R females (80.187 ± 18.47 mg) was heavier than that of NR females (70.90 ± 20.15 mg) ($t = 3.696$, $p < 0.05$) for the same size range distribution.

Based on the annual growth, ring counts of 173 (75%) readable female otoliths ranged from 2 to 18 years (age). Fish younger than 2 years were absent in the study sample. The youngest R individual was 8 years. The *von Bertalanffy growth curves* for observed TL and tTL at age of R and NR females are shown in Fig. 5. *Hotelling's T^2-test* showed significant differences in the growth parameters between R and NR females ($T^2 = 106.930$, $p < 0.05$). Differences in growth between both groups increased with longevity. NR and R individuals at 9 years exhibit differences of 18 mm in TL (NR, 252 mm TL; R, 234 mm tTL), and this value increased in individuals aged 17 years: 44 mm in TL (NR, 345 mm TL; R, 301 mm tTL).

3.4. *Total fecundity, offspring and maternal fitness*

The fecundity outputs by ontogeny are summarized in Table 1. There were no significant differences between mean values of TF and BF between the NR and R groups ($t > 0.840$, $p > 0.05$). Throughout ontogeny, mean fecundity outputs between NR and R groups showed no significant differences within young-adults. Nevertheless, R old-adults showed lower BF than NR old-adults ($t = 2{,}180$, $p < 0.05$) (Table 1). TF and BF plotted against TL and tTL for NR and R, respectively, showed significant differences between groups (Fig. 6a) ($F > 5.03$, $p < 0.05$), wherein the slope of TF plotted against size was lower in R females than NR females. This difference was greater when TF and BF data were plotted and compared against the ages of the individuals (Fig. 6b) ($F > 180.30$, $p < 0.05$).

4. Discussion

Our study describes a remarkable capacity to withstand sublethal tail loss in *Physiculus cyanostrophus* a fish species not listed in previous reviews of sublethal tissue loss in freshwater or marine ecosystems (Maginnis, 2006; Unguez, 2013).

4.1. *Regenerated individuals in natural populations*

Regenerated individuals represent a large fraction of the population (27.0%). This is a high prevalence of tail loss in a marine species far exceeding the 3.1–15.5% observed in the winter flounder in which the cause is bacterial fin-rot disease (Ziskowski et al., 2008). However, the distribution of regenerated individuals and its importance change within the natural population. Thus, the frequency of R individuals increases throughout ontogeny (16.8–67.5%), whereas females dominate the long-lived fraction of the population. This phenomenon may be because the species studied shows a marked sexual dimorphism, where R or NR females are bigger and more abundant than R or NR males; a common strategy in deep-water species to avoid intraspecific competition for resources (Shine, 1989; Fairbairn, 1997). An important consequence of ontogenetic niche shifts is that a population can

Table 1

Mean values (± standard deviation) and range (minimum-maximum) of total fecundity (TF) and batch fecundity (BF) for non-regenerated (NR) and regenerated (R) individuals of *Physiculus cyanostrophus* in young-adults and old-adults ontogenetic groups. *Significant differences ($p < 0.05$) between bold values.

	young-adults (200 < TL < 300 mm TL)								old-adults (TL > 300 mm TL)							
	Non-regenerated (n = 31)				Regenerated (n = 27)				Non-regenerated (n = 20)				Regenerated (n = 25)			
	Min	Max.	Mean	SD	Min	Max.	Mean	SD	Min	Max.	Mean	SD	Min	Max.	Mean	SD
TF	12,545.19	69,902.06	35,558.39	2993.72	23,700.58	46,756.23	31,143.98	1400.24	33,056.43	137,322.37	65,999.81	5821.83	8320.83	117,309.64	53,907.20	6623.64
BF	2212.05	29,766.23	10,018.10	1080.44	4651.03	14,930.94	9140.64	783.87	8488.68	44,959.84	**18,254.08***	1705.28	1632.03	27,698.11	**12,473.30***	1758.57

potentially be divided into ecologically distinct stages (Olson, 1996). Concerning the subject of ontogeny, early stages and juveniles of our studied species exhibit a pelagic behaviour, in contrast with adults, which are benthopelagic (Okamoto et al., 2007), as has been described in closely related groups, such as macrourids (Bergstad and Gordon, 1994). These differences in ontogenetic niches could explain the absence of regenerated juvenile specimens, because predation is more likely to be lethal.

4.2. *Body losses in caudal region*

The ability to withstand body losses varies with size and is higher in large individuals, which can survive losses of up to 28 vertebrae, equivalent to 45% of total length. However, the capacity to regenerate the caudal zone in our studied species is limited. The balance between body lost length in a sublethal attack and the length of the newly regenerated caudal region shows a limit of maximum recovery of 19% in tTL versus a maximum of 45% of the body lost length. This limited regeneration of the caudal zone could be an adaptive mechanism, as an imperfect or limited regeneration could represent an optimal investment into the regeneration process for the injured animal (see Bely and Nyberg, 2010). This result is in line with those of studies on caudal fin regeneration in fishes (e.g., Fu et al., 2013).

4.3. *Tissue loss allocation cost in growth*

Our results describe a smaller somatic growth in regenerated females than NR females. This statement was achieved through two approaches. On the one hand, a close relationship between otolith mass and age exists (e.g., Boehlert, 1985; Pawson, 1990; Worthington et al., 1995; Cardinale et al., 2000). Taking into account that otolith mass continues to increase throughout the life of an individual, even if somatic growth is small or null (e.g., Fowler and Doherty, 1992; Ashworth et al., 2016), a different context can be considered when comparing regenerated and non-regenerated individuals. We found that predation does not affect the increments in otolith mass with age. Nevertheless, injuries change the growth rate, resulting in the R individuals showing a lower phenotypic growth compared to non-regenerated individuals. On the other hand, estimates of age based on the number of growth increments also reveal differences between R and NR individuals. Our results showed that the youngest R individual was 8 years old. The magnitude and effects of the body loss on growth have a different degree of influence according to the percentage of body lost and the elapsed time from the injury. This can be seen in the disribution of age data. Therefore, the size of R individuals compared to NR individuals depends on the time since the injury, and on the percentage of body loss. When a natural population is studied, the period in which the sublethal attack occurred on individuals is unknown. Therefore, our results indicate that regeneration implies a reduction in long-term growth. The benefit of structure replacement in their lifetime will depend on the age of the animal at injury and its expected longevity (Vitt and Cooper, 1986). The slow growth and long age (18 years) observed in our species compensates for the energy allocation during the regeneration process, since in the long term, it benefits from producing offspring during many seasons.

4.4. *Tissue loss effects in offspring and maternal fitness*

In nature, two well-differentiated strategies can be developed by a species depending on whether natural selection maximizes the maternal or offspring fitness. Species in which evolution has prioritized offspring fitness tends to produce a single, very large offspring (Bernardo, 1996). In contrast, species wherein selection favours maternal fitness tend to have a greater number of offspring with low fitness. The ability of mothers to produce lower quality offspring (selfish maternal effect) does not imply a worsening of maternal fitness, but quite the opposite

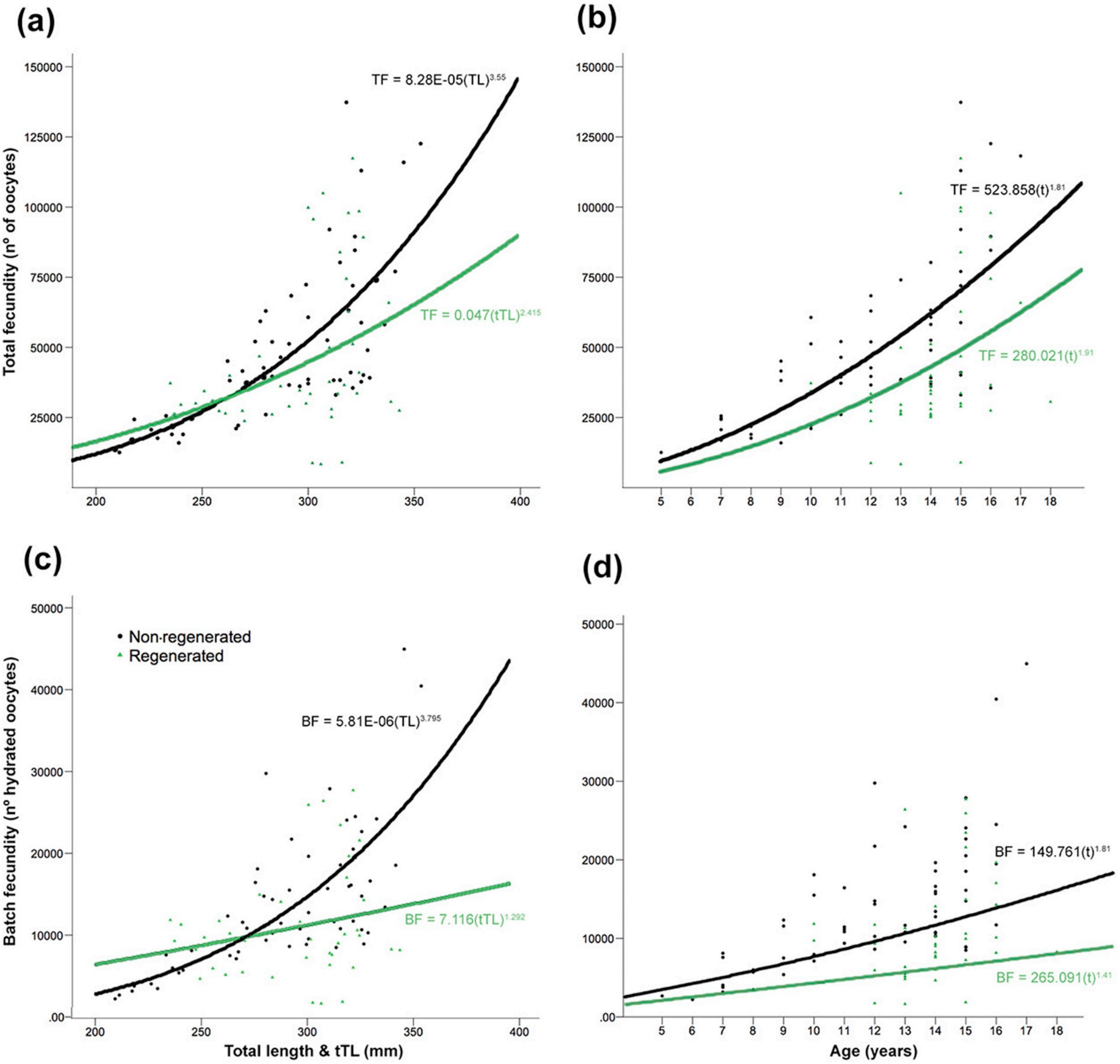

Fig. 6. Power function relationship of total (TF; a and b) and batch fecundity (BF; c and d) between length (a and c) and age (b and d) of *Physiculus cyanostrophus*. Black circles are non-regenerated (NR) individuals, whereas the green triangles are regenerated (R) individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Marshall and Uller, 2007). Our studied species is a batch spawner. This reproductive strategy maximizes maternal fitness and produces numerous smaller offspring (batches). Our comparative results on fecundity outputs between R and NR groups showed no significant differences in mean values. However, across the ontogeny, the R older-adults showed low offspring fitness. Indeed, the slope of the relationship between fecundity or offspring and size for the whole population showed lower values in R individuals. If we add growth as a factor in offspring fitness, these differences become greater. Since there are regenerated individuals with less growth than individuals without regeneration allocations (NR), the ability to regenerate the lost caudal area allows the population to maintain a large number of mothers that contribute significantly to the next generation. It is important to bear in mind that, in this population group (old-adults), a higher frequency of regenerated specimens was found (67.5%). Some authors argued that the contribution of larger females to self-recruitment is significantly greater than the expected on the basis of the relationship between body size and fecundity, indicating that female size has an important maternal effect on traits in their offspring (see Beldade et al., 2012).

Survivorship of R individuals in the population of our studied species, even at the expense of a decrease in offspring, generates a relevant contribution to maternal fitness at the population level. Following Einum and Fleming (2000), selection acts to maximize maternal fitness. Mothers tend to make smaller, more numerous offspring, effectively sacrificing individual offspring fitness for maternal fitness.

4.5. *Loss of the tail*

While it is true that sublethal predation implies an important allocation cost in different groups of metazoans (Alvarado, 2000), it should be noted that the most widespread sublethal predation in teleosts is reduced to scale-eating and fin-nipping specialized predators (e.g., Sazima, 1983; Winemiller, 1990). In this scenario, sublethal predation in fishes has been usually considered as an opportunistic mechanism to keep prey abundant as a rapidly renewable resource for specialized predators (Northcote et al., 1986; Nico and Taphorn, 1988). Our study suggests a well developed capacity of *Physiculus cyanostrophus* to survive following a predator attack. However, the putative predator has not been identified. The loss of the tail and regrowth with a pseudohypural plate suggests the tail loss was traumatic event rather than disease as in the winter flounder (Ziskowski et al., 2008).

Competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2019.06.008.

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IV. General conclusions

Chapter 2

1. The low number of individuals of by-catch species caught confirmed the high selectivity of shrimp traps.
2. The differences found, among archipelagos, in the relative composition of the SSTF catches indicate that the fishing system affects the by-catches in a different way.
3. The archipelagos that showed the greatest differences in by-catch were the Canary Islands and the Cape Verde, i.e. the most exploited and the unexploited marine areas, respectively.
4. The use and development of this kind of selective fishing system makes an important contribution to reducing bycatch and conserving the community and habitat, especially in deep-sea marine ecosystems.

Chapter 3

5. The *Plesionika edwardsii* macroscopic maturity scale known to date based on the morphology of the gonads was revised and modified after histological examination. Only histological images allowed the correct and unambiguous application of maturity scales in genus *Plesionika*.
6. Egg development scale in *Plesionika* species based on the colouration was revealed as wrong. Image analysis was necessary to establish a correct and unambiguous scale, at least for *P. edwardsii*.
7. Size at sexual maturity estimation based on physiological maturity instead of ovigerous condition was more reliable. Size at sexual maturity estimation based on ovigerous condition method could lead to an overestimation of the size at maturity.
8. Differences in reproductive output through different regions also indicated that *P. edwardsii* invests more energy in the production of eggs in Madeira than in the Cape Verde Islands, with females in the latter locality producing smaller eggs.

9. Patterns in life-history traits of *P. edwardsii* showed latitudinal variations. A latitudinal north-south pattern was observed for the three archipelagos studied.
10. This pattern may result as a consequence of the temperature experienced during their development. Temperature induces phenotypic plasticity with size decreasing as temperature increases.
11. The growth strategy of *P. edwardsii* may be the result of a mixture of both forms of latitudinal compensation by adapting to differences in the temperature and length of growing season.
12. Thoracic teeth can be used to determine sex in pandalid shrimps of the genus *Plesionika*. This morphological trait has been ignored across the taxonomy in pandalids.
13. Maturity of *Plesionika* females is linked to the fading of immature thoracic teeth. Thoracic teeth are a valuable tool to determine the first maturity of the *Plesionika* species.

Chapter 4

14. A new species of *Physiculus*, *P. caboverdensis* n. sp., is described from the outer shelf and upper slope of the Cape Verde Islands. This species mainly differs from all other congeners from the Atlantic Ocean by its peculiar dentition.
15. The relative position and size of the light organ among Atlantic species of *Physiculus* are taxonomic tools used for species identification.
16. The ability to withstand body losses in *P.* c*yanostrophus* varies with size and is higher in large individuals, which can survive losses of up to 28 vertebrae, equivalent to 45% of its total length.
17. In *P.* c*yanostrophus,* tissue losses represent a significant allocation of costs in terms of growth and offspring production. Nevertheless, regeneration capability decreases mortality in the large breeding females of a population, maximizing maternal fitness.

V. Resumen en español

Capítulo 1

Introducción general

1.1 Preámbulo

A lo largo de las últimas décadas, la sobrepesca en aguas costeras ha resultado en la expansión de parte de la actividad extractiva hacia aguas más profundas (Morato et al. 2006; Norse et al. 2012; Wehrtmann et al. 2012). El desarrollo sin precedentes de la pesca de profundidad ha provocado una sobreexplotación temprana de diversas especies (Koslow et al. 2000; Roberts 2002). Este hecho ha dirigido el interés de la comunidad científica en lograr y contribuir a la sostenibilidad de las pesquerías de profundidad (Norse et al. 2012). En este sentido, el estudio de los ecosistemas marinos profundos representa un verdadero desafío, debido a que son poco conocidos y vulnerables a la actividad extractiva (Pajuelo et al. 2016). Los camarones de aguas profundas del género *Plesionika* Spence Bate, 1888 son el objetivo principal de algunas pesquerías, tanto comerciales como artesanales, realizadas en el mar Mediterráneo y en islas del Atlántico centro-oriental (González et al. 1992). Es necesario discutir y estudiar en detalle las lagunas que existen sobre el impacto de estas pesquerías y priorizar el estudio del ciclo de vida de las especies sobre las que se desarrolla esta actividad.

La primera parte del núcleo central de la tesis, tiene como objetivo conocer el impacto de la pesca con nasas camaroneras semi-flotantes (SSTF) en los ecosistemas de aguas profundas más someras (100-450 m) (Pajuelo et al. 2018). El estudio se basa en el comportamiento de SSTF en tres archipiélagos del Atlántico centro-este: Madeira, Islas Canarias y Cabo Verde. Se plantea el análisis de la composición de las capturas en relación con las diferentes bio-regiones y características oceanográficas. Se discute la relación entre las capturas accesorias y el grado de explotación humana, abordando uno de los mayores problemas relacionados con la pesca (Wilcox & Donlan 2007). En el Capítulo 2 son presentados los principales actores de la tesis. Las nasas camaroneras semi-flotantes como pesquería a pequeña escala y el método de muestreo exploratorio. Los camarones pandálidos de profundidad (Capítulo 3) representados por *Plesionika edwardsii* (Brandt, 1851), principal especie objetivo del SSTF, y finalmente los móridos (Capítulo 4) representados por el género *Physiculus* Kaup, 1858 como parte de la captura accesoria de SSTF en Cabo Verde.

La segunda parte del núcleo central de tesis, tiene como objetivo conocer los principales rasgos del ciclo de vida de *Plesionika edwardsii*. Se discuten las metodologías que existen en la literatura para describir aspectos de la biología reproductora, con el objetivo de contribuir a una mejor estimación de estos parámetros (Triay-Portella et al. 2017). El estudio sobre los caracteres sexuales secundarios de estas especies concluye con la descripción de una nueva estructura morfológica en el género *Plesionika*. Esta estructura es útil en diferentes campos de estudio, tales como la taxonomía, el comportamiento o las estrategias reproductivas (Triay-Portella et al. 2018). Finalmente, la variación en los rasgos del ciclo de vida de *Plesionika edwardsii* se presentan como un indicador de las tendencias biogeográficas a lo largo de un gradiente latitudinal en tres archipiélagos del Atlántico centro-este (González et al. 2018; Triay-Portella et al. 2018). Desde un punto de vista de gestión pesquera, es esencial conocer la estrategia reproductiva, fecundidad, crecimiento y mortalidad de las especies objetivo para garantizar la sostenibilidad de las poblaciones.

A pesar de que el grupo de los *Physiculus* es el más diverso dentro de la familia Moridae Moreau, 1881 (Paulin 1989), hasta la presente tesis los estudios sobre su ecología son escasos. La última parte del núcleo central de la tesis tiene como objetivo ampliar el conocimiento del género *Physiculus* en el Atlántico, destacando aspectos de su ecología que lo hacen particularmente excepcional. El primer enfoque se basa en un estudio taxonómico, que ha resultado en el descubrimiento de una nueva especie, *Physiculus caboverdensis* n. sp., un endemismo de Cabo Verde (González et al. 2018). Además, los datos morfológicos obtenidos de las especies de *Physiculus* en el Océano Atlántico proporcionan nuevas herramientas de identificación en un grupo poco conocido (presentado por Triay-Portella et al. sometido). Por último, se ha descrito y evaluado la notable capacidad de regenerar la región caudal en *Physiculus cyanostrophus* Anderson y Tweddle, 2002, incluyendo las consecuencias en su dinámica poblacional, crecimiento y *fitness* maternal (Triay-Portella et al. 2019).

1.2 Dimensión espacial: zona de penumbra y archipiélagos del Atlántico centro-este

La presente tesis tiene dos dimensiones espaciales. Desde un punto de vista ecológico la extensión batimétrica, que pertenece al margen continental, cubre aproximadamente de 175 a 500 m de profundidad, el hábitat llamado zona de penumbra o crepuscular. Este hábitat es la frontera entre los ecosistemas mesofóticos y afóticos (batiales). En segundo lugar, una dimensión latitudinal integra tres archipiélagos del Océano Atlántico centro-oriental: Madeira, Islas Canarias y Cabo Verde (Fig. 1).

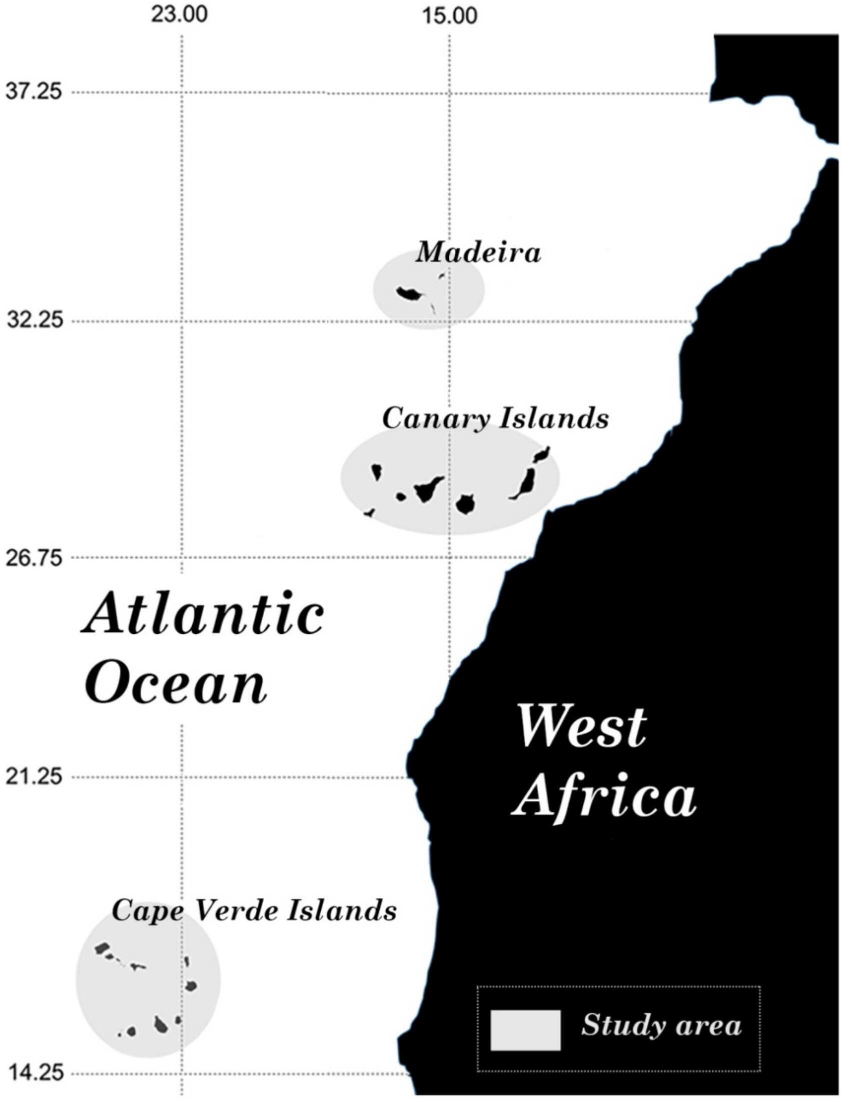

Figura 1. La dimensión latitudinal del trabajo integra tres archipiélagos del Océano Atlántico centro-oriental: Madeira, Islas Canarias y Cabo Verde.

En la zona de penumbra, las especies se adaptan a un entorno de transición entre la luz y la oscuridad (Marshall 1971). En este hábitat, la bioluminiscencia es un recurso utilizado por los organismos para comunicarse, depredar y evitar ser depredados (Herring 1996; Haddock et al. 2010). A estas profundidades, persisten grandes brechas en los aspectos fundamentales del conocimiento ecológico.

La dimensión latitudinal del trabajo se desarrolla a lo largo del Sistema de la Corriente de Canarias, uno de los Grandes Ecosistemas Marinos del Mundo y Cuencas Hidrográficas Vinculadas (LME) en los océanos globales (Sherman & Hempel 2009). Se caracterizan por su singular batimetría, hidrografía y productividad, así como su capacidad para soportar poblaciones marinas que han adatado sus ciclos de vida a estas condiciones (Hernández-León et al. 2007). La región de Madeira está dominada por el sistema de la Corriente de Canarias, que induce un transporte neto hacia el sur (Caldeira & Sangrà 2012). La presencia de una montaña submarina en el extremo sureste de Madeira produce una afluencia insular localizada de aguas frías ricas en nutrientes alrededor de las costas (Caldeira et al. 2002). Las Islas Canarias se caracterizan por la presencia en los primeros 500 m de profundidad del Agua Central del Atlántico Norte Oriental (Hernández-Guerra et al. 2002). Mientras tanto, las aguas de Cabo Verde están bajo la influencia de la contracorriente ecuatorial del norte y la corriente de Canarias. Los patrones de circulación estacional de esta contracorriente muestran principalmente su influencia en la parte sureste del archipiélago (Lázaro et al. 2005).

1.3 Nasas camaroneras semi-flotantes: pesquería y técnica de muestreo

En los últimos años, las pesquerías a pequeña escala (SSF, de sus siglas en inglés), como la pesca del camarón con nasas, se consideran un buen ejemplo para promover la prosperidad de las comunidades pesqueras en el mar Mediterráneo (Kalogirou et al. 2017; Vasilakopoulos et al. 2019) y los archipiélagos del Atlántico centro-oriental (González et al. 1997). Estas pesquerías a menudo se han descrito como más selectivas y sostenibles que la actividad pesquera comercial (Zimmerhackel et al. 2015). Además, SSF se encuentran actualmente en medio de un debate sustantivo dentro de la Unión Europea, debido a la falta y baja calidad de los datos existentes en este sector de la flota (STECF 2018).

Desde 1975, los camarones del género *Plesionika* son objeto de las nasas camaroneras semi-flotantes (NCSF) (Fig. 2) que operaba entre 100 y 500 m de profundidad en todo el Mar Mediterráneo (González et al. 1992; García-Rodríguez et al. 2000). El éxito de estas pesquerías produjo su expansión a los archipiélagos del Atlántico centro-oriental (Santana et al. 1997), donde se desarrolló una pesquería a pequeña escala, en las Azores (Martins & Hargreaves 1991), Archipiélago Canario (González et al. 2001) y Madeira (Sousa et al. 2014). En Cabo Verde, solo se han realizado pescas experimentales, donde las poblaciones y hábitats de aguas profundas permanecen inexplotados.

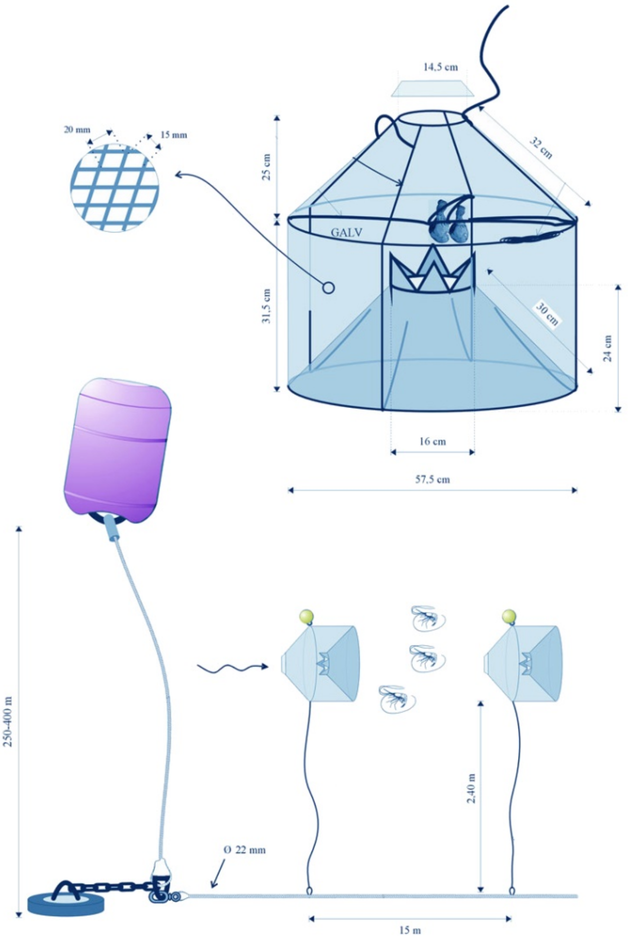

Figure 2. EL tren de nasas camaroneras semi-flotantes (SST) es la técnica de muestreo principal de la presente tesis.

El objetivo del Capítulo 2 es evaluar la composición de las capturas de las pesquerías de camarón soldado con nasas semi-flotantes frente a las costas de Madeira, Islas Canarias y Cabo Verde. Conocer la cantidad y diversidad de las especies que conforman las capturas incidentales y accesorias es relevante para la política pesquera de la Unión Europea, que persigue reducir las capturas (desembarques) de algunos grupos de especies a cero en el horizonte de 2019 (UE 2018). El segundo objetivo del presente capítulo es evaluar el comportamiento del sistema de pesca, a través de sus capturas, a diferentes niveles de explotación del ecosistema.

El impacto ambiental de la pesca de arrastre de fondo en los ecosistemas profundos excede los límites éticos y ecológicos (Thrush & Dayton 2002). Por este motivo, es razonable que la comunidad científica utilice métodos de muestreo respetuosos para estudiar los ecosistemas profundos. Entre los métodos de pesca, las nasas son menos destructivas para los hábitats profundas que los artes de arrastre de fondo (Roberts 2002). Las nasas camaroneras semi-flotantes (SST, de sus siglas en inglés) son la principal técnica de muestreo de la presente tesis. Las nasas están suspendidas 2,4 m por encima del fondo. Se trata de una nasa troncocónica con una longitud de base de 56 cm y una altura de 57 cm, cubierta con una malla de plástico de 15×20 mm. Cada nasa tiene una abertura truncada en forma de cono con un diámetro externo de 23 cm y un diámetro interno de 19 cm (Pajuelo et al. 2018). El arte de pesca consiste en 75 nasa unidas a una línea madre, separadas entre sí cada 15 m. Se utiliza la caballa (*Scomber colias*) como carnada y los tiempos efectivos de pesca rondan las 20 h.

1.4 Camarones de aguas profundas (Pandalidae)

Las especies del género *Plesionik*a juegan un papel ecológico importante en los ecosistemas bentónicos, sus rasgos en el ciclo de vida, como es el caso de *Plesionika edwardsii* (Fig. 3), están adaptados a los ambientes profundos (Carbonell & Abelló 1998; Vafidis et al. 2005). *Plesionika edwardsii* tiene una distribución circuntropical (ausente en el Pacífico oriental) y habita una gran variedad de fondos, entre los que se incluyen fondos de fango, arena, arrecifes rocosos y corales a profundidades entre 110 y 680 m, con mayor frecuencia entre los 250-380 m (González et al. 2001). En el Atlántico oriental, esta especie se ha encontrado desde el suroeste de España hasta Angola, incluidos los archipiélagos de la Macaronesia, Cabo Verde y toda la región mediterránea (García-Rodríguez et al. 2000; González et al. 2001). Las características del ciclo vida de *P. edwardsii*, como son la estrategia reproductora, el crecimiento, la dieta y la mortalidad, se han estudiado en el Pacífico (King & Moffitt 1984; King 1987), el Océano Índico (Intès et al. 1989) y en el Mediterráneo (Cartes 1993a, 1993b; García-Rodríguez et al. 2000; Colloca 2002; Vafidis et al. 2005; Possenti et al. 2007). Sin embargo, la información sobre el crecimiento, la maduración sexual, el desarrollo ovárico y el tamaño de las puestas es escasa en general y deficitaria de las poblaciones atlánticas.

El primer objetivo del tercer capítulo es contribuir al conocimiento en los aspectos reproductivos de *P. edwardsii*, abarcando el desarrollo ovárico y embrionario, estimando el tamaño de las puestas y estableciendo una escala de madurez para la especie en el Atlántico centro-oriental. El segundo objetivo estudia la variación latitudinal de los diferentes parámetros del ciclo de vida de *P. edwardsii*, incluyendo su distribucion batimétyrica y la estructura demografía. El conocimineto de su ecología, junto con el estudio de los cambios a lo largo de un gradiente latitudinal representan valiosas herramientas para su correcta gestión, desde una perspectiva en la que las especies de aguas profundas son vulnerables a la sobrexplotación. Finalmente, se describe y se discute la importancia de una esructura morfológica o carcater sexual secundario, que representa un considerable avance en la ecología del género *Plesionika*.

Figura 3. Captura de *Plesionika edwardsii.*

1.5 Mólleras (Moridae)

Las mólleras se distribuyen en todos los mares tropicales, subtropicales y templados del mundo entre los 100 y 600 m de profundidad (Paulin 1989). Se conocen principalmente desde una perspectiva taxonómica, pero hay pocos datos disponibles sobre su ecología y estructura de población. La mayoría de las especies son muy similares externamente y por tanto difíciles de identificar. Por este motivo, en general son poco conocidos (Paulin 1989; Prokofiev 2006). El género *Physiculus* está representado por 42 especies válidas (Froese & Pauly 2019), 41 según Biscoito & González (2018), distribuidas en todo el mundo, nueve de las cuales se encuentran en el Océano Atlántico. De entre estas, siete ocurren en el Océano Atlántico oriental: *P. cyanostrophus* (Fig. 4); *P. dalwigki* Kaup, 1858; *P. helenaensis* Paulin, 1989; *P. huloti* Poll, 1953; *P. karrerae* Paulin, 1989; *P. maslowskii* Trunov, 1991 y *P. microbarbata* Paulin & Matallanas, 1990.

El primer objetivo del Capítulo 4 es la descripción de una nueva especie, *Physiculus caboverdensis* (Fig. 4), un endemismo de las Islas de Cabo Verde (González et al. 2018). Por otro lado, se realiza un estudio morfométrico y merístico de *Physiculus cyanostrophus* basado en una amplia muestra de individuos. La combinación de estos dos objetivos iniciales se tradujo en la actualización de los rasgos distintivos entre las especies de *Physiculus* presentes en el Océano Atlántico.

A pesar de que la presencia de peces con la cola regenerada, o falsa cola, se ha estudiado poco en los ecosistemas profundos, la presencia de individuos con la región caudal regenerada es un rasgo característico en algunas especies de *Physiculus.* Brüss (1986) describió este hecho por primera vez en *P. marisrubri* Brüss, 1986. Más tarde, algunos autores describieron este fenómeno en otras especies de *Physiculus* (Paulin 1989; Paulin & Matallanas 1990; Prokofiev 2006). La parte final del Capítulo 4, tiene como objetivo describir la extraordinaria capacidad de regeneración en condiciones naturales de *P. cyanostrophus* y evalúa sus efectos a través de los principales rasgos de su ciclo de vida e importancia a nivel poblacional.

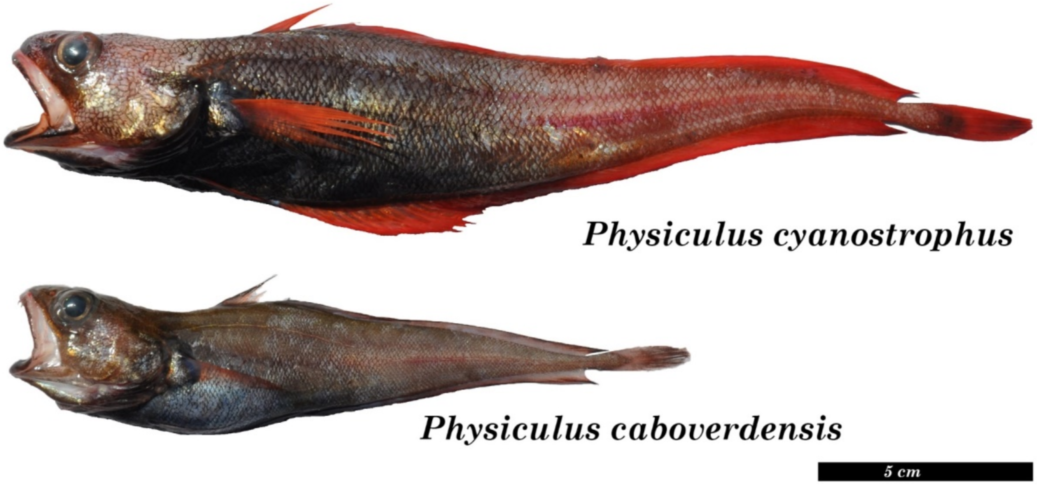

Figura 4. Individuos de *Physiculus cyanostrophus* y *Physiculus caboverdensis*.

1.6 Estructura de la tesis doctoral

La presente tesis, efectuada por compendio de artículos, tiene dos protagonistas principales: *Plesionika edwardsii* y *Physiculus cyanostrophus*. La relación entre ambas especies, más allá del hábitat que comparten, puede resumirse como la especie objetivo de una pesquería artesanal y una de las principales especies accesorias, respectivamente. Por lo tanto, la tesis se estructura en base a esta relación. El segundo capítulo, y primera parte del cuerpo principal de la tesis, está compuesto por un artículo que presenta la pesquería de nasas camaroneras semi-flotante y sus capturas accesorias. El tercer capítulo está compuesto por tres artículos publicados sobre la ecología de *P. edwardsii* en particular y el género *Plesionika* en el Atlántico centro-oriental en general. Del mismo modo, el cuarto capítulo está constituido por tres artículos (dos publicados y otro sometido) sobre la ecología de *P. cyanotrophus* y algunas contribuciones ictiológicas al género *Physiculus* en el Atlántico centro-oriental. Las conclusiones generales se dividen en base a estos tres pilares.

Finalmente, además de este argumento principal, se han desarrollado otros trabajos que han formado parte del proceso de aprendizaje y de integración del candidato en un grupo de investigación consolidado. A pesar de que estas publicaciones no se enmarcan directamente en el contexto lógico de la tesis, en cambio sí comparten un denominador común, los ecosistemas semi-profundos y profundos. Se han incluido nueve artículos publicados como sección VII. La intención es proporcionar una visión más amplia y detallada sobre las contribuciones realizadas durante el aprendizaje pre-doctoral en lo relativo a especies de crustáceos y peces del Atlántico centro-oriental. Estas contribuciones pueden clasificarse en tres grandes bloques. Un primer bloque englobaría las contribuciones al conocimiento sobre la biodiversidad de los ecosistemas marinos en los archipiélagos de la Macaronesia y Cabo verde (Artículos; Sección VII, Art. 9, 10, 11, 13 & 16). Un segundo bloque aunaría los trabajos referidos a la distribución espacial y abundancia de algunas especies de crustáceos decápodos en los ecosistemas profundos de Canarias y su relación con la existencia de cañones submarinos (Artículos; Sección VII, Art. 8 & 12). Por último, las contribuciones a la ecología de dos especies de crustáceos de aguas profundas (Artículos; Sección VII, Art. 14 & 15).

Conclusiones generales

Capítulo 2

1. El bajo número de individuos capturados considerados como especies accesorias confirmó la alta selectividad de las nasas camaroneras semi-flotantes (SSTF, de sus siglas en inglés).
2. Las diferencias encontradas en la composición relativa de las capturas de SSTF indican que el sistema de pesca afecta a las capturas accesorias de una manera diferente en cada archipiélago.
3. Los archipiélagos que mostraron mayores diferencias en la captura accesoria fueron las Islas Canarias y Cabo Verde, es decir, las áreas marinas con mayor presión pesquera y no explotadas, respectivamente.
4. El uso y desarrollo de este tipo de sistemas de pesca selectivos hacen una contribución importante en la reducción de las capturas accesorio, conservación de las comunidades y hábitats, especialmente en los ecosistemas marinos de aguas profundas.

Capítulo 3

5. La escala de madurez macroscópica para *Plesionika edwardsii* se revisó y se modificó después de un examen histológico. Sólo las imágenes histológicas permitieron la aplicación correcta e inequívoca de las escalas de madurez macroscópica en el género *Plesionika*.
6. Las escalas de desarrollo embrionaria en especies de *Plesionika* que se basan en la coloración de las cargas ovígeras son poco precisas. El análisis a través de imágenes es necesario para establecer una escala correcta e inequívoca, al menos para *P. edwardsii*.
7. La estimación de la talla de primera madurez sexual basada en la madurez fisiológica es más precisa. La estimación de la talla de primera madurez sexual basada en el método de la condición ovígera podría conducir a una sobreestimación del tamaño en la madurez sexual.
8. Las diferencias en la fecundidad para las diferentes regiones indicaron que *P. edwardsii* invierte más energía en la producción de huevos en Madeira que en

las Islas de Cabo Verde, además las hembras de Cabo Verde producen huevos más pequeños.

9. Los parámetros estudiados en los ciclos de vida de *P. edwardsii* mostraron cambios latitudinales. Se observó un patrón latitudinal norte-sur para los tres archipiélagos estudiados.
10. Este patrón puede ser debido a la temperatura experimentada durante su desarrollo. La temperatura induce plasticidad fenotípica, el tamaño de los ejemplares de una población es menor a medida que aumenta la temperatura.
11. La estrategia de crecimiento de *P. edwardsii* puede ser el resultado de la mezcla de dos factores, la adaptación a la temperatura con un marcado gradiente longitudinal y la duración de las épocas de mayor crecimiento.
12. Los dientes torácicos pueden utilizarse para determinar el sexo en los camarones pandálidos del género *Plesionika*. Este carácter morfológico ha sido ignorado a lo largo de los estudios taxonómicos en pandálidos.
13. La madurez sexual de las hembras de *Plesionika* está relacionada con la desaparición de los dientes torácicos inmaduros. Los dientes torácicos son una herramienta valiosa para determinar la talla de primera madurez fisiológica en las hembras del género *Plesionika*.

Capítulo 4

14. Se describe una nueva especie de *Physiculus*, *P. caboverdensis* González, Triay-Portella & Biscoito, 2019, presente desde la plataforma exterior hasta el talud superior de las islas de Cabo Verde. Esta especie se diferencia de todos los demás congéneres del Océano Atlántico por su peculiar dentición.
15. La posición y tamaño relativos del órgano luminoso de las especies de *Physiculus* del Atlántico es una herramienta taxonómica útil para su correcta identificación.
16. La capacidad de soportar pérdidas de masa corporal en *Physiculus cyanostrophus* varía según el tamaño de los ejemplares, los ejemplares mayores son los que presentan mayores pérdidas, estos pueden sobrevivir a la pérdida de 28 vértebras en la región caudal, equivalente a la pérdida del 45% de la longitud total.

17. En *P. cyanostrophus*, la pérdida de tejidos representa la asignación de costes en términos de fecundidad y crecimiento. Sin embargo, la capacidad de regenerar la región caudal contribuye a disminuir la mortalidad en las grandes hembras reproductoras, maximizando el *fitness* maternal.

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VII. Other contributions in the doctoral learning process

Other contributions in the doctoral learning process

Despite they do not fall within main scope of this thesis, these nine published articles have also been included as other contributions to provide a broader and deeper view about research on deep-sea species in the Eastern Central Atlantic. These contributions have been obtained during the same period as it is not possible to separate the different components that are obtained during the same research surveys on deep-water species. (In reverse chronological order of publication)

(Article 8) Triay-Portella, R., Pajuelo, J.G. & González, J.A. (2017). Spatio-temporal variation in biomass of the deep-sea red crab *Chaceon affinis* in Gran Canaria Island (Canary Islands, Eastern-Central Atlantic). *Marine Ecology*, 38(5), e12462.

(**Article 9**) González, J.A., **Triay-Portella, R**., Martins, A. & Lopes, E. (2017). Checklist of brachyuran crabs (Crustacea: Decapoda) from the Cape Verde Islands, with a biogeographic comparison with the Canary Islands (Eastern Atlantic). *Cahiers de Biologie Marine*, 58, 137–51.

(**Article 10**) González, J.A., **Triay-Portella, R**., Santana, J.I., Correia, S., Monteiro, C. & Martins, A. (2017). Three new decapods (Aristeidae, Chirostylidae, Pandalidae) from the Cape Verde Islands (NE Atlantic). *Crustaceana*, 90(3), 349–358.

(**Article 11**) González, J.A., **Triay-Portella, R**. & Santana, J.I. (2016). Southernmost record of *Spongiocaris koehleri* (Decapoda, Stenopodidea, Spongicolidae) off the Canary Islands. *Crustaceana*, 89(10), 1233–1238.

(**Article 12**) Pajuelo, J.G., **Triay-Portella, R**., Santana, J.I. & González, J.A. (2015). The community of deep-sea decapod crustaceans between 175 and 2600 m in submarine canyons of a volcanic oceanic island (central-eastern Atlantic). *Deep-Sea Research Part I: Oceanographic Research Papers*, 105, 83–95.

(**Article 13**) González, J.A., González-Jiménez, J.F., **Triay-Portella, R**., Jiménez, S., González-Lorenzo, G. & Biscoito, M. (2016). On the presence of *Trachinus pellegrini* (Trachinidae) in the Canary and Cape Verde Islands (north-eastern Atlantic). *Cybium*, 40(2), 173–177.

(**Article 14**) Biscoito, M., Freitas, M., Pajuelo, J.G., **Triay-Portella, R**., Santana, J.I., Costa, A.L., Delgado, J. & González, J.A., (2015). Sex-structure, depth distribution, intermoult period and reproductive pattern of the deep-sea red crab *Chaceon affinis* (Brachyura, Geryonidae) in two populations in the north-eastern Atlantic. *Deep-Sea Research Part I: Oceanographic Research Papers*, 95, 99–114.

(**Article 15**) **Triay-Portella, R**., González, J.A., Santana, J.I., García-Martín, V., Romero, M., Jiménez-Martín, S., Hernández-Castro, D. & Pajuelo, J.G. (2014). Reproductive pattern and egg development of the deep-sea crab *Paromola cuvieri* (Brachyura, Homolidae) around the Canary Islands (NE Atlantic). *Deep-Sea Research Part I: Oceanographic Research Papers*, 85, 1–14.

(**Article 16**) González, J.A., Martins, A., Santana, J.I., **Triay-Portella, R**., Monteiro, C., García-Martín, V., Jiménez, S., González-Lorenzo, G., Pajuelo, J.G., Lorenzo, J.M. & Biscoito, M. (2014). New and rare records of teleost fishes from the Cape Verde Islands (eastern-central Atlantic Ocean). *Cybium*, 38(4), 289–300.

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ORIGINAL ARTICLE

WILEY marine ecology

Spatio-temporal variation in biomass of the deep-sea red crab *Chaceon affinis* in Gran Canaria Island (Canary Islands, Eastern-Central Atlantic)

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Abstract

The spatial and temporal biomass distribution of *Chaceon affinis* and its vulnerability to fishing activity in Gran Canaria (Canary Islands) were investigated. The first goal was to assess the influence of the slope steepness and substrate on the size of crab patches, size of the crabs, and crab biomass. The second goal was to evaluate spatial and temporal variation in the biomass over a 15-month period. The last goal was to assess the influence of fishing activity upon the reduction in the biomass over the same 15-month period. Only two or three locations in the sampling area generated high-biomass contour patches. When these patches were superimposed on the isobath lines, they were coincident with the main depth range described for the species in the area. The map of the biomass values clearly showed three structures with cores of the highest biomass in both muddy and rocky-muddy areas. The biomass was higher on muddy than on rocky-muddy bottoms. Biomass was twice as high when steepness was reduced to one third between isobaths of 500 and 900 m. The size of crab patches increases linearly with the decrease in slope steepness. The spatial structure of crabs remained fairly stable over time, showing that biomass changes with depth over time. Maps of the estimated biomass values over the 15-month period showed the same two main patches over time with the cores of highest biomass separated by a distance of between 4.2 and 4.5 km. Although the bathymetric distribution by sexes showed temporal changes, with a displacement to deeper areas made by both sexes over the studied period, only a partial temporal segregation between males and females was observed. During the study period, crabs underwent a significant decline in biomass and this was consistent with the combined catches of both commercial and experimental fishing in the area. Due to its low mobility, *C. affinis* is highly vulnerable to local depletion by intensive fishing efforts.

KEYWORDS
biomass, *Chaceon affinis*, deep-sea red crab, spatio-temporal variation

1 | INTRODUCTION

In recent years, the importance of spatial data for understanding the dynamics and ecology of marine resource populations has been increasing due to recognition of the risks of ignoring the spatial structure of exploited populations (Ciannelli, Fauchald, Chan, Agostini, & Dingsor, 2008; Pelletier & Mahevas, 2005; Punt, 2003). Specifically, there has been an increasing interest in understanding the ecological mechanisms responsible for species' distributions (Castrejón, Pérez-Castañeda, & Defeo, 2005). In this regard, geostatistics has become a powerful tool for modeling and estimation of spatial patterns (Castrejón et al., 2005; Rossi, Mulla, Journel, & Franz, 1992). Distribution data along the same isobath are generally obtained at the macroscale (>100 km; Gutiérrez, Masello, Uscudun, & Defeo, 2011; Jensen & Miller, 2005; Rufino, Maynou, Abelló, Gil de Sola, & Yule, 2005; Rufino, Maynou, Abelló, & Sarda, 2006) or mesoscale (10–100 km; Castrejón et al., 2005; González-Gurriarán, Freire, & Fernández, 1993; Maynou, 1998; Rufino, Maynou, Abelló, & Yule, 2004; Rufino, Maynou, Abelló, Yule, & de Sola, 2006), but data at smaller scales (<10 km) are scant (Defeo & Rueda, 2002; Freire, Fernández, Muiño, & González-Gurriarán, 1993; Ríos-Lara, Salas, Bello-Pineda, & Ayora, 2007). Studies on the changes of species' spatial distribution patterns over time are less common (Jensen & Miller, 2005; Rufino, Maynou, Abelló, Yule et al., 2006). Spatial distributions change over a range of spatial and temporal scales and because of the inter-play among the physical environment and ecological and behavioral interactions (Ciannelli et al., 2008; Mann & Lazier, 1991; Wiens, 1989). While on a macro-scale the ocean's physical conditions limit the habitat of an organism, the small-scale distribution may be determined by biotic factors, such as competition and predation, or by abiotic conditions such as substrate type (Ciannelli et al., 2008). Small-scale data of species' distributions are fundamental to understand the spatial patterns related to the type of substrate; this is because in studies conducted at the macro- or mesoscale, the type of substrate is usually not homogeneous and it is not possible to observe the substrate-related pattern (Ríos-Lara et al., 2007; Rufino et al., 2004). The relationships between spatial patterns and ecological processes over a range of spatial scales is one of the most important research topics and most unsolved problems in ecology (Steinhardt & Volk, 2003).

The spatial distribution of geryonid crabs through their bathymetric range is heterogeneous and dependent on many factors such as the type of the bottom, oceanographic conditions, spawning migrations or agonistic intra- and inter-specific competition (Beyers & Wilke, 1980; Haefner & Musick, 1974; Melville-Smith, 1988). Deep-sea red crabs are slow-growing, long-lived animals restricted to low temperatures at 300–1,500 m depth, and reach maturity at 5–15 years (Hines, 1990; Steimle, Zetlin, & Chang, 2001; Wahle, Bergeron, Chute, Jacobson, & Chen, 2008). These features, combined with very irregular and aperiodic recruitment pulses (Steimle et al., 2001), result in high variability in stock sizes and high susceptibility to overexploitation. Species of the genus *Chaceon* support fisheries of high commercial value (Defeo, Little, & Barea, 1991; Guerrero & Araña, 2009; Steimle et al., 2001; Wahle et al., 2008) and some have shown signs of overexploitation or depletion during recent years (Robinson, 2008). A biomass reduction of the *Chaceon maritae* (Manning & Holthuis, 1981) population of Southwestern Africa was described by Melville-Smith (1988). Additionally, a drastic depletion of the *Chaceon fenneri* (Manning & Holthuis, 1984) populations of the South Atlantic Bight and the Gulf of Mexico was reported by Armstrong (1990). Similar patterns of depletion have also been described for *Chaceon* populations in other areas (Hastie, 1995). Vulnerability to fishing activity increases with the aggregation process and with a reduction in species' displacements (Holt, Jones, Hawkins, & Hartnoll, 1995; Tyler-Walters, Hiscock, Lear, & Jackson, 2001). Knowing the species' spatial distribution, their biological characteristics and the magnitude of their spatio-temporal variation permits the determination of their degree of vulnerability. Additionally, biomass maps derived from a time series of data permit the examination of potential changes in habitat use and aggregation through time (Jensen & Miller, 2005).

The Canary Islands are located in the Canary Current System, which is one of the Large Marine Ecosystems of the world (Sherman & Hempel, 2008), characterized by their singular bathymetry, hydrography, productivity and their ability to support marine populations, which have adapted their feeding, reproductive and growth strategies to this specific locations (Hernández-León, Gómez, & Arístegui, 2007). Hydrologically, this archipelago is characterized by the presence of three water masses in the first 1,000 m depth, the Eastern North Atlantic Central Water (ENACW), the Antarctic Intermediate Water (AIW) and the Mediterranean Water (MW), which are located at different depths and have characteristic thermohaline properties (Fraile-Núñez et al., 2010; Hernández-Guerra et al., 2002; Machín, Hernández-Guerra, & Pelegrí, 2006). The start of the lower thermocline and the end of the ENACW occur at a depth of approximately 700 m (Hernández-Guerra, López-Laatzen, Machín, de Armas, & Pelegrí, 2001; Machín et al., 2006). Deep waters between 700 and 1,000 m are characterized by the AIW and the MW, the latter of which extends up to 2,000 m depth (Hernández-Guerra et al., 2001; Machín et al., 2006). These changes in temperature and salinity with depth result in the presence of thermal and density barriers that affect the vertical distribution of decapods (Pajuelo, Triay-Portella, Santana, & González, 2015). In addition, the Canary Islands are biogeographically included in the Azores-Madeira-Canaries ecoregion, within the Lusitanian province of the Temperate Northern Atlantic realm (Spalding et al., 2007).

The deep-sea red crab *Chaceon affinis* (A. Milne-Edwards & Bouvier, 1894) is distributed in waters of the Northeastern Atlantic Ocean from Iceland to Senegal, including all of the Macaronesian islands (Biscoito et al., 2015; Manning & Holthuis, 1981). The burrowing behavior of geryonids has been described by Attrill, Hartnoll, and Rice (1991) and specifically observed for *C. affinis* (Biscoito et al., 2015). Off the coast of Gran Canaria Island (Canary Islands, Northwest Africa), the population of *C. affinis* is near-pristine natural condition. However, in recent years a small-scale deep crab fishery started (Biscoito et al., 2015). This fishery uses strings of rectangular-based trunco-pyramidal crab traps, has only one fishing vessel exploiting the resource, has an absence of reliable landing statistics, has no regulation measures, and there is a lack of knowledge on its population biomass. Through mark and recapture experiments, Biscoito et al. (2015) indicated that this species remained in the same area over time for at least 3 years. This population of *C. affinis* is considered an ideal case for the application of a geostatistics approach to studying its spatio-temporal patterns due to its low mobility, burrowing behavior and the pristine level of this population.

Geostatistics is a set of techniques focused on the modelling of spatio-temporal patterns inherent to a particular species (Matheron, 1971; Rossi et al., 1992). This information is used to estimate maps of density or biomass (Lembo, Silecchia, Carbonara, Acrivulis, &

Spedicato, 1999; Petitgas, 1993, 2001), and these maps (over time) provide an insight into biomass and/or density changes. Geostatistics is used to evaluate spatial management measures and to improve stock assessment to avoid overexploitation (Addis et al., 2009; Castrejón et al., 2005; Jansen et al., 2016; Moura & Fernandes, 2009) .

The main goals of this work are to estimate the spatial and temporal biomass distribution of the deep-sea red crab *C. affinis* and its vulnerability to fishing activity in Gran Canaria Island (Canary Islands, Eastern-Central Atlantic). The specific goals are to evaluate in Gran Canaria Island: (i) the influence of the muddy and rocky-muddy substrata on the size of crab patches, size of the crabs, and crab biomass; (ii) the influence of the slope steepness on the size of patches and the biomass; (iii) the spatial and temporal variation in the biomass, as a whole and by sex, in the same area; and (iv) the influence of fishing activity on the observed reduction in the biomass.

2 | MATERIAL AND METHODS

2.1 | Sampling areas, surveys and sampling procedure

Three areas, designed as South 1, South 2 and East, were selected off Gran Canaria to assess the spatial and temporal variation in the biomass of *Chaceon affinis* between the isobaths of the species' maximum abundance, at 500–900 m (Biscoito et al., 2015; Figure 1). The selected areas were small portions (between 0.49% and 3.10%) of the total island slope, which is situated approximately parallel to the coastline (Figure 1). The South 1 area has dimensions of 1.37 × 3.56 km with muddy substrate and a slope steepness of 37.26° (Figure 1). The South 2 area is 1.86 × 3.60 km with rocky-muddy substrate (slope steepness = 36.93°; Figure 1). The East area is 4.25 × 6.75 km with gently sloping muddy substrate (slope steepness = 12.28°; Figure 1). The specific dimensions for the selected areas were chosen based on the largest areas with homogeneous substrate excluding submarine canyons. The substrate in each area was determined by multibeam echo-sounding. In these areas, five research cruises were conducted to perform two experiments with different sampling designs to assess the spatial and temporal variation in the biomass of the *C. affinis* population at a small scale (<10 km). The cruises conducted were: Chace 1 (23–31 July 2010), Chace 2 (3–11 September 2010), Chace 3 (7–15 March 2011), Chace 4 (3–11 December 2011) and Chace 5 (20–28 July 2012). Two replicates of 360 samples were developed for both South 1 and South 2 areas in July 2010 and July 2012, and three replicates of 620 samples in the East area in September 2010, March 2011 and December 2011 (Figure 2).

The sampling gear used during the five research cruises was a rectangular-based trunco-pyramidal crab trap with a bottom base of 1.15 × 0.80 m, a top base of 1.15 × 0.70 m, 0.50 m in height and covered with a 15 × 15 mm metallic mesh. Each trap had one trunco-conical opening with a 23 cm outer and 19 cm inner diameter. Traps were deployed parallel to the coastline in strings of 20 traps and equally spaced (100 m) along the length of each fishing rope. Standard immersion times ranged from 44 to 46 h with Spanish mackerel (*Scomber colias*) used as bait. The radius of influence used to provide biomass estimates was 30 m. This radius has been considered reliable for the assessment of geryonid crabs (Gutiérrez et al., 2011; McElman & Elner, 1982; Melville-Smith, 1986, 1988; Stone & Bailey, 1980) and for *C. affinis* in particular (González et al., 1998). Each trap was georeferenced (latitude–longitude) by global positioning system using a urchin tracking module projection. The total carapace width (mm), total wet weight (g), sex and ovigerous condition of each crab were recorded for each line of the traps. The biomass was calculated by considering the population of individuals with a carapace width larger than 50 mm as vulnerable to trapping. Data on the salinity and temperature 0.5 m above the sea floor were recorded using a CTD sensor for each string of traps.

2.2 | Sampling design and analysis

The goal of the first sampling design was to assess the influence of the habitat (substrate or slope) on the biomass of *Chaceon affinis* aggregations. To evaluate the influence of the substrate (muddy versus

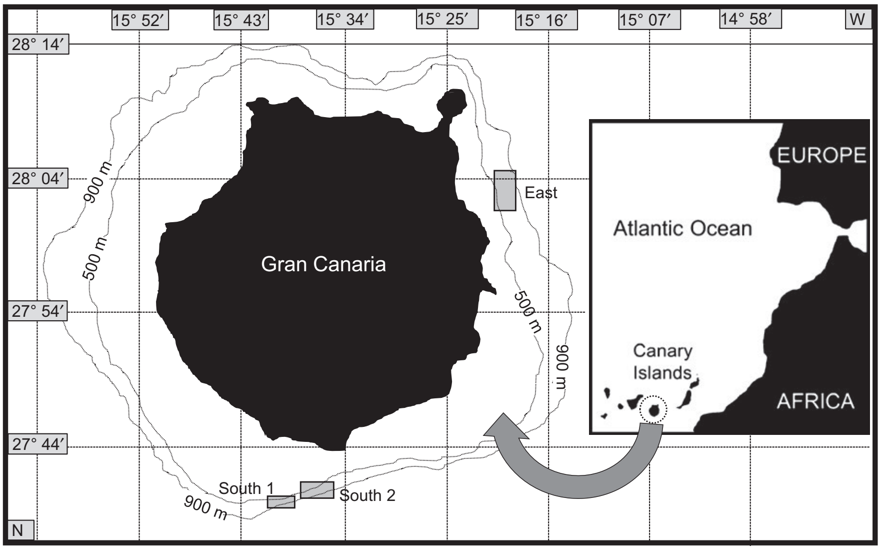

FIGURE 1 Sampling areas off Gran Canaria Island, Canary Islands. South 1, muddy area with steep slope; South 2, rocky-muddy area with steep slope; East, muddy area with gentle slope

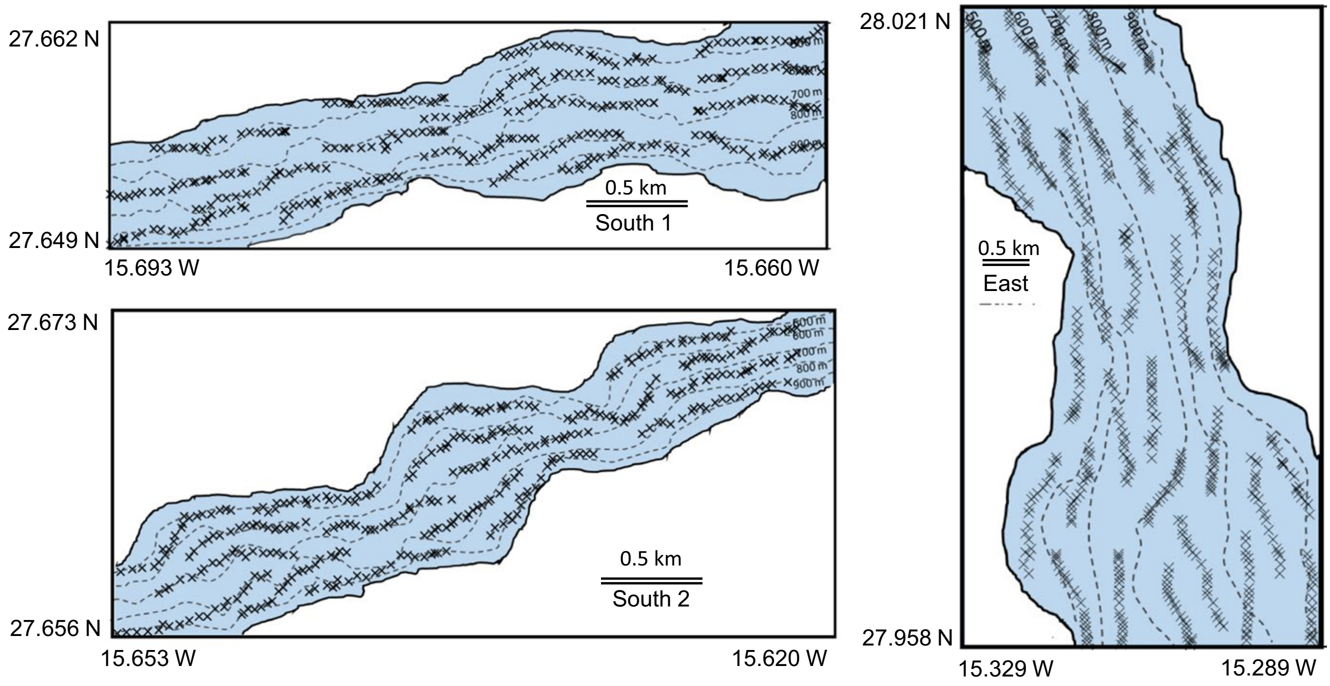

FIGURE 2 Selected areas with positions of crab trap strings used for collecting *Chaceon affinis*. South 1, muddy area with steep slope; South 2, rocky-muddy area with steep slope; East, muddy area with gentle slope

rocky-muddy), data from the two replicates of the South 1 and South 2 areas, taken in July 2010 and July 2012, were examined by means of geostatistical analysis. A Student's *t*-test was used to evaluate the null hypothesis of equality in mean size of the patches and equality in mean biomass between steep muddy and steep rocky-muddy substrata, as well as between replicates for the same substrate type (*H*0: $\mu_1 = \mu_2$) with a significance level of 5% ($\alpha = 0.05$) and a critical value of $t_{0.05,<10} = 2.228$. Differences in carapace width distribution between substrata were analysed using a Kolmogorov–Smirnov nonparametric *Z*-test. This test evaluated the null hypothesis of equality in carapace width distribution between substrata (*H*0: $F_1[x] = F_2[x]$) with a significance level of 5% ($\alpha = 0.05$) and a critical value of $Z_{0.05} = 1.96$ (Sachs, 1982; Sokal & Rohlf, 2012). To assess the influence of the slope (gender versus steep) on the biomass, data from South 1 (July 2010) and East (September 2010) areas were examined by means of geostatistical analysis. A *t*-test was used to test differences in mean size of the patches and mean biomass between steep muddy and gentle muddy substrata.

The aim of the second sampling design was to assess the spatial and bathymetric variation in the biomass of *C. affinis* with time, and the influence of fishing activity on the species' biomass. For these goals, data from the three replicates in the East area, taken in September 2010, March 2011 and December 2011, were analysed, as a whole and by sex, by means of geostatistical analysis.

The size of the patches and biomass over time in the gentle slope muddy substrate were compared with an analysis of variance (ANOVA). This analysis was used to evaluate the null hypothesis of equality in size of the patches and biomass over time (*H*0: $\mu_1 = \mu_2 = \ldots = \mu_n$), with a significance level of 5% ($\alpha = 0.05$) and a critical value of $F_{0.05,2,<20} = 3.49$. Correlations between temperature or salinity with the size distribution of crabs and with the weight of catches were examined using the Spearman's correlation test. The impact of the fishery on the species' biomass was assessed following the fishing activity developed in the East area by a professional fisherman, operating an average of two fishing trips with traps per month during the same 15-month period. The traps used by the fisherman were similar to those used in the present study. The data from both commercial and experimental catches were used to evaluate the impact of the fishery.

A geostatistical tool, formed by a set of statistical techniques, was applied to detect, model and estimate the spatial distribution of the crab species using GS+ version 9 software (Robertson, 2008). Geostatistical analysis is generally undertaken using two techniques, the variographic and the kriging methods (Rossi et al., 1992). The variographic technique is a structural analysis in which the spatial correlation among the observations is modeled using a function named a semivariogram (Robertson, 1987). The kriging technique uses the model estimated in the variographic stage to provide estimates for unmeasured points (Robertson, 1987; Petitgas, 2001). These data are used to estimate maps of densities or biomasses, and also to estimate biomasses or abundances in an area (Maynou, Sardà, & Conan, 1998; Simard, Legendre, Lavoie, & Marcotte, 1992).

The analyses were applied to georeferenced data of the biomass (in kg km^{-2}) of *C. affinis*. The data were square-root-transformed to fulfil normality requirements and back-transformed for mapping purposes (Robertson, 2008). The semivariogram $\gamma(h)$, which is a form of computing the variance of a population and considers the spatial position of the samples, was estimated according to Matheron (1971) as $\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} (Z(x_i + h) - Z(x_i))^2$, where $Z(x_i)$ is the biomass of

C. affinis at location x_i; $Z(x_i+h)$ is the biomass of *C. affinis* at location x_j, which is within distance h of location x_i; and N(h) is the number of pairs of observations used to compute the experimental semivariogram separated by h. Anisotropy was checked by constructing directional variograms. Theoretical models (spherical, exponential, Gaussian and linear) were fitted to the experimental semivariograms. The semivariogram is defined by three parameters, namely the nugget (C_0), the sill (C_0+C) and the range (A_0). The nugget is a discontinuity at the origin of the semivariogram due to small-scale spatial phenomena and can be attributed to measurement errors, white noise, microscale variability or/and small-scale spatial structure (Cressie, 1991; Matheron, 1971; Maynou, 1998). The sill can be defined as the maximum variability point beyond which the semivariance values become asymptotic, and the range represents the distance within which the data remain autocorrelated (Maynou, 1998; Maynou et al., 1998). The proportion of variance explained by the spatially structured component [$C/(C_0+C)$], the co-efficient of determination (r^2), and the residual sum of squares (RSS) were defined as the criteria with which to determine the goodness of fit (Cressie, 1991; Robertson, 2008).

A punctual kriging analysis was used to estimate the biomass at the locations not sampled and obtain a cartography of the crabs by means of bidimensional biomass maps estimated using the experimental semivariogram parameters of the selected model (Castrejón et al., 2005; Maynou, 1998). The expected biomass among the stations was estimated following Matheron (1971) and Cressie (1991). Block kriging was used to produce global estimates of the total and mean biomass over the three areas studied (Matheron, 1971; Maynou et al., 1998).

The appropriateness of the models fitted in the variographic analysis and kriging interpolations was evaluated through jack-knife cross-validation, which sequentially excludes one sampling point and uses the remaining data to estimate it (Addis et al., 2009; Isaaks & Srivastava, 1989). The observed and estimated biomass values were fitted to a linear regression (Addis et al., 2009; Castrejón et al., 2005). Departures from a one-to-one line through the origin indicate model inadequacy, and differences between the estimated and hypothetical regression co-efficient (b = 1) and axis intercept (a = 0) were tested by a Student's t-test (Sachs, 1982). The kriging analysis was implemented with the geostatistics software GS+ version 9 (Gamma Design Software; Robertson, 2008).

3 | RESULTS

3.1 | Habitat substrate: muddy versus rocky-muddy area

The map of the biomass values estimated by the punctual kriging technique clearly showed three structures with cores of the highest biomass in both muddy (South 1; Figure 3) and rocky-muddy areas (South 2; Figure 4) in July 2010 and July 2012. In the muddy area (South 1), patches showed maximum diameters of 0.58–0.82 km with a mean size of 0.71 km during both periods. In the rocky-muddy area (South 2), patches presented maximum diameters of 0.51–0.66 km with a mean size of 0.56 km. The t-test showed significant differences in mean size of the maximum diameter between the patches of muddy and rocky-muddy areas (t = 3.32, p = .0077), with higher values (27%) for the muddy area.

Mean biomass values in both periods were higher in the muddy area (South 1) than in the rocky-muddy area (South 2) (Figure 5). The

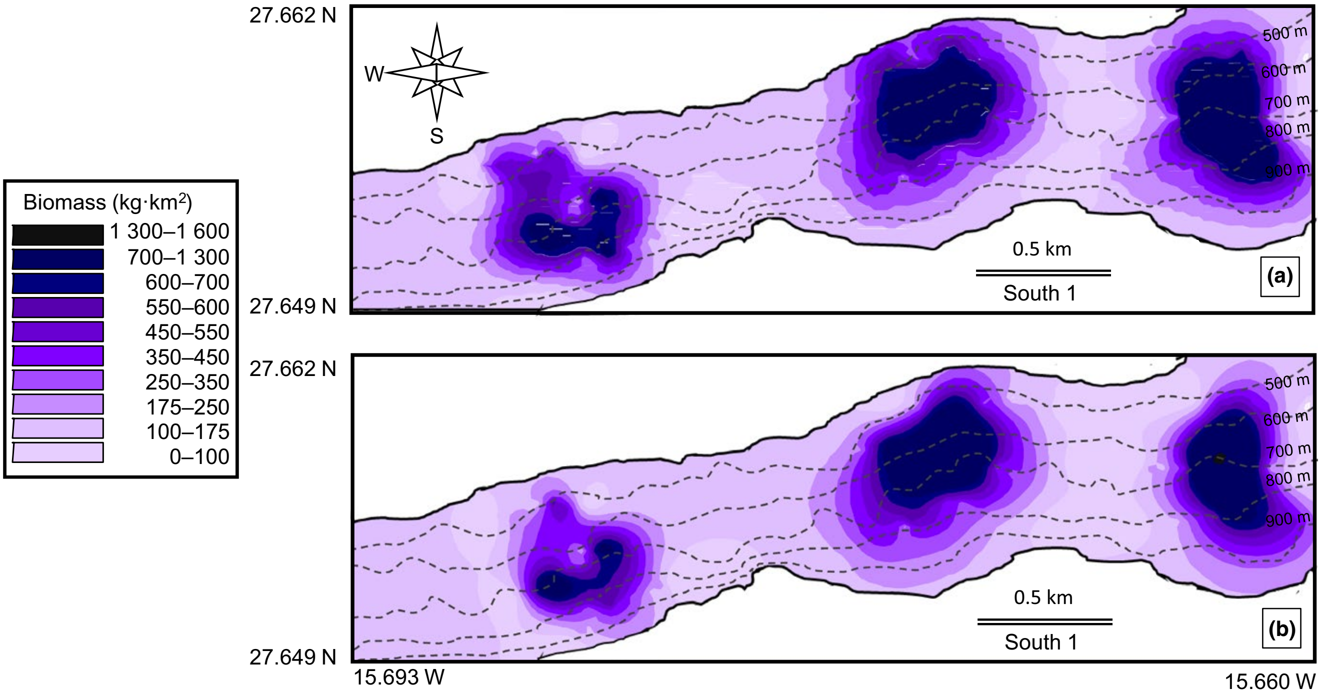

FIGURE 3 Spatial distribution of the biomass of *Chaceon affinis* (kg km^{-2}) off Gran Canaria Island on muddy bottoms with steep slope (South 1) in (a): July 2010 and (b): July 2012

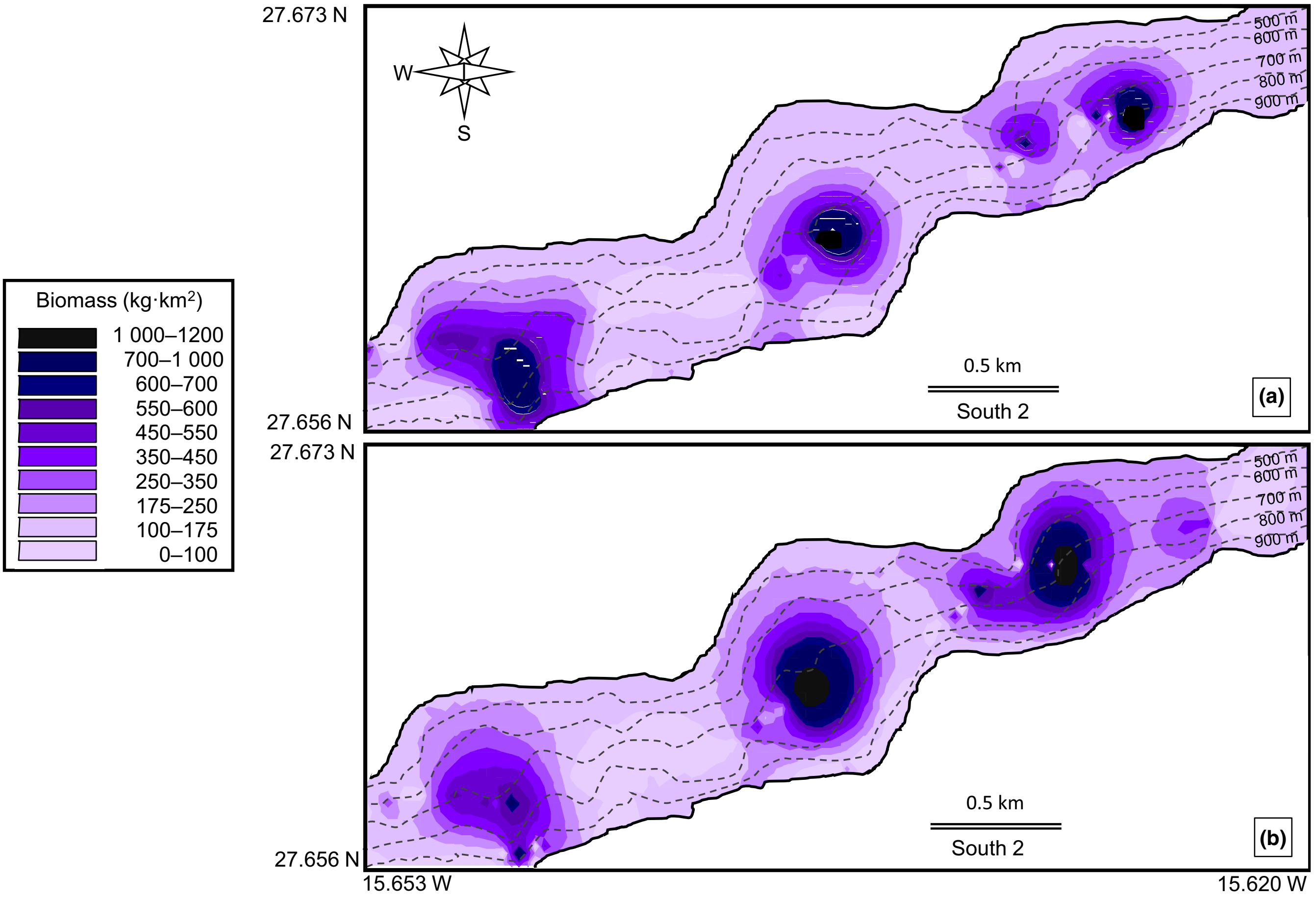

FIGURE 4 Spatial distribution of the biomass of *Chaceon affinis* (kg km^{-2}) off Gran Canaria Island on rocky-muddy bottoms with a steep slope (South 2) in (a): July 2010 and (b): July 2012

t-test showed significant differences in the mean biomass in both periods between muddy and rocky-muddy areas ($t > 19.24$, $p < .0001$) with higher (>65%) values observed in the muddy area. A Student's *t*-test also showed no significant differences in the estimated mean biomasses between July 2010 and July 2012 for both areas ($t < 1.92$, $p > .0562$). It can be also observed that the highest values of biomass in the rocky-muddy area (South 2) are located at greater depth than in the muddy area (South 1). The *Z*-test showed significant differences in carapace width distribution between areas ($Z = 1.44$, $p = .032$). In the muddy area (South 1) the three patches observed revealed different biomass distributions with depth. One patch showed higher biomass in deeper water, from 650 to 1,000 m depth, with a high predominance of ovigerous females. However, the other two patches showed distribution of the higher biomass from 550 to 850 m (Figure 3).

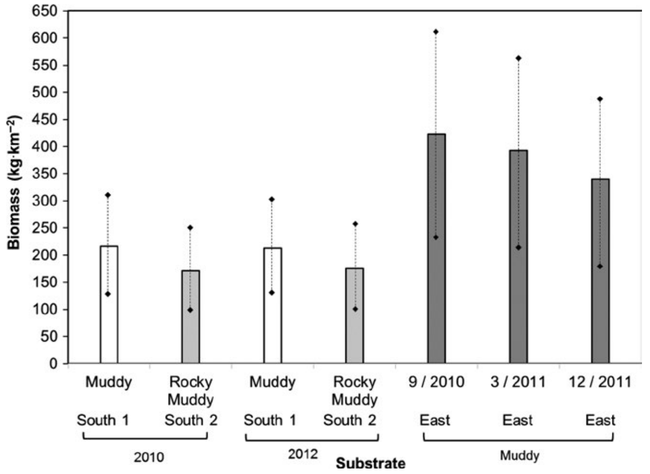

FIGURE 5 Mean biomass of *Chaceon affinis* (kg km^{-2}) off Gran Canaria Island estimated on muddy bottoms with steep slope (South 1) in July 2010 and July 2012, on rocky-muddy bottoms with steep slope (South 2) in July 2010 and July 2012, and on muddy bottoms with gentle slope (East) in September 2010, March 2011 and December 2011. Vertical bars indicate SD

The models obtained with the geostatistical approach in muddy (South 1) and rocky-muddy (South 2) areas with steep slope showed that the range A_0, defined as the distance of spatial influence, was higher in the muddy areas (between 518 and 558 m) than in the rocky-muddy ones (between 397 and 448 m) for the two periods analysed (July 2010 and July 2012) (Table 1). The values of the nugget C_0 (muddy <7.1%; rocky-muddy <15.3%) indicated that the utilized sampling spatial resolution was appropriate in both habitats and periods (Table 1). The spatially structured biomass component ($C/[C_0+C]$) was highly reflecting the well-defined patches of *Chaceon affinis* in both areas and periods (Table 1). A comparative analysis of goodness of fit estimates showed that the isotropic spherical model consistently provided the lowest RSS and the highest r^2 in all analysed models, successfully explaining the spatial population structure in the two areas studied in both periods analysed (Table 1). Basic assumptions of the geostatistical method were met in the muddy and rocky-muddy areas; no trend was observed for the *C. affinis* biomass data versus depth, and data were not related to time or geographic direction. A cross-validation analysis supported the appropriateness of the model and the predictions, and model inadequacy in the estimation of the biomass values was not observed in any case, with the regression co-efficients of all models not differing from 1, and the axis intercepts of all models not differing from 0 (*t*-test $t \le 0.97$, $p > .335$).

3.2 | Habitat slope: steep versus gentle slope

In the area with gentle slope (East), the map of the estimated biomasses revealed two main patches showing maximum diameters between 1.32 and 2.08 km and a mean size of 1.69 km (Figure 6). In the area with steep slope (South 1), patches presented maximum diameters of 0.58–0.73 km with a mean size of 0.69 km (Figure 3). A Student's *t*-test showed significant differences in mean size of the maximum diameter between the gentle (East) and steep slope (South 1) ($t = 3.21$, $p = .0074$). However, when the ratio between the maximum diameter of the patch and the maximum distance between isobaths was calculated for each area, Student's *t*-test showed no significant differences in the ratio between gentle (East, 71%) and steep slope (South 1, 86%) ($t = 1.54$, $p = .149$). This indicated that a diminution in the slope steepness produces a proportional increase in the patch size.

Mean biomasses for the area with gentle slope (East) were higher than for the area with steep slope (South 1) (Figure 5). The *t*-test showed significant differences in mean biomass between areas with gentle (East) and steep slope (South 1) ($t = 22.40$, $p < .0001$).

The models obtained with the geostatistics approach showed that the distances of spatial influence (A_0) were higher in the area with gentle slope (East, 1,639 m) than in the area with steep slope (South 1, 518 m) (Table 1). The value of the nugget C_0 (gentle <8.12%) indicated that the sampling spatial resolution used in the area with gentle slope (East) was also appropriate (Table 1). The spatially structured biomass component ($C/[C_0+C]$) was 95.0% in the area with steep slope (South 1) and 95.2% for the gentle slope (East), which reflects the same well-defined structure of *Chaceon affinis* in both areas (Table 1). An analysis of goodness of fit showed that the isotropic spherical model for the muddy area with gentle slope (East) consistently provided the lowest RSS and the highest r^2 in all models analysed, successfully explaining the spatial population structure of this crab (Table 1). The cross-validation analysis also supported the appropriateness of the model and predictions, and no model inadequacies were observed in the estimation of the biomasses in any case with the regression co-efficients of all models not differing from 1, and the axis intercepts of all models not differing from 0 (*t*-test $t \le 1.13$, $p > .262$).

3.3 | Spatial and temporal variation within the muddy area with gentle slope

Maps of the estimated biomass values for the East area showed the same two main patches over time with the cores of highest biomass

TABLE 1 Parameters of the semivariograms and goodness of fit criteria for variographic analysis based on *Chaceon affinis* density data from off Gran Canaria (Canary Islands). Muddy areas with steep (South 1) and gentle (East) slopes and rocky-muddy area with steep slope (South 2)

			Parameters			Goodness of fit		
Area	Month/year	Model	C_0	C_0+C	A_0	$(C/[C_0+C])$	r^2	RSS
Total								
South 1	07/2010	Spherical	22.1	436.6	0.518	95.0	0.958	3,973
South 1	07/2012	Spherical	24.1	339.7	0.558	92.9	0.943	4,357
South 2	07/2010	Spherical	44.1	359.2	0.397	87.8	0.808	5,804
South 2	07/2012	Spherical	48.7	318.3	0.448	84.7	0.892	3,841
East	09/2010	Spherical	35.4	726.1	1.639	95.2	0.870	13,958
East	03/2011	Gaussian	20.0	767.2	1.285	97.4	0.872	15,131
East	12/2011	Gaussian	68.0	837.9	1.963	91.8	0.912	12,732
Males								
East	09/2010	Spherical	23.0	440.4	1.435	94.8	0.894	14,943
East	03/2011	Gaussian	11.2	489.7	1.134	97.8	0.876	14,722
East	12/2011	Gaussian	40.3	522.7	2.310	92.2	0.946	13,902
Females								
East	09/2010	Spherical	10.1	377.5	2.301	97.3	0.903	15,071
East	03/2011	Gaussian	32.2	334.6	1.252	90.3	0.898	13,638
East	12/2011	Gaussian	21.7	292.9	2.332	92.8	0.887	14,104

C_0 = the nugget effect corresponding with the minimum semivariance; A_0 = range of the semivariogram; C_0+C = sill corresponding with the maximum semivariance; $(C/[C_0+C])$ = proportion of variance explained; r^2 = co-efficient of determination; RSS = residual sum of squares.

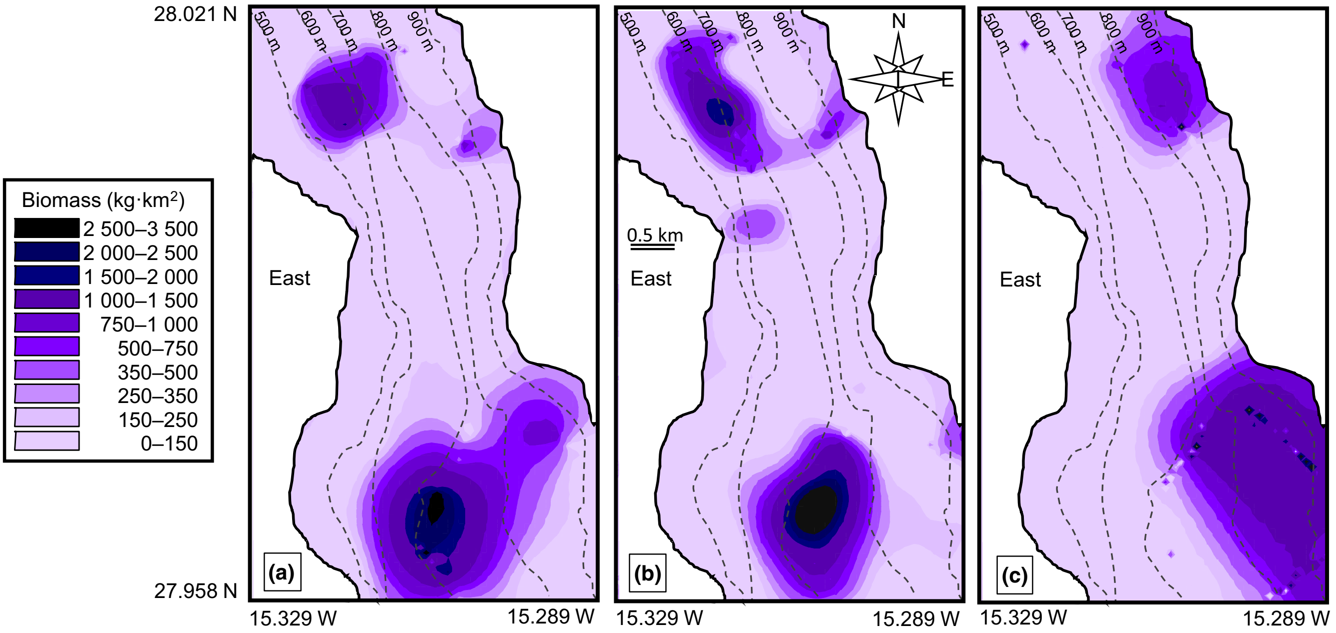

FIGURE 6 Spatial distribution of the biomass of *Chaceon affinis* (kg km^{-2}) off Gran Canaria Island on muddy bottoms with gentle slope (East) in (a): September 2010, (b): March 2011 and (c): December 2011

separated by a distance between 4.2 and 4.5 km (Figure 6). The main patches showed maximum diameters from 1.32 to 2.08 km in September 2010 with a mean size of 1.69 km; from 1.57 to 2.01 km in March 2011 with a mean size of 1.79 km; and from 1.64 to 2.81 km in December 2011 with a mean size of 2.23 km (Figure 6). The ANOVA showed no significant differences in size of the patches for the East area over time ($F = 0.449$, $p = .667$). The two main biomass patches remained over time, showing an eastward displacement of 1.4–1.8 km from the core of the structure of the biomass on the bathymetric line of 600 m to the isobath of 900 m (Figure 6). The map of estimated biomass for females in September 2010 showed a second patch with high level of abundance deeper than the both sex all over rest of time studied (Figure 8). Maps of estimated biomasses for each sex showed the same two main patches over time and the same pattern distribution (Figures 7 and 8). These maps also showed a higher biomass of females (Figure 8) than males (Figure 7) in deeper areas during September and March. Males showed higher biomass values than females in shallower areas (Figures 7 and 8). Temperature and salinity showed a low Spearman's correlation with the carapace width (temperature $\rho = 0.023$, salinity $\rho = 0.017$, $p < .008$) or the weight of the catches (temperature $\rho = 0.0001$; salinity $\rho = 0.0001$; $p < .0001$).

Total biomass and mean biomass showed a decreasing pattern over time (Figure 5). ANOVA showed significant differences in biomass in the East area over time ($F = 9.54$, $p < .0002$). Dunnett's *T3* post-hoc test showed significant differences in mean biomass in the East area among the three periods ($p < .05$). For the 15-month period, the estimated biomass reached a variation of 1.66 t. Catches of *Chaceon affinis* by both commercial and experimental fishing in the East area were 1.2 t (0.52 t between September 2010 and March 2011, and 0.68 t between March and December 2011).

Models obtained with the geostatistics method for September 2010, March 2011 and December 2011 showed that the distance of spatial influence (A_0) changed over the year and ranged between 1,285 and 1,963 m (Table 1). The values of the nugget C_0 (<8.12%) indicated that the utilized sampling spatial resolution was appropriate throughout the year (Table 1). The spatially structured biomass component (C/[C_0+C]) was high in the three periods analysed, reflecting the well-defined patches of *C. affinis* in the area over time (Table 1). The same pattern was recorded for males and females when analysed separately. Analysis of goodness of fit estimates showed that the isotropic Gaussian models consistently provided the lowest RSS and the highest r^2 in all analysed models, successfully explaining the spatial population structure over time (Table 1). The cross-validation analysis supported the appropriateness of the models and the predictions over time of the biomass of *C. affinis* as a whole and by sex. Model inadequacy in the estimation of the biomass values were not observed in any case with the regression co-efficients of all models not differing from 1, and the axis intercepts of all models not differing from 0 (*t*-test $t \le 1.27$, $p > .209$).

4 | DISCUSSION

The size of the patches of *Chaceon affinis* on muddy bottoms changes with slope steepness. *Chaceon affinis* has a patch size related to steepness of the slope between 500 and 900 m isobaths, and showed an increase in patch size when the steepness decreased (South 1 versus East). This species also showed a biomass level related to the substrate type; the same size of patch was found higher on the muddy bottoms than on the rocky-muddy ones (South 1 versus South 2), and in relation to the slope steepness an increase of biomass occurred when the

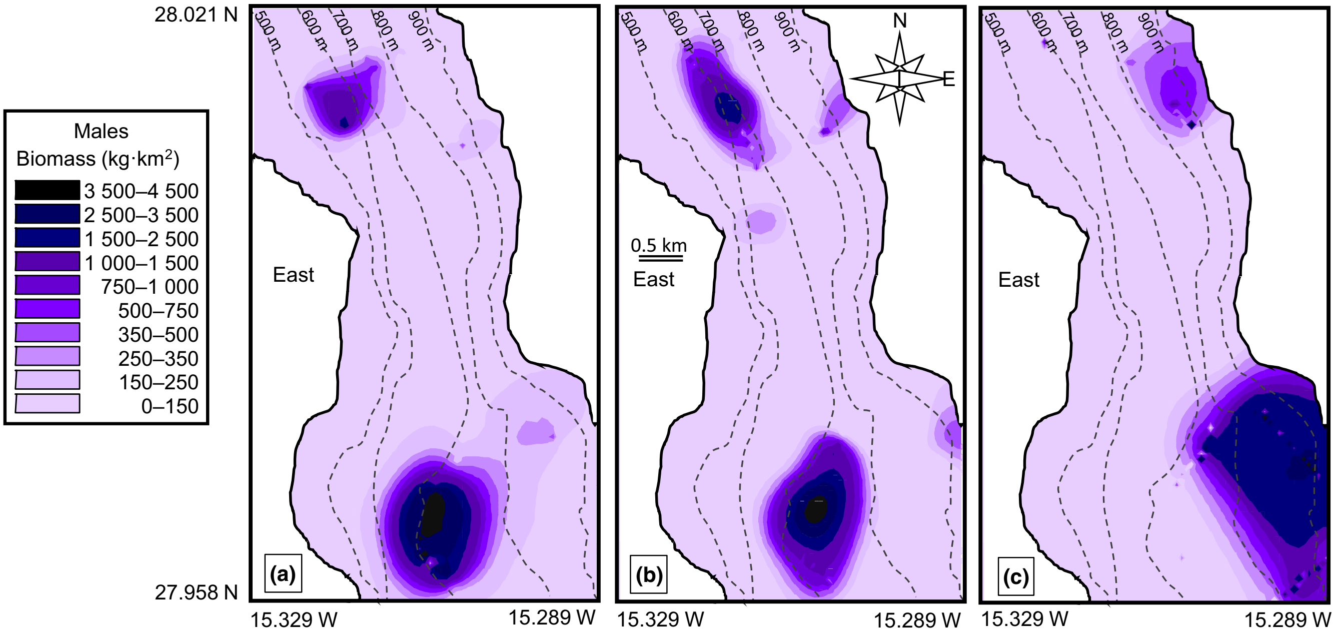

FIGURE 7 Spatial distribution of the biomass of *Chaceon affinis* males (kg km^{-2}) off Gran Canaria Island on muddy bottoms with gentle slope (East) in (a): September 2010, (b): March 2011 and (c): December 2011

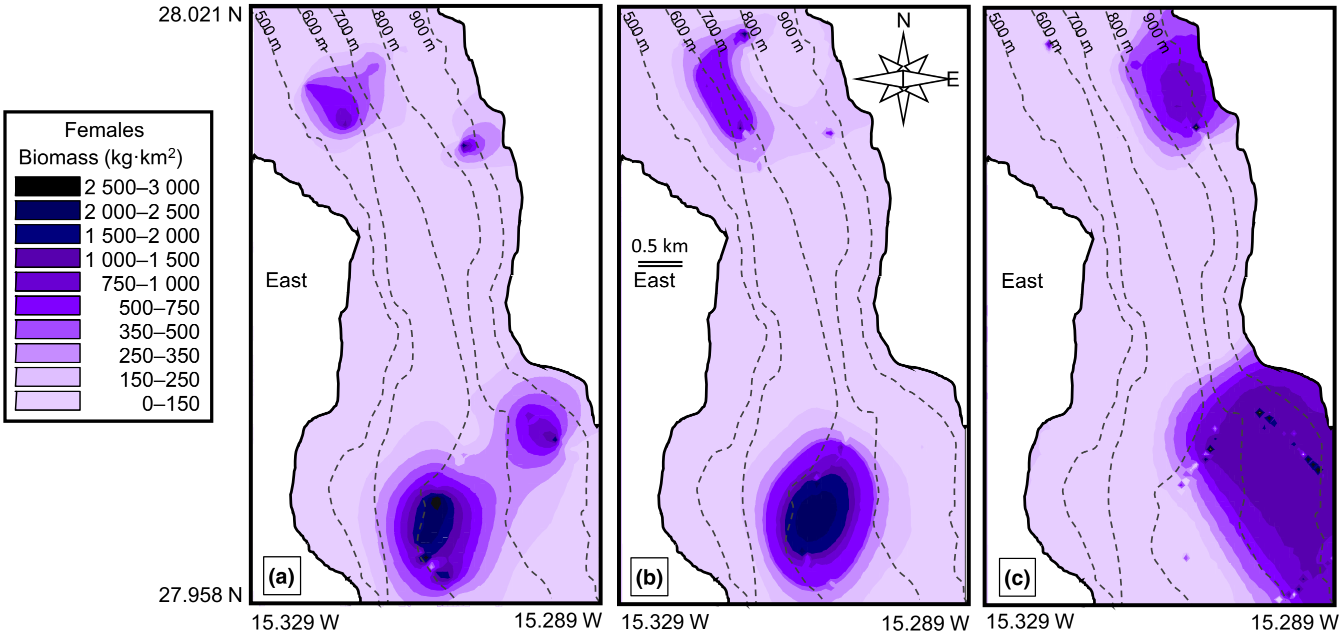

FIGURE 8 Spatial distribution of biomass of *Chaceon affinis* females (kg km^{-2}) off Gran Canaria Island on muddy bottoms with gentle slope (East) in (a): September 2010, (b): March 2011 and (c): December 2011

steepness decreased (South 1 versus East). These patterns are considered habitat-dependent and linked to a differential rate of settlement, with muddy bottoms favored over rocky-muddy ones and to a differential rate of post-settlement survival among the types of bottoms and to differences in food availability (Gutiérrez et al., 2011). Muddy bottoms should be the preferred substrate of the species because they allow the crabs to dig burrows as hiding strategies during the molting and hardening of the carapace in the pre-pubertal stage (Biscoito et al., 2015). Molting is very frequent in small individuals, and nine molts have been observed before reaching a 40 mm carapace width in *Chaceon maritae* (Melville-Smith, 1989). The results obtained for the carapace width distribution showed differences between substrate types, with a higher number of small individuals on muddy bottoms.

Results showed that the biomass level is higher on muddy substrate. The occurrence and distribution of many benthic decapod crustaceans are strongly influenced by bottom characteristics, with a preference for soft bottoms, especially in burrowing species (Comeau et al., 1998; Rufino et al., 2004). Additionally, within each study area,

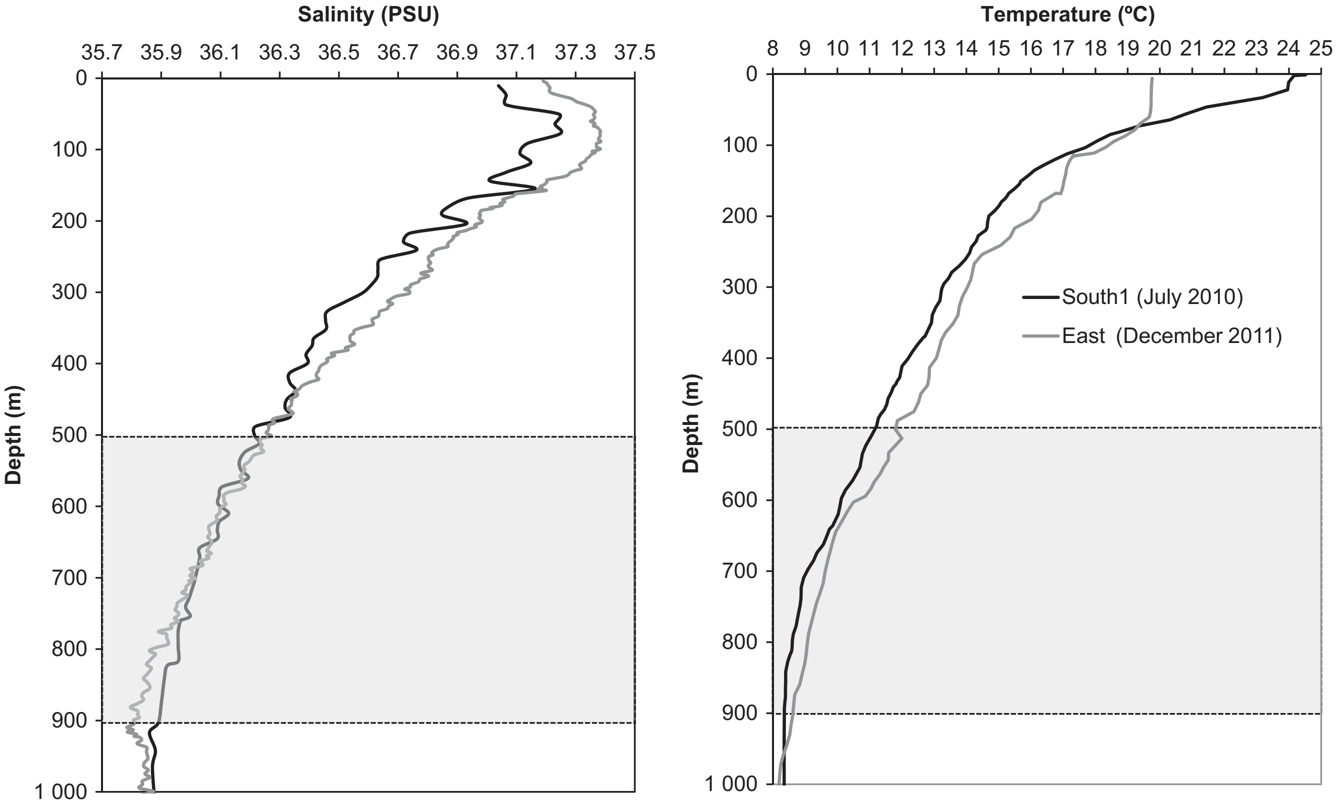

FIGURE 9 Changes in both salinity and temperature with depth corresponding to the extreme values observed for seasons and areas in Gran Canaria Island

the estimated maps showed the existence of various patches of different biomasses and sizes. These results contrasted with those obtained in larger areas (Castrejón et al., 2005; Gutiérrez et al., 2011; Rufino et al., 2004; Rufino, Maynou, Abelló, Yule et al., 2006) where patches are extensive (over distances of 30 km) and it is not possible to observe this habitat-related pattern. In geryonid crabs, differential substrate preferences have been related to burrowing capability, sediment type and food availability (Castrejón et al., 2005; Comeau et al., 1998). The deeper biomass distribution observed in one patch of the muddy area (South 1) can be related to the different sex ratio composition observed in each patch. In the deeper patch, females were more abundant than males. Males showed a depth distribution mainly between 600–800 m, while females tended to be found in deeper waters (Biscoito et al., 2015). In Azorean waters, Pinho, Gonçalves, Martins, and Menezes (2001) also found that male abundance decreased significantly with depth, thus females were more abundant than males below 900 m depth.

In other studies, the environmental conditions, such as temperature or salinity, have been shown to determine the distribution of benthic crabs (Cartes & Carrassón, 2004; Rosa et al., 2012; Rufino et al., 2004). In distribution of *C. affinis*, neither temperature nor salinity exhibit high oscillations or correlation that could explain variations in size or location. On the contrary, distribution in *C. affinis* in these areas show changes between seasons in each area were less than 0.75 °C and 0.024 PSU for each 50 m in the bathymetric area of distribution (Figure 9). Related with this, Pajuelo et al. (2015) also found that the bathymetric distribution of *C. affinis* is not linked to a specific water mass with certain conditions of salinity and temperature.

Only two or three locations in the study areas generated high biomass contour patches. When these patches were superimposed on the isobath lines (range: 500–900 m), they were coincident with the main depth range described for the species in the area (Biscoito et al., 2015). In this regard, the upper bathymetric limit of abundances in this species has been considered in the analysis, and in shallower waters the biomass of *C. affinis* is low as a consequence of the presence of the aggressive crabs *Cancer bellianus* Johnson, 1861 and *Paromola cuvieri* (Risso, 1816), which mainly inhabit areas at depths of 400–700 m, creating a border of competition among the species (Biscoito et al., 2015; Pinho, Gonçalves, & Martins, 2001; Pinho, Gonçalves, Martins, and Menezes, 2001; Triay-Portella et al., 2014). The deeper location of the highest values of biomass in the rocky-muddy area (South 2) with respect to the muddy area (South 1) can be related to the variable upper limit of vertical distribution of *C. affinis* that is influenced by the presence of the aggressive crabs of other species in a variable competition border (Biscoito et al., 2015).

The spatial structure of *C. affinis* remained fairly stable over time showing that biomass changes with depth over time. The stable patches of biomass found in the study areas may be related to the presence of nearby submarine canyons crossing the insular slope. These canyons represent zones of organic matter (OM) and energy transfer between the shelf and the deep slope (Amaro, de Stigter, Lavaleye, & Duineveld, 2015; Amaro et al., 2010; Cunha et al., 2011;

De Leo, Smith, Rowden, Bowden, & Clark, 2010; Mamouridis, Cartes, Parra, Fanelli, & Saiz Salinas, 2011). The energy and OM are channeled along canyons, enhancing benthic biodiversity and creating biomass hotspots (De Leo, Vetter, Smith, Rowden, & McGranaghan, 2014; De Leo et al., 2010; Mamouridis et al., 2011).

During the time period studied, the deep-sea red crab underwent a substantial decline in biomass. This decline is consistent with the combined catches of both commercial and experimental fishing in the area. We argue that the reduction is associated with three main factors: low mobility of individuals of the species, a small increase in biomass due to growth, and a low increase in biomass due to recruitment. The small changes in the temporary location of the patches showed the low mobility of the species. However, it is well known that geryonid species perform migrations related to reproduction (Biscoito et al., 2015; Erdman et al., 1991; López-Abellán, Balguerías, & Fernández-Vergaz, 2002). Off the coasts of the Canary Islands, the low mobility of *C. affinis* is a consequence of the steep slope of the islands and the proximity of the isobaths. Hilário and Cunha (2013) and Biscoito et al. (2015) indicated that this limited temporary movement into deeper waters is due to a combination of a mating-related migration and the presence of competitors. Additionally, López-Abellán et al. (2002) noted that these seasonal displacements are related to strategies to diminish competition with other crabs such as *Cancer bellianus* or *P. cuvieri*. Considering that vulnerability is a measure of the degree of exposure to a fishing pressure (Hiscock, 1999; Roberts, Smith, Tillin, & Tyler-Walters, 2010), the low observed mobility makes the species highly vulnerable to overexploitation. Exposure to fishing increases more as the resource is grouped and is reduced when the resource exhibits dispersion and mobility. Exposure will also be conditioned by the extent, magnitude and duration of the fishing pressure (Roberts et al., 2010), and therefore more fishing activity will increase the vulnerability. Deep-sea crabs are very sensitive to fishing activity with baited traps, which has been observed in other fisheries that have collapsed (Armstrong, 1990; Melville-Smith, 1988; Robinson, 2008). In *C. affinis*, reproduction is biennial with a very low rate of growth and late first sexual maturity (Biscoito et al., 2015). This life pattern results in a low rate of resilience or recoverability, and as a consequence larvae re-colonization from other areas and their growth will take a long time.

A different bathymetric distribution by sex is a common pattern in deep-sea red crabs (Beyers & Wilke, 1980; Haefner & Musick, 1974; Masello & Defeo, 2016; McElman & Elner, 1982; Melville-Smith, 1988), but it is not a fixed rule (Wenner, Ulrich, & Wise, 1987) because different types of bathymetric distribution by sex or ontogenic stage have been described even for the same species in different geographic areas (Erdman et al., 1991).

Although the bathymetric distribution by sex showed temporal changes, with a displacement to deeper areas made by both sexes over the studied period, only a partial temporal segregation between males and females was observed. As our results indicate, mating-related migration during winter months reveals that deep-water crustacean species have higher mating and feeding activities in winter, which are related to seasonal changes in the availability of food (Briones-Fourzán, Barradas-Ortiz, Negrete-Soto, & Lozano-Álvarez, 2010). This pattern coincides with that observed for *C. affinis* by Biscoito et al. (2015), who indicated that the sex ratio is linked to depth and males are mainly located at 600–800 m while females are at 800–1,000 m. The deeper patch observed for females may be related to the seasonal downward movements of ovigerous females (Biscoito et al., 2015). López-Abellán et al. (2002) indicated that these seasonal displacements of ovigerous females could be related to strategies to diminish competition with other aggressive crabs. The presence of females in deeper areas has also been attributed to the oceanographic conditions in these areas, which favor larger amounts of food (Biscoito et al., 2015; Hilário & Cunha, 2013).

The biennial individual reproductive cycle of *C. affinis*, as indicated by Pinho, Gonçalves, Martins, and Menezes (2001), Hilário and Cunha (2013) and Biscoito et al. (2015), results in both low reproductive potential and low recruitment of the species. Moreover, after crabs reach sexual maturity, the poor rate of increase in biomass is likely due to limited growth of individuals with inter-molt periods longer than 3 years (Biscoito et al., 2015).

Due to its very low mobility, *C. affinis* is highly vulnerable to local depletion by intensive fishing efforts. Robinson (2008) and Biscoito et al. (2015) proposed some regulatory measures for the exploitation of this species such as a minimum landing size of 120–130 mm carapace width, closed areas to protect the spawning females, and/or a catch prohibition on females carrying eggs to preserve their reproductive potential. These authors also suggested the need to implement additional management measures. Consequently, the results obtained in the present work suggest that management measures based on rotational fishing strategies could be implemented to avoid overexploitation. This management would be to open areas on a rotational basis and allow fishing during a few months in each area (depending on the limit of fixed catches) at intervals of 2 years. This resting period should allow crabs to reproduce and grow before the next period of fishing activity. Moreover, the establishment of closure areas as reproductive refugia, fixed through regulation and excluded from fishery operations, would be potential areas for larval advection for the eventual re-colonization of fished areas. Considering the aggregated nature and stability of the distribution of *C. affinis*, these spatial management measures should be used simultaneously with regulation measures in a framework of management redundancy (Caddy, 1999).

Finally, spatial analysis techniques have been previously used to estimate the biomass of exploited invertebrate populations using data from spatially extensive surveys to examine seasonal and biomass-related changes in distribution patterns in large (Gutiérrez et al., 2011; Jensen & Miller, 2005; Lembo et al., 1999; Rufino, Maynou, Abelló, Yule et al., 2006) and small marine areas (Ríos-Lara et al., 2007; Rufino et al., 2004; Rufino, Maynou, Abelló, & Sarda, 2006). In the case of deep-sea crab species, many studies have shown that the study of large areas masks the variation in the patterns of distribution and the biomass of these species at a much smaller scale, which shows the true vulnerability of these species to exploitation as a consequence of the low sampling density relative to the sampled area (Rufino, Maynou, Abelló, Yule et al., 2006).

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Checklist of brachyuran crabs (Crustacea: Decapoda) from the Cape Verde Islands, with a biogeographic comparison with the Canary Islands (Eastern Atlantic)

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Abstract: In the current scenario of defaunation and bioinvasion, increasing the knowledge about the composition in marine species and monitoring are an emergency need to control the biodiversity. Nearly 35 years have passed since Türkay (1982) published the decapod crustaceans of the Cape Verde islands. No checklists of decapod fauna specifically covering this area have been published since then, and an update is needed. The current list of Cape Verdean brachyuran crabs comprises 125 species, grouped in 83 genera and 40 accepted families. Additional species have been mainly recorded thanks to intensified research into deep water and description of new taxa. *Anamathia rissoana* and *Macropipus rugosus* are recorded for the first time and the occurrence/absence of some species confirmed in the area. This work summarizes all recent changes in Cape Verdean brachyurans and makes biogeographic remarks, with a comparison with the Canary Islands brachyurans. It presents a literature review and overview about the species previously recorded in the area. It still aims to be a tool to support further monitoring to identify the absence or appearance of invasive species.

Résumé : *Crabes brachyoures (Crustacea : Decapoda) des îles du Cap Vert, comparaison biogéographique avec les îles Canaries (Atlantique Est)*. Dans les conditions actuelles de disparition d'espèces et d'invasion biologique, la connaissance de la composition en espèces marines et la surveillance représentent une nécessité émergente de contrôler le niveau de la biodiversité. Presque 35 ans se sont écoulés depuis que Türkay (1982) a publié la liste des crustacés décapodes des iles du Cap Vert. Aucune liste équivalente couvrant spécifiquement cette zone n'ayant été publiée depuis, une mise à jour était nécessaire. La liste actuelle des brachyoures du Cap Vert comprend 125 espèces regroupées en 83 genres et 40 familles validées. De nouvelles espèces ont été signalées principalement grâce à l'intensification des recherches en eau profonde et à la description de nouveaux taxa. *Anamathia rissoana* et *Macropipus rugosus* ont été signalées pour la première fois et la presence ou l'absence de certaines espèces est confirmée. Ce travail synthétise les récents changements au sein des brachyoures du Cap Vert et apporte des remarques biogéographiques par une comparaison avec les brachyoures des Îles Canaries. Il présente une revue de la littérature sur le thème et les espèces précédemment signalées dans la région. Il constitue un outil pour de futures observations afin d'identifier l'apparition d'espèces invasives.

Keywords: Checklist ● Biogeography ● Brachyura ● Decapoda ● Cape Verde Islands ● Canary Islands

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Introduction

In the current scenario of defaunation and bioinvasion, increasing the knowledge about the composition of marine species that occur in different regions by using their checklists and support monitoring is an emergency need to control the biodiversity (e.g. Araújo & Wirtz, 2015). For this purpose, the appropriateness of decapod crustaceans is evident because decapods is one of the most diverse taxa in marine and coastal ecosystems, as well as one of the most representative groups of the benthic environment.

Placed in the NE Atlantic, the Cape Verde archipelago has about 965 km of coastline, the islands lying within the 4000 m marine contour. The islands are separated from the coasts of Western Africa by great depths (> 3000 m), being Boa Vista located 570 km from Senegal. Most of the islands arise from great depths, but the windward island chain, and Boa Vista and Maio are linked by relative shallows (< 200 m) (Fig. 1). These characteristics are manifest by the absence of wide shelves, with a bottom depth of 300 m near the coast except around Boa Vista and Maio. The islands show an increase of age from west (< 3 my) to east (8-16 my) (Madeira et al., 2008). Their waters are under the influence of the North Equatorial Counter-Current and the Canary Current (e.g. Lázaro et al., 2005), and sea surface are normally higher than 20°C all year long (Wirtz et al., 2013). This could explain the great diversity in the biogeographic patterns of their biota. The Cape Verde islands eco-region is included within the West African Transition province of the Tropical Atlantic realm (Spalding et al., 2007).

Nearly 35 years have passed since Türkay (1982) published his work on decapod crustaceans of the Cape Verde islands. The systematic research landscape on brachyurans has changed drastically in the last few decades (e.g. Marco-Herrero et al., 2015; González, 2016), and a great number of changes to the species found around the Cape Verde islands have also taken place; so an update is needed for this area.

This work summarizes all changes in Cape Verdean brachyurans since Türkay (1982) and makes biogeographic remarks, with a comparison with the Canary Islands brachyurans. It presents a literature review and overview about the species previously recorded in the area, with two new records and some presence/absence confirmations. It still aims to be a useful tool to support further monitoring to identify the absence or appearance of invasive ones.

Materials and Methods

This list covers all brachyuran crabs present in the Cape Verde islands from intertidal to deep waters. The study area is bounded by the 14º50'N-17º20'N parallels and the 22º40'W-25º30'W meridians, covering an area of about 800560 km^2 (Fig. 1).

Families are arranged in taxonomical order, and species alphabetically within each family. This systematic classification follows Ng et al. (2008), but also takes into account the latest changes in particular taxa: Schubart & Reuschel (2009) and Spiridonov et al. (2014) for Cancroidea and Portunoidea; Marco-Herrero et al. (2013) for Majoidea, with larvae and DNA data supporting that *Ergasticus clouei* should be moved from Inachidae to Oregoniidae; Shih et al. (2016) for Ocypodidae. Data from WoRMS database (http://www. marinespecies.org/) were also checked.

For each crab species, the publication that (to our knowledge) gives the first record (with its original name) from the study area is listed. When the Cape Verde islands were type-locality, all available data on that type-material is given. Additionally, main references used to check the occurrence of each one of the brachyuran species are listed as follow: A, Monod (1956); B, Manning & Holthuis (1981); C, Türkay (1982); D, Fransen (1991); E, d'Udekem d'Acoz (1999); F, González et al. (2004); G, González et al. (2009); and present work when enlarging the bathymetric range of a species. In some cases, a common synonym used in the literature is given.

For each species, previously reported or unpublished data (from six campaigns with different types of traps) on regional depth range are given, as well as their vertical distribution elsewhere. Each species is classified into the following 12 biogeographic pattern categories adapted from González (2016): cosmopolitan or worldwide; pantropical or circuntropical; amphi-Atlantic of wide distribution; amphi-Atlantic of warm affinity; eastern Atlantic of wide distribution; eastern Atlantic cold-temperate; eastern Atlantic warm-temperate; Atlanto-Mediterranean; Guinean (restricted to tropical and subtropical eastern Atlantic); eastern-central Atlantic islands (from Azores to Cape Verde islands, and southwards even to St. Helena); insular West African (around Cape Verde islands and islands of the Gulf of Guinea); and endemic to Cape Verde islands. Global and regional distribution is given if necessary. A description of different components of this brachyuran fauna is performed, followed by a second approach where both pelagic and deep-water benthic species were excluded, in order to compare the littoral and upper bathyal benthic species (0-300 m) from Cape Verde (Menezes et al., 2015) and Canary Islands (González, 2016).

For newly recorded species from the study area, measurements taken (using callipers, ± 0.1 mm) and abbreviations used were: CL - carapace length; CW - carapace width. Sex and ovigerous condition were also noted.

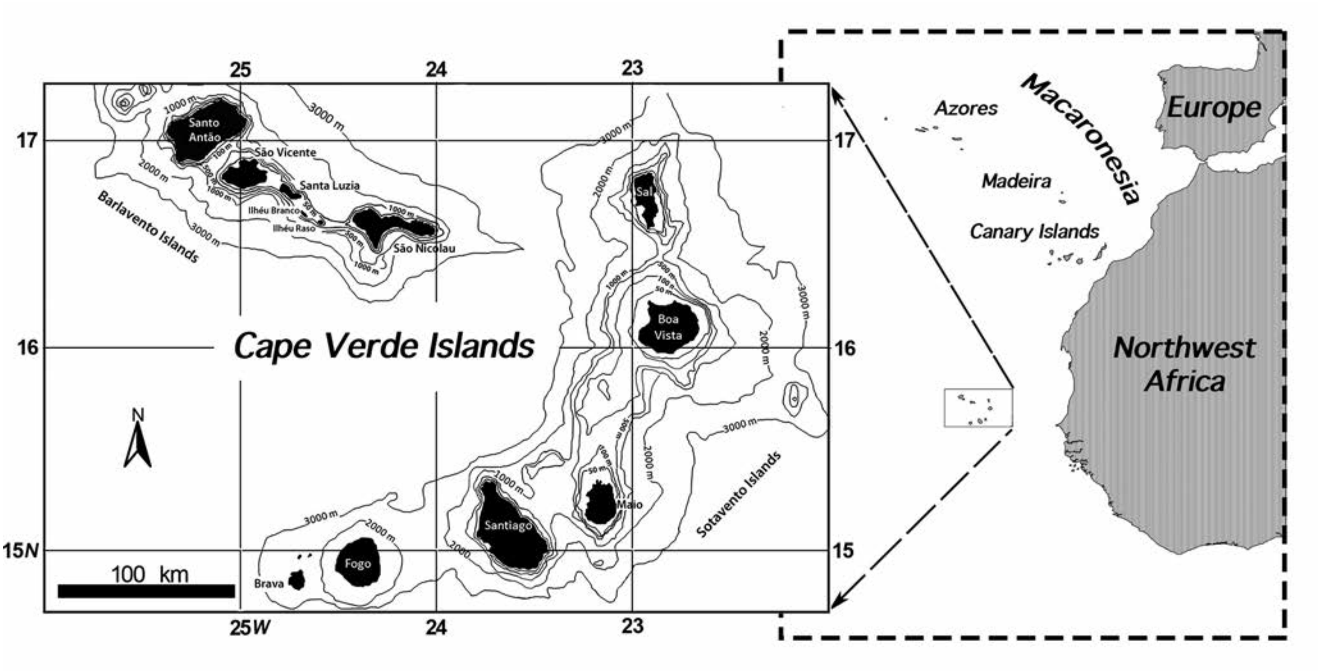

Figure 1. Map of the Cape Verde Islands (eastern Atlantic) showing their geographic situation and bathymetric characteristics.

Results

A total of 125 crab species and subspecies are reported herein around the Cape Verde islands. Of them, *Cardisoma armatum* Herklots, 1851 is terrestrial and 124 species are marine forms; *Planes minutus* (Linnaeus, 1758) is essentially pelagic and 123 species are benthic.

Superfamily DROMIOIDEA de Haan, 1833
Family Dromiidae de Haan, 1833
Dromia marmorea Forest, 1974

First record: A. Milne-Edwards & Bouvier (1899: 15, as *D. vulgaris*). Main references: A, B, C, D, E. Depth range: 10-30 m; elsewhere, 0-76 m. A Guinean species.

Dromia nodosa A. Milne-Edwards & Bouvier, 1898

First record: A. Milne-Edwards & Bouvier (1898: 75; five males; type-locality, Cape Verde islands; 75 m of depth). Main references: A, B, C, D, E. Depth range: 75-90 m; elsewhere, 75-95 m. A Guinean species.

Sternodromia spinirostris (Miers, 1881)

First record: Forest (1974: 101, as *Dromia spinirostris*). Main references: B, C, E, this work. Depth range: 40-122 m; elsewhere, 7.5-108 m. A Guinean species.

Family Dynomenidae Ortmann, 1892
Dynomene filholi Bouvier, 1894

First record: Bouvier (1894: 6; type-locality, Cape Verde islands). Main references: A, B, C, D. Depth range: 58-1477 m; elsewhere, 23-85 m. An insular West African species; also known from Príncipe and Annobon Islands.

Superfamily HOMOLOIDEA de Haan, 1839
Family Homolidae de Haan, 1839
Homola barbata (Fabricius, 1793)

First record: Bouvier (1922: 51). Main references: A, B, C, this work. Depth range: 91-165 m; elsewhere, 2-637 m. An amphi-Atlantic species of wide distribution.

Paromola cuvieri (Risso, 1816)

First record: Manning & Holthuis (1981: 27). Main references: E, F, G, this work. Depth range: 80-700 m; elsewhere, 10-1212 m. An eastern Atlantic species of wide distribution.

Family Latreilliidae Stimpson, 1858
Latreillia elegans Roux, 1830

First record: A. Milne-Edwards & Bouvier (1900: 13-14). Main references: A, B, D, E, F, G, this work. Depth range: 100-475 m; elsewhere, 35-405 m. An Atlanto-Mediterranean species.

Superfamily RANINOIDEA de Haan, 1839
Family Raninidae de Haan, 1839
Ranilia constricta (A. Milne-Edwards, 1880)

First record: Fransen (1991: 46, 180). No further records. Depth range: 76-76 m; elsewhere, 40-481 m. An amphi-Atlantic species of warm affinity.

Superfamily CALAPPOIDEA de Haan, 1833
Family Calappidae de Haan, 1833
Calappa galloides Stimpson, 1859

First record: Miers (1886: 286, as *C. gallus*). Main references: A, B, C, D, E, this work. Depth range: 0-80 m; elsewhere, 15-218 m. An amphi-Atlantic species of warm affinity.
Remarks: Generally referred erroneously as *Calappa gallus* (Herbst, 1803). In WoRMS it is currently noted "between Cape Verde islands and Senegal …". However, d'Udekem d'Acoz (1999) stated that Indo-Pacific species was misidentified with *C. galloides* for a long time.

Calappa granulata (Linnaeus, 1758)

First record: A. Milne-Edwards & Bouvier (1900: 59-60). Main references: A, B, C, D, E, G, this work. Depth range: 75-233 m; elsewhere, 10-400 m. An Atlanto-Mediterranean species.

Calappa sp. Fransen, 1991

First record: Fransen (1991: 38, 84). No further records. Depth range: 92-92 m; elsewhere, 80-192 m. An eastern-central Atlantic islands species; also known from the Canary and Selvagens Islands (González, 2016).

Cryptosoma cristatum Brullé, 1837

First record: Lucas (1882: 15). Main references: A, B, C, D, E. Depth range: 40-50 m; elsewhere, 2-89 m. An eastern-central Atlantic islands species; also known from Madeira, Canaries and St. Helena (González, 2016).

Superfamily CANCROIDEA Latreille, 1802
Family Atelecyclidae Ortmann, 1893
Atelecyclus rotundatus (Olivi, 1792)

First record: A. Milne-Edwards & Bouvier (1900: 60-61, as *A. septemdentatus*). Main references: A, B, C, D, E, this work. Depth range: 102-275 m; elsewhere, 0-795 m. An eastern Atlantic species of wide distribution.

Atelecyclus undecimdentatus (Herbst, 1783)

First record: A. Milne-Edwards & Bouvier (1900: 61, as *A. rotundatus*). Main references: A, C, E. Depth range: 0-51 m; elsewhere, same range. An Atlanto-Mediterranean species.

Superfamily DORIPPOIDEA MacLeay, 1838
Family Dorippidae MacLeay, 1838
Phyllodorippe armata (Miers, 1881)

First record: A. Milne-Edwards & Bouvier (1900: 32-33, as *Dorippe armata*). No further records. Depth 60 m; elsewhere, 7-105 m. A Guinean species.
Remarks: First recorded for the area based on three 1883 Talisman specimens caught off São Vicente Island and eight specimens from off Branco Islet at 60 m of depth; these records were surprisingly not compiled by none main reference.

Family Ethusidae Guinot, 1977
Ethusa rosacea A. Milne-Edwards & Bouvier, 1897

First record: Bouvier (1922: 53). Main references: A, E. Depth range: 628-660 m; elsewhere, 100-1013 m. A Guinean species.

Ethusa rugulosa A. Milne-Edwards & Bouvier, 1897

First record: A. Milne-Edwards & Bouvier (1897: 297-298; type-locality, Cape Verde islands; 150-275 m). Main references: A, B, C, D. Depth range: 88-275 m; elsewhere, 60-305 m. A Guinean species.

Ethusa vossi Manning & Holthuis, 1981

First record: A. Milne-Edwards & Bouvier (1900: 22-24, as *E. mascarone*). Main references: A, B, D. Depth range: 40-69 m; elsewhere, 6-96 m. A Guinean species.

Ethusina alba Filhol, 1884

First record: A. Milne-Edwards & Bouvier (1900: 29-30, as *E. abyssicola*). Main references: A, B, D, E. Depth range: 3000-3890 m; elsewhere, 2800-4265 m. An eastern Atlantic cold-temperate species.

Superfamily ERIPHIOIDEA MacLeay, 1838
Family Menippidae Ortmann, 1893
Menippe nodifrons Stimpson, 1859

First record: A. Milne-Edwards (1878: 264, as *M. rudis*). Main references: A, B, C, this work. Depth range: 3-3 m; elsewhere, 0-20 m. An amphi-Atlantic species of warm affinity.

Family Oziidae Dana, 1851
Epixanthus helleri A. Milne-Edwards, 1867

First record: A. Milne-Edwards & Bouvier (1900: 83-85). Main references: A, B, C, D. Depth range: 0-6 m; elsewhere, 0-10 m. A Guinean species.

Eupilumnus africanus (A. Milne-Edwards, 1867)

First record: Miers (1886: 146, 150, as *Pilumnus* *africanus*). Main references: A, B, C, D, E. Depth range: 0-15 m; elsewhere, 0-35 m. A Guinean species.

Eupilumnus aff. **stridulans** (Monod, 1956)

First record: Fransen (1991: 54-55, 101, as *Globopilumnus* aff. *stridulans*). No further records. Depth range: 0-6 m. Likely endemic to the area.

Superfamily GONEPLACOIDEA MacLeay, 1838
Family Acidopsidae Števčić, 2005
Acidops cessacii (A. Milne-Edwards, 1878)

First record: A. Milne-Edwards (1878: 227, as *Epimelus Cessaci*; two specimens; type-locality, Cape Verde islands). Main references: A, B, C, D. Depth range: 0.5-61 m; elsewhere, intertidal. A Guinean species.

Family Chasmocarcinidae Serène, 1964
Typhlocarcinodes integrifrons (Miers, 1881)

First record: Fransen (1991: 36, 192). No further records. Depth range: 70-88 m; elsewhere, 12-90 m. A Guinean species.

Family Goneplacidae MacLeay, 1838
Goneplax barnardi (Capart, 1951)

First record: Fransen (1991: 36, 38-39, 50, 85-86, as *Carcinoplax barnardi*). Main references: E. Depth range: 328-590 m; elsewhere, 200-590 m. A Guinean species.

Goneplax rhomboides (Linnaeus, 1758)

First record: Fransen (1991: 36, 102-103). Main references: E. Depth range: 310-310 m; elsewhere, 0-600/700 m. An eastern Atlantic warm-temperate species.

Superfamily LEUCOSIOIDEA Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Atlantolocia laevidorsalis (Miers, 1881)

First record: A. Milne-Edwards & Bouvier (1900: 58, as *Philyra laevidorsalis*). Main references: A, B, C. Depth range: neritic littoral; elsewhere, 4-30 m. A Guinean species.

Ebalia affinis Miers, 1881

First record: A. Milne-Edwards & Bouvier (1898: 32-34, as *E. (Phlyxia) atlantica*). Main references: A, C, E. Depth range: 60-60 m; elsewhere, 4-140 m. A Guinean species.

Ebalia nux A. Milne-Edwards, 1883

First record: A. Milne-Edwards & Bouvier (1900: 45-47). Main references: A, B. Depth range: 219-875 m; elsewhere, 80-2983 m. An eastern Atlantic cold-temperate species.

Ebalia tuberculata Miers, 1881

First record: A. Milne-Edwards & Bouvier (1900: 50-51). Main references: A, B, C, E. Depth range: 60-60 m; elsewhere, 12-110 m. A Guinean species.

Ilia nucleus (Linnaeus, 1758)

First record: A. Milne-Edwards & Bouvier (1900: 40-41). Main references: A, B, C, E. Depth range: 60-60 m; elsewhere, 0.5-80 m. An Atlanto-Mediterranean species.

Ilia spinosa Miers, 1881

First record: Guinot & Ribeiro (1962: 30). Main references: B, C, D, E, this work. Depth range: 8-150 m; elsewhere, 5-132 m. A Guinean species.

Merocryptus obsoletus A. Milne-Edwards & Bouvier, 1898

First record: A. Milne-Edwards & Bouvier (1898: 34-35; one male; type-locality, W of the Cape Verde islands; 75 m of depth). Main references: A, B, C, E, this work. Depth range: 75-122 m; elsewhere, 75-132 m. A Guinean species.

Superfamily MAJOIDEA Samouelle, 1819
Family Epialtidae MacLeay, 1838
Subfamily Epialtinae MacLeay, 1838
Acanthonyx brevifrons A. Milne-Edwards, 1869

First record: Miers (1886: 43, as *A. lunulatus*). Main references: A, B, C, E. Depth range: 75-110 m; elsewhere, 0-110 m. An eastern-central Atlantic islands species; also known from Canary, Madeira and Azores archipelagos (González, 2016).

Acanthonyx depressifrons Manning & Holthuis, 1981

First record: Türkay (1982: 98, 111). No further records. Depth range: 5-5 m; elsewhere, 5-10 m. A Guinean species.

Acanthonyx lunulatus (Risso, 1816)

First record: Guinot & Ribeiro (1962: 76). B, C, D, E, this work. Depth range: 0-90 m; elsewhere, same range. An eastern Atlantic warm-temperate species.

Subfamily Pisinae Dana, 1851
Anamathia rissoana (Roux, 1828)

First record: present work; ICCM413, one male, CL/CW 33.5/23.3 mm, Santiago Island, Ponta Água Doce, cruise *CAMARÃO-1*, stn 5, 15°09'N 23°47'W, 220-258 m, rocky bottom, 19 Nov. 2011, semi-floating trap. Elsewhere, 100-730 m. An Atlanto-Mediterranean species.

Apiomithrax violaceus (A. Milne-Edwards, 1868)

First record: A. Milne-Edwards (1868: 50-52, as *Micropisa violacea*). Main references: A, C, D. Depth range: 3-110 m; elsewhere, 3-36 m. A Guinean species.

Herbstia rubra A. Milne-Edwards, 1869

First record: A. Milne-Edwards (1869: 354; one female; type-locality, Cape Verde islands). Main references: A, B, C, D, E, this work. Depth range: 0.5-75 m; elsewhere, same depth. A Guinean species.

Micropisa ovata Stimpson, 1858

First record: Stimpson (1858: 217). Main references: A, B, C, D, E. Depth range: 0-110 m; elsewhere, same depth. A Guinean species.

Pisa armata (Latreille, 1803)

First record: Studer (1883: 9, as *P. Gibsii*). Main references: A, B, C, D, E. Depth range: 70-110 m; elsewhere, 18-162 m. An eastern Atlantic warm-temperate species.

Pisa nodipes (Leach, 1815)

First record: A. Milne-Edwards & Bouvier (1900: 129-130, as *P. armata*). Main references: A, B, C, E. Depth range: 75-75 m; elsewhere, 0-100 m. An Atlanto-Mediterranean species.

Family Inachidae MacLeay, 1838

Dorhynchus thomsoni Thomson, 1873

First record: A. Milne-Edwards & Bouvier (1900: 148-152, as *Lispognathus Thomsoni*). Main references: A, B, D. Depth range: 225-1200 m; elsewhere, 106-2080 m. A cosmopolitan or worldwide species.

Inachus grallator Manning & Holthuis, 1981

First record: ?A. Milne-Edwards & Bouvier (1900: 143-144, as *I. dorsettensis*). Main references: A, B. Depth range: 90-318 m; elsewhere, 36-325 m. A Guinean species. Remarks: Probably first recorded from the Cape Verde islands by Milne-Edwards & Bouvier (1900), based on collections on sand with shells at São Vicente-Santo Antão channel (75-90 m) and at E of Santo Antão Island (318 m) (Manning & Holthuis, 1981).

Inachus phalangium (Fabricius, 1775)

First record: Studer (1883, as *Stenorhynchus phalangium*). Main references: A, B, C, E. Depth range: unknown; elsewhere, 0.5-160 m. An eastern Atlantic cold-temperate species.

Inachus sp.2 Fransen, 1991

First record: Fransen (1991: 40-42, 50-52, 120-121). No further records. Depth range: 50-110 m. Likely endemic to the area.

Macropodia doracis Manning & Holthuis, 1981

First record: A. Milne-Edwards & Bouvier (1900: 155, as *Stenorhynchus aegyptius* [part]). Main references: A, B, C. Depth range: 110-180 m. Endemic to the area.

Macropodia aff. ***doracis*** Manning & Holthuis, 1981

First record: Fransen (1991: 40, 49, 52, 127). No further records. Depth range: 60-90 m. Likely endemic to the area.

Macropodia longicornis A. Milne-Edwards & Bouvier, 1899

First record: A. Milne-Edwards & Bouvier (1899: 48, as *Stenorhynchus longicornis*; type-locality, Praia, Santiago Island, Cape Verde islands). Main references: A, B, C. Depth range: 150-275 m. Endemic to the area.

Macropodia longipes (A. Milne-Edwards & Bouvier, 1899)

First record: A. Milne-Edwards & Bouvier (1900: 156-157, as *Stenorhynchus longicornis*). Main references: A, B, D. Depth range: 318-318 m; elsewhere, 50-445 m. An Atlanto-Mediterranean species.

Macropodia aff. ***parva*** van Noort & Adema, 1985

First record: Fransen (1991: 46, 128). Main references: E. Depth range: 30-90 m; elsewhere, 20-90 m. A Guinean species; also known from off Mauritania and the Canary Islands (Fransen, 1991).

Macropodia spinulosa (Miers, 1881)

First record: Studer (1882: 7, as *Stenorhynchus phalangium*). Main references: A, B, C. Depth range: 70-70 m; elsewhere, 1-126 m. A Guinean species.

Macropodia tenuirostris (Leach, 1814)

First record: Fransen (1991: 51, 129-130, as *M. longipes*). Main references: D, E. Depth range: 115-115 m; elsewhere, 9-748 m. An eastern Atlantic cold-temperate species.

Macropodia sp.3 Fransen, 1991

First record: Fransen (1991: 41, 46, 48-51, 131-132). No further records. Depth range: 61-1200 m. Likely endemic to the area.

Stenorhynchus lanceolatus (Brullé, 1837)

First record: Miers (1886: 4, as *Leptopodia sagittaria*). Main references: A, B, C, D, E. Depth range: 5-90 m; elsewhere, 5-96 m. A Guinean species.

Family Majidae Samouelle, 1819
Eurynome aspera (Pennant, 1777)

First record: A. Milne-Edwards & Bouvier (1900: 125-127). Main references: A, D, E. Depth range: 61-318 m; elsewhere, 10-1216 m. An eastern Atlantic species of wide distribution.

Maja brachydactyla Balss, 1922

First record: Türkay (1982: 99, as *M. squinado*). No further records. Depth range: unknown; elsewhere, 0-91 m. An eastern Atlantic cold-temperate species.

Maja crispata Risso, 1827

First record: A. Milne-Edwards & Bouvier (1900: 127-128, as *Maia verrucosa*). Main references: A, B, C, E. Depth range: 84-84 m; elsewhere, 0.5-95 m. An Atlanto-Mediterranean species.

Family Mithracidae MacLeay, 1838
Mithrax caboverdianus Türkay, 1986

First record: Türkay (1982: 113, as Majidae gen. sp. indet.). Main references: Türkay (1986) and Fransen (1991: 54, 139-140, one intertidal specimen from Sal Island). Endemic to the area.
Remarks: Described as a new species by Türkay (1986), on the basis of two males with type-locality at Ponta Rodrigo, NE of Boa Vista Island, Cape Verde islands, at 0.5-2 m of depth.

Family Oregoniidae Garth, 1958
Ergasticus clouei A. Milne-Edwards, 1882

First record: Studer (1882: 8). Main references: A, C, D, E. Depth range: 70-400 m; elsewhere, 70-1000 m. An Atlanto-Mediterranean species.

Superfamily PALICOIDEA Bouvier, 1898
Family Palicidae Bouvier, 1898
Palicus caronii (Roux, 1828)

First record: Miers (1886: 334, as *Cymopolia caronii*). Main references: A, B, C, D, E. Depth range: 20-100 m; elsewhere, 18-220 m. An Atlanto-Mediterranean species.

Superfamily PARTHENOPOIDEA MacLeay, 1838
Family Parthenopidae MacLeay, 1838
Subfamily Daldorfiinae Ng & Rodríguez, 1986
Daldorfia bouvieri (A. Milne-Edwards, 1869)

First record: A. Milne-Edwards (1869: 350-351, as *Parthenope bouvieri*; one male; type-locality, São Vicente Island, Cape Verde islands). Main references: A, B, C, D. Depth range: 0.5-91 m; elsewhere, 4-5 m. A Guinean species.

Subfamily Parthenopinae MacLeay, 1838
Distolambrus maltzami (Miers, 1881)

First record: A. Milne-Edwards & Bouvier (1900: 121-122, as *Heterocrypta Maltzani* [sic]). Main references: A, B, C, D. Depth range: 24-347 m; elsewhere, 22-550 m. An eastern Atlantic warm-temperate species.

Parthenopoides massena (Roux, 1830)

First record: Stimpson (1858: 220, as *Lambrus rugosus*). Main references: A, C, D, E. Depth range: 20-110 m; elsewhere, 3-141 m. An Atlanto-Mediterranean species.

Spinolambrus macrochelos (Herbst, 1790)

First record: Bouvier (1922: 76, as *Lambrus Miersi*). Main references: A, B, D, E. Depth range: 91-91 m; elsewhere, 5-1478 m. An Atlanto-Mediterranean species.

Spinolambrus notialis (Manning & Holthuis, 1981)

First record: Fransen (1991: 40, 158, as *Parthenope notialis/miersi*). No further records. Depth range: 55-80 m; elsewhere, 18-162 m. A Guinean species; known from the Western Sahara to Angola (Manning & Holthuis, 1981).
Remarks: Its presence in the area is based on the report by Fransen (1991) of specimens (one from the Cape Verde islands, and 15 from Mauritania) showing intermediate features between *S. notialis* and *S. macrochelos*. Then, it was erroneously compiled by d'Udekem d'Acoz (1999) as a Cape Verdean species on the basis of the Manning & Holthuis (1981) citation from Cap Vert, Senegal.

Velolambrus expansus (Miers, 1879)

First record: A. Milne-Edwards & Bouvier (1900: 117, as *Parthenolambrus expansus*). Main references: A, B, C, D, E. Depth range: 69-90 m; elsewhere, 30-170 m. An Atlanto-Mediterranean species.
Remarks: Also reported as *Parthenope expansa* (Miers, 1879), as accepted taxonomic status (Marco-Herrero et al., 2015; González, 2016).

Superfamily PILUMNOIDEA Samouelle, 1819
Family Pilumnidae Samouelle, 1819
Pilumnus hirtellus (Linnaeus, 1761)

First record: Manning & Holthuis (1981: 152). Main references: B, C, E. Depth range: unknown; elsewhere, 0-90 m. An eastern Atlantic cold-temperate species.

Pilumnus inermis A. Milne-Edwards & Bouvier, 1894

First record: A. Milne-Edwards & Bouvier (1900: 73, as *P. hirtellus* var. *inermis*). Main references: A, B, C, D, E, this work. Depth range: 3-225 m; elsewhere, 5-400 m. An Atlanto-Mediterranean species.

Pilumnus perrieri A. Milne-Edwards & Bouvier, 1898

First record: A. Milne-Edwards & Bouvier (1898: 183-185; type-locality, Cape Verde islands; 75 m). Main references: A, B, C, D, E. Depth range: 40-91 m; elsewhere, 20-91 m. A Guinean species.

Pilumnus spinifer H. Milne Edwards, 1834

First record: Bouvier (1922: 61, as *P. hirtellus* var. *spinifer*). Main references: A. Depth range: 61-91 m; elsewhere, 1-179 m. An Atlanto-Mediterranean species.
Remarks: The first record for the area by Bouvier (1922) was based on specimens caught in the SW of Boa Vista Island at 61 m depth. That record was compiled by Monod (1956), but not in subsequent publications.

Superfamily PORTUNOIDEA Rafinesque, 1815

Family Carcinidae MacLeay, 1838

Xaiva biguttata (Risso, 1816)

First record: A. Milne-Edwards & Bouvier (1900: 61-62, as *Portumnus biguttatus*). Main references: A, B, C, E. Depth range: unknown; elsewhere, 1-10 m. An eastern Atlantic warm-temperate species.

Family Geryonidae Colosi, 1923

Chaceon affinis (A. Milne-Edwards & Bouvier, 1894)

First record: Bouvier (1922: 70-71, as *Geryon affinis*). Main references: B, E, F, G, this work. Depth range: 692-1300 m; elsewhere, 130-2047 m. An eastern Atlantic cold-temperate species.

Chaceon gordonae (Ingle, 1985)

First record: Ingle (1985: 95-97, as *Geryon gordonae* [in part], not as part of type-material). Main references: E. Depth range: 628-628 m; elsewhere, 1183-1183 m. A Guinean species.

Chaceon maritae (Manning & Holthuis, 1981)

First record: González et al. (2004: 1-76). Main references: F, G. Depth range: 301-1000 m; elsewhere, 100-1000 m. A Guinean species.

Family Pirimelidae Alcock, 1899

Pirimela denticulata (Montagu, 1808)

First record: Cunningham (1871: 492). Main references: A, C, E. Depth range: unknown; elsewhere, 0-250 m. An eastern Atlantic cold-temperate species.

Family Polybiidae Ortmann, 1893

Bathynectes maravigna (Prestandrea, 1839)

First record: González et al. (2004: 1-76). Main references: F, G. Depth range: 301-700 m; elsewhere, 60-1410 m. An eastern Atlantic cold-temperate species.
Remarks: First recorded for the area on the basis of 19 specimens from off Boa Vista Island and 23 from off Santiago Island (cruise *TALIARTE 2003-08*, R/V "Taliarte", Aug. 2003). A total of 107 specimens (accumulate) of this species were reported by González et al. (2009, same islands, 301-700 m, cruise *CABO VERDE 2005-06*, R/V "Pixape II", Jun. 2005).

Bathynectes piperitus Manning & Holthuis, 1981

First record: Filhol (1885, as *Bathynectes*). Main references: A, B, D, this work. Depth range: 108-628 m; elsewhere, 200-546 m. A Guinean species.
Remarks: Of minor interest, it is probably the unique brachyuran species regularly exploited in the area, as by-catch in the specialised trap fishery for the Cape Verde spiny lobster, *Palinurus charlestoni* Forest & Postel, 1964.

Liocarcinus corrugatus (Pennant, 1777)

First record: Miers (1881: 200-201, as *Portunus corrugatus*). Main references: A, B, C, D, E. Depth range: 35-68 m; elsewhere, 1-147 m. An eastern Atlantic warm-temperate species.

Macropipus rugosus (Doflein, 1904)

First record: present work; ICCM410, one male, CL/CW 16.3/20.2 mm, Boa Vista Island, Ponta Lacacão, cruise *CAMARÃO-2*, stn 15-D4, 15°55'N 22°57'W, 113-133 m, rocky bottom, 14 Mar. 2012, bottom trap; ICCM411, one male, CL/CW 22.6/28.8 mm, ICCM412, one non-ovigerous female, CL/CW 20.1/25.7 mm, both specimens from cruise *CAMARÃO-3*, stn 22, 16°47'N 22°53'W, Sal Island, Calhetinha, 125-130 m, rocky bottom, 18 Jul. 2012, bottom trap. Elsewhere, 5-400 m. A Guinean species.

Family Portunidae Rafinesque, 1815

Subfamily Portuninae Rafinesque, 1815

Callinectes amnicola (De Rochebrune, 1883)

First record: Guinot & Ribeiro (1962: 50, as *C. latimanus*). Main references: B, C. Depth range: inshore estuarine; elsewhere, 0-30 m. A Guinean species.

Callinectes marginatus (A. Milne-Edwards, 1861)

First record: A. Milne-Edwards (1878: 229, as *C. africanus* [var. de *diacanthus*]). Main references: A, B, C. Depth range: shallow waters; elsewhere, similar range. A Guinean species.

Cronius ruber (Lamarck, 1818)

First record: A. Milne-Edwards (1869: 54, as *Goniosoma Milleri*). Main references: A, B, C, D. Depth range: 2.5-20 m; elsewhere, 5-69 m. A pantropical or circuntropical species.

Laleonectes vocans (A. Milne-Edwards, 1878)

First record: A. Milne-Edwards (1878: 225-226, as *Neptunus vocans*; one carapace; type-locality, Cape Verde islands). Main references: A, B, C, E. Depth range: 5-6 m; elsewhere, 6-37 m. An amphi-Atlantic species of warm affinity.

Portunus (Portunus) hastatus (Linnaeus, 1767)

First record: Fransen (1991: 37, 41-42, 46, 56, 178-179). Main references: D, E. Depth range: 20-40 m; elsewhere, 2-32 m. A Guinean species.

Portunus (Portunus) inaequalis (Miers, 1881)

First record: Monod (1956: 201, as *Neptunus inaequalis*). Main references: A, B, C. Depth range: 4-15 m; elsewhere, 4-73 m. A Guinean species.

?**Sanquerus validus** (Herklots, 1851)

First record: González et al. (2004: 28, 35, as *Portunus validus*). Main references: B. Depth range: 150-280 m; elsewhere, 3-55 m. A Guinean species, known from Mauritania to Angola (Manning & Holthuis, 1981).
Remarks: The citation by González et al. (2004) was based on two specimens from Santiago Island (Ponta Covinha, and Ponta do Lobo, both at 140-150 m), and another specimen from Boa Vista Island (Ponta Taráfe, 280-300 m). This record was then reported by González et al. (2004: 53, 58: as *Portunus* cf. *validus*). The species' original name of *Portunus (Posidon) validus* Herklots, 1851 was reassigned to the currently valid name of *Sanquerus validus*. Unfortunately this material was lost during the sinking of R/V "Taliarte" and its preliminary on-board identification not corroborated at laboratory. Moreover, these specimens were caught well out of the known depth range for this species. So authors have decided to consider as doubtful the presence of this species in the study area.

Subfamily Thalamitinae Paul'son, 1875
Thalamita poissonii (Audouin, 1826)

First record: Guinot & Ribeiro (1962: 46, as *T. africana*). Main references: C, E. Depth range: 2-8 m; elsewhere, 0.5-20 m. A pantropical or circuntropical species.

Superfamily PSEUDOZIOIDEA MacLeay, 1838
Family Pseudoziidae MacLeay, 1838
Euryozius bouvieri (A. Milne-Edwards, 1869)

First record: A. Milne-Edwards (1869: 377-378, as *Xantho Bouvieri*; type-locality, Cape Verde islands). Main references: A, B, C, D, E. Depth range: 0-30 m; elsewhere, 6-23 m. An eastern-central Atlantic islands species; also known from the Canary, Madeira and Azores archipelagos (González, 2016).

Superfamily TRAPEZIOIDEA Miers, 1886
Family Domeciidae Ortmann, 1893
Domecia acanthophora africana Guinot, 1964

First record: Bouvier (1922: 273, *as D. hispida*). Main references: A, B, C, D, E. Depth range: 2.5-22 m; elsewhere, 0-35 m. An insular West African species.

Superfamily XANTHOIDEA MacLeay, 1838
Family Panopeidae Ortmann, 1893
Eurypanopeus blanchardi (A. Milne-Edwards, 1881)

First record: Dana (1852: 170, as *Xanthus (Xantho) parvulus*). Main references: A, B, C, D, this work. Depth range: 0-22 m; elsewhere, 0-6 m. A Guinean species.

Panopeus africanus A. Milne-Edwards, 1867

First record: Fransen (1991: 55, 153). Main references: D. Depth range: 0-8 m; elsewhere, 0-140 m. A Guinean species.

Family Xanthidae MacLeay, 1838
Xanthidae sp. Fransen, 1991

First record: Fransen (1991: 40, 48, 53-54, 193). Main references: D. Depth range: 0-312 m; elsewhere, 0-0.5 m. A Guinean species; also known from Senegal (Fransen, 1991).

Subfamily Actaeinae Alcock, 1898
Paractaea margaritaria (A. Milne-Edwards, 1867)

First record: A. Milne-Edwards (1867: 41-42, as *Actaea margaritaria*; type-locality, São Vicente, Cape Verde islands). Main references: A, B, C, D, this work. Depth range: 3-91 m; elsewhere, 4/5-45 m. A Guinean species.

Paractaea monodi Guinot, 1969

First record: A. Milne-Edwards & Bouvier (1900: 100-101, as *Actaea margaritaria*). Main references: A, B, C, D, E.

Depth range: 0.5-91 m; elsewhere, 0.5-200 m. An Atlanto-Mediterranean species.

Paractaea rufopunctata (H. Milne Edwards, 1834)

First record: A. Milne-Edwards (1868: 63, as *Actaea rufopunctata*). Main references: A. Depth range: 30-91 m; elsewhere, 0-69 m. A pantropical or circuntropical species.

Subfamily Euxanthinae Alcock, 1898
Glyptoxanthus cavernosus (A. Milne-Edwards, 1878)

First record: A. Milne-Edwards (1878: 226-227, as *Actaea cavernosa*; type-locality, Cape Verde islands). Main references: A, B, C, D, E. Depth range: 0-17 m; elsewhere, same range. An eastern-central Atlantic islands species; also known from the Canaries (González, 2016).

Glyptoxanthus corrosus (A. Milne-Edwards, 1869)

First record: A. Milne-Edwards (1869: 376-377, as *Xantho corrosus*; type-locality, Cape Verde islands). Main references: A, B, C. Depth range: neritic littoral. Endemic to the area.

Monodaeus couchii (Couch, 1851)

First record: A. Milne-Edwards & Bouvier (1900: 95, as *Xantho tuberculatus*). Main references: A, D, E. Depth range: 110-594 m; elsewhere, 0-1415 m. An eastern Atlantic warm-temperate species.

Subfamily Xanthinae MacLeay, 1838
Coralliope parvula (A. Milne-Edwards, 1869)

First record: A. Milne-Edwards (1869: 412, as *Actumnus parvulus*; type-locality, Cape Verde islands). Main references: A, B, C, D, E. Depth range: 5-110 m; elsewhere, 0-355 m. A Guinean species.

Cycloxanthops occidentalis (A. Milne-Edwards, 1867)

First record: A. Milne-Edwards (1867: 36-38, as *Xantho occidentalis*; type-locality, Cape Verde islands). Main references: A, B, C. Depth range: 0-3 m; elsewhere, 0-23 m. A Guinean species.

Microcassiope minor (Dana, 1852)

First record: A. Milne-Edwards (1869: 409-410, as *Xanthodes rufopunctatus*). Main references: A, B, C, D, E. Depth range: 0.5-61 m; elsewhere, 0-220 m. An amphi-Atlantic species of warm affinity.

Nanocassiope melanodactyla (A. Milne-Edwards, 1867)

First record: Dana (1852: vol I, 170, as *Xantho parvulus*). Main references: A, B, D, E. Depth range: 4-225 m; elsewhere, 5-200 m. A Guinean species.

Paraxanthias eriphioides (A. Milne-Edwards, 1867)

First record: A. Milne-Edwards (1867: 38-39, as *Xanthodes eriphioides*; type-locality, São Vicente, Cape Verde islands). Main references: A, B, C, D, E. Depth range: 0.5-85 m; elsewhere, unknown. An eastern-central Atlantic islands species; also known from the Azores (cf. d'Udekem d'Acoz, 1999).

Xantho hydrophilus (Herbst, 1790)

First record: A. Milne-Edwards & Bouvier (1900: 95-96, as *X. floridus*). Main references: A, B, C, D, E. Depth range: 0-30 m; elsewhere, 0-37 m. An Atlanto-Mediterranean species.

Xantho sexdentatus (Miers, 1881)

First record: Fransen (1991: 53, 199-200). Main references: D, this work. Depth range: 0-15 m; elsewhere, 0-35 m. A Guinean species.

Xantho sp. Fransen, 1991

First record: Fransen (1991: 52, 200). Main references: D. Depth range: 0-15 m (likely); elsewhere, 0-15 m. A Guinean species.

Xanthodius inaequalis faba (Dana, 1852)

First record: ?Dana (1852: 195-196 as *Actaeodes faba*); A. Milne-Edwards (1869: 410-412, as *Chlorodius (Leptodius) convexus*). Main references: A, B, C, this work. Depth range: 0.5-10 m. Endemic to the area.

Subfamily Zosiminae Alcock, 1898
Platypodiella picta (A. Milne-Edwards, 1869)

First record: A. Milne-Edwards (1869: 410, as *Lophactaea picta*; type-locality, Santa Luzia and Salamança, São Vicente, Cape Verde islands). Main references: A, B, C, D, E. Depth range: 0.5-28 m; elsewhere, 0-30 m. A Guinean species.

Superfamily GRAPSOIDEA MacLeay, 1838
Family Gecarcinidae MacLeay, 1838
Cardisoma armatum Herklots, 1851

First record: Stimpson (1858: 100, as *C. Guanhumi*). Main references: A, B, C. Terrestrial. A Guinean species.

Family Grapsidae MacLeay, 1838
Geograpsus lividus (H. Milne Edwards, 1837)

First record: A. Milne-Edwards & Bouvier (1900: 110).

Main references: A, B, C. Depth range: 10-10 m; elsewhere, shallow waters. A pantropical or circuntropical species.

Subfamily Grapsinae MacLeay, 1838
Grapsus adscensionis (Osbeck, 1765)

First record: Dana (1852: 336-337 (Atlas, 1855), as *G. pictus*). Main references: A, B, C, D, E, this work. Depth range: 0-10 m; elsewhere, 0-4 m. A Guinean species.

Pachygrapsus maurus (Lucas, 1846)

First record: ?Monod (1956: 422, as *Goniograpsus simplex*; Fransen, 1991: 44, 149-150). Main references: ?A, D. Depth range: 0-0 m; elsewhere, 0-6 m. An Atlanto-Mediterranean species.

Pachygrapsus transversus (Gibbes, 1850)

First record: Miers (1886: 259-260). Main references: A, B, C, D, E. Depth range: 0-6 m; elsewhere, 0-7 m. A pantropical or circuntropical species.

Planes minutus (Linnaeus, 1758)

First record: Fransen (1991: 49, 170-171). Main references: D. Depth range: 0-31 m; elsewhere, same range. A pantropical or circuntropical species.

Family Percnidae Števčić, 2005
Percnon gibbesi (H. Milne Edwards, 1853)

First record: A. Milne-Edwards & Bouvier (1900: 114-115, as *Leiolophus planissimus*). Main references: A, B, C, D, E, this work. Depth range: 0.5-29 m; elsewhere, same range. A pantropical or circuntropical species.

Family Plagusiidae Dana, 1851
Euchirograpsus liguricus H. Milne Edwards, 1853

First record: A. Milne-Edwards & Bouvier (1900: 107-108, as *E. americanus*). Main references: A, B, C, E. Depth range: 110-180 m; elsewhere, 10-359 m. An eastern Atlantic cold-temperate species.

Plagusia depressa (Fabricius, 1775)

First record: Miers (1886: 272). Main references: A, B, C, D, E, this work. Depth range: 0-5 m; elsewhere, same range. An amphi-Atlantic species of warm affinity.

Family Varunidae H. Milne-Edwards, 1853
Subfamily Cyclograpsinae H. Milne Edwards, 1853
Cyclograpsus integer H. Milne Edwards, 1837

First record: A. Milne-Edwards (1878: 228, as *C. occidentalis*). Main references: A, B, this work. Depth range: 0-10 m; elsewhere, 2-5 m. An amphi-Atlantic species of warm affinity.

Superfamily OCYPODOIDEA Rafinesque, 1815
Family Ocypodidae Rafinesque, 1815
Subfamily Ocypodinae Rafinesque, 1815
Ocypode africana de Man, 1881

First record: Bouvier (1922: 74). Main references: A, C. Depth range: 0-3 m; elsewhere, same range. A Guinean species; known from Mauritania to SW Africa (Manning & Holthuis, 1981).
Remarks: According to Monod (1956) and Türkay (1982), this species was first recorded from the study area by Bouvier (1922), based on material collected at Branco Islet. Ribeiro (1964) reported on *Ocypoda* (sic) sp. from Santo Antão Island (Bay of Monte do Trigo) and from Boa Vista Island (Bay of Sal Rei, and Curralinho). However, it was not compiled by Manning and Holthuis (1981), and there are no further records for the area.

Ocypode cursor (Linnaeus, 1758)

First record: Stimpson (1858: 100). Main references: A, B, C, D, E, this work. Depth range: 0-3 m; elsewhere, same range. An eastern Atlantic warm-temperate species.

Subfamily Ucinae Dana, 1851
Afruca tangeri (Eydoux, 1835)

First record: Monod (1956: 403). Main references: A, C, E. Depth range: 0-2 m; elsewhere, same range. A Guinean species.

Superfamily PINNOTHEROIDEA de Haan, 1833
Family Pinnotheridae de Haan, 1833
Viridotheres marionae Manning, 1996

First record: Manning (1996: 271-273; one specimen; type-locality, Boa Vista Island, Cape Verde islands, 91 m). Main references: Manning (1996). Depth range: 91-91 m. Endemic to the area.

Viridotheres viridis (Manning, 1993)

First record: Fransen (1991: 54, 166, as *Pinnotheres* sp.; one specimen, type-locality, Branco Islet, Cape Verde islands, 12-15 m). Main references: Manning (1993) and Wirtz (2009). Depth range: 3-15 m. Endemic to the area.
Remarks: After this species was first recorded for the area, it was assigned to *Nepinnotheres viridis* by Manning (1993), but currently reassigned to genus *Viridotheres* Manning, 1996 by Manning (1996).

Discussion

The 125 crab species and subspecies reported herein around the Cape Verde islands are grouped in 40 accepted families and 83 genera. This represents a number of species very close to the 132 brachyuran species recently reported from the Canary Islands, grouped in 39 families and 77 genera (González, 2016).

Seven benthic species seem to occur in waters of the Cape Verde islands at the shallowest depth ever recorded elsewhere: *D. bouvieri*, *P. inermis*, *C. gordonae*, *B. piperitus*, *C. ruber*, *P. margaritaria* and *N. melanodactyla*; sixteen benthic species seem to occur at the greatest depth ever recorded elsewhere: *S. spinirostris*, *D. filholi*, *L. elegans*, *A. cessacii*, *I. spinosa*, *A. violaceus*, *C. maritae*, *B. piperitus*, *P. (P.) hastatus*, *E. bouvieri*, *E. blanchardi*, *P. margaritaria*, *P. rufopunctata*, *N. melanodactyla*, *G. adscensionis* and *C. integer*. This work enlarges the known depth lower limit in the area for *H. barbata*, *P. cuvieri*, *C. granulata* and *M. obsoletus*, and newly provides vertical ranges for *M. nodifrons* and *X. inaequalis faba*.

When compared both brachyuran catalogues, the Cape Verde and Canary Islands have divergent composition of species. Taking into account the supra-species taxa, the Cape Verdean superfamily Raninoidea does not currently occur around the Canary archipelago, and the Canarian superfamily Cryptochiroidea has not been found in Cape Verde islands. The Cape Verdean tropical-subtropical Dynomenidae, Raninidae, Menippidae, Acidopsidae, Chasmocarcinidae, Mithracidae and Gecarcinidae do not currently occur around the Canaries; the Canarian cold/warm-temperate Cancridae, Eriphiidae, Euryplacidae, Mathildellidae, Progeryonidae, Thiidae and Cryptochiridae have not been found in the Cape Verde islands.

Regarding the species' biogeographic patterns, a first preliminary description of all components of the Cape Verdean brachyuran fauna (125 species) shows just one main group: 51 tropical and subtropical eastern Atlantic (Guinean) species (40.8%), distantly followed by 18 Atlanto-Mediterranean species (14.4%), 11 species endemic to the area (8.8%), and 10 eastern Atlantic warm-temperate species (8.0%, Table 1). A second description of the Cape Verdean benthic littoral and/or upper-bathyal species (96 species, depth 0-300 m) reveals the same principal group now formed by 42 Guinean species (43.8%), followed far behind by 12 Atlanto-Mediterranean species (12.5%), and 10 endemic to the area (10.4%, Table 1). On the contrary, according to González (2016) the Canarian brachyuran crabs living shallower than the upper slope (123 species, depth 0-300 m) showed three main groups: 39 Atlanto-Mediterranean species (31.7%), 28 Guinean species (22.8%), and 21 eastern Atlantic cold-temperate species (17.1%, Table 2).

The greater number of coastal crabs endemic to the Cape Verde islands than those of the Macaronesian archipelagos has been interpreted as a combined result of the Cape Verde islands' isolation, their generally young geological age, and the shortening of their shallow habitats and oceanographic bottlenecks during the most recent glaciations; on the contrary, the coastal fish communities of the Macaronesian archipelagos are characterized by low endemism rates (e.g. Brito et al., 2007; Wirtz et al., 2008).

In the study area, the fourth biogeographic component in number of species is formed by the amphi-Atlantic species of warm affinity (7.3% versus 4.1% in the Canaries, González, 2016) (Table 2), suggesting according to Spalding et al. (2007) a relatively good bio-connexion between the Cape Verde eco-region and the Guianan and Amazonia eco-regions (both forming the North Brazil Shelf province). Present results seem to corroborate the role played by the Cape Verde islands and nearby seamounts/banks as stepping stones anchored in the middle of the ocean, but connecting the western and eastern Atlantic basins.

Twenty-four brachyuran benthic species (19.5% of the 123 crabs listed) occurring in the Cape Verde islands currently have their southern limit of distribution in this archipelago: *D. nodosa*, *L. elegans*, *E. alba*, *E. nux*, *A. brevifrons*, *A. rissoana*, *P. nodipes*, *I. phalangium*, *M. longipes*, *M.* aff. *parva*, *M. crispata*, *E. clouei*, *S. macrochelos*, *P. hirtellus*, *P. spinifer*, *C. affinis*, *P. denticulata* (also in Senegal), *B. maravigna*, *E. bouvieri*, *P. monodi*, *G. cavernosus*, *P. eriphioides*, *X. sexdentatus*, *Xantho* spec. (also Senegal) and *P. maurus*. Seventeen benthic species (13.8%) occurring in the Cape Verde islands currently have their northern limit of distribution in this archipelago: *D. filholi*, *R. constricta*, *E. rugulosa* (also Senegal), *M. nodifrons* (also Senegal in the East Atlantic), *E. helleri* (also Senegal), *A. cessacii* (also Senegal), *T. integrifrons* (also Senegal), *I. nucleus*, *A. depressifrons*, *M. spinulosa* (also Senegal), *D. bouvieri*, *P. perrieri* (also Senegal), *C. gordonae*, *B. piperitus*, *P. margaritaria*, *C. occidentalis* (also Senegal) and *G. lividus* (in the East Atlantic). Seventy-two brachyuran benthic species occur in both the Cape Verde and Canary archipelagos, representing 57.6% of species shared with the Canaries. As the Cape Verde Islands belong to its own eco-region, whereas the Canaries to the Macaronesian eco-region (Spalding et al., 2007), the above-mentioned information could be relevant in the context of faunal movements derived from the eastern Atlantic warming.

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Table 1. Composition of the Cape Verdean brachyuran fauna showing the number of species (N) grouped by biogeographic pattern.

Species' biogeographic pattern	All Cape Verdean brachyuran (125 species, depth 0 -> 2000 m) Species		Littoral and upper bathyal benthic (96 species, depth 0-300 m) Species	
	N	%	N	%
Tropical and subtropical eastern Atlantic (TSEA)	51	40.8	42	43.8
Atlanto-Mediterranean (ATLM)	18	14.4	12	12.5
Endemic to the Cape Verde Islands (ECVI)	11	8.8	10	10.4
Eastern Atlantic warm-temperate (EAWT)	10	8.0	7	7.3
Eastern Atlantic cold-temperate (EACT)	8	6.4	3	3.1
Amphi-Atlantic of warm affinity (AAWA)	7	5.6	7	7.3
Pantropical or circumtropical (PANT)	7	5.6	7	7.3
Eastern-central Atlantic islands (ECAI)	6	4.8	6	6.3
Eastern Atlantic of wide distribution (EAWD)	3	2.4	1	1.0
Insular West African (IWAF)	2	1.6	1	1.0
Amphi-Atlantic of wide distribution (AAWD)	1	0.8	0	0.0
Cosmopolitan or worldwide (COSM)	1	0.8	0	0.0

Table 2. Comparison between components of the Cape Verdean and Canarian littoral and upper bathyal benthic brachyurans, showing the number of species (N) grouped by biogeographic pattern.

Species' biogeographic pattern	Littoral and upper bathyal benthic (depth, 0-300 m)			
	This work Cape Verde Islands 96 species		González (2016) Canary Islands 123 species	
	N	%	N	%
Tropical and subtropical eastern Atlantic (TSEA)	42	43.8	28	22.8
Atlanto-Mediterranean (ATLM)	12	12.5	39	31.7
Endemic to the Cape Verde Islands (ECVI)	10	10.4	-	-
Amphi-Atlantic of warm affinity (AAWA)	7	7.3	5	4.1
Eastern Atlantic warm-temperate (EAWT)	7	7.3	10	8.1
Pantropical or circumtropical (PANT)	7	7.3	4	3.3
Eastern-central Atlantic islands (ECAI)	6	6.3	5	4.1
Eastern Atlantic cold-temperature	3	3.1	21	17.1
Eastern Atlantic of wide distribution (EAWD)	1	1.0	6	4.9
Insular West African (IWAF)	1	1.0	-	-
Amphi-Atlantic of wide distribution (AAWD)	0	0.0	1	0.8
Cosmopolitan or worldwide (COSM)	0	0.0	1	0.8
Macaronesian (MAC)	-	-	3	2.4

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BRILL

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CRUSTACEANA

THREE NEW DECAPODS (ARISTEIDAE, CHIROSTYLIDAE, PANDALIDAE) FROM THE CAPE VERDE ISLANDS (NE ATLANTIC)

BY

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ABSTRACT

In the present article three benthic decapods, *Aristeus varidens* Holthuis, 1952 (Aristeidae), *Gastroptychus formosus* (Filhol, 1884) (Chirostylidae) and *Plesionika longicauda* (Rathbun, 1901) (Pandalidae), are recorded for the first time from the Cape Verde Islands. This is the southernmost record of *G. formosus*, as well as the northernmost of *P. longicauda* ever recorded from the eastern Atlantic. Preliminary data on batch fecundity and egg size of the pandalid shrimp are provided. Studied specimens were caught in the frame of a scientific trapping survey.

RESUMEN

En el presente informe tres decápodos bentónicos, *Aristeus varidens* Holthuis, 1952 (Aristeidae), *Gastroptychus formosus* (Filhol, 1884) (Chirostylidae) y *Plesionika longicauda* (Rathbun, 1901) (Pandalidae), son citados por primera vez en aguas de las Islas Cabo Verde. Se trata del registro más meridional de *G. formosus*, así como del registro más septentrional de *P. longicauda* en el Atlántico Oriental. Se aportan datos preliminares sobre la fecundidad parcial y el tamaño de huevos del camarón pandálido. Los ejemplares estudiados fueron capturados en el marco de campañas experimentales con nasas.

INTRODUCTION

The Cape Verde Islands are located in the north-eastern Atlantic. Lying within the 4000 m marine contour, the islands are separated from the coasts of West Africa by depths greater than 3000 m and located 570 km from Cape Verde, Senegal. Their volcanic characteristics are manifest by the absence of wide insular

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shelves, with a bottom depth of 300 m near the coast except around Boa Vista and Maio. These islands show an increase of age from west (<3 million years) to east (15.8 million years) (Ramalho, 2011). Their waters are under the influence of the North Equatorial Counter-Current and the Canary Current, with sea-surface temperature normally higher than 20°C over the year (González et al., 2009a). Biogeographically, the Cape Verde Islands ecoregion is included in the West African Transition province of the Tropical Atlantic realm (Spalding et al., 2007).

Nearly 35 years have passed since Türkay (1982) published his work on decapod crustaceans of the Cape Verde Islands (in German), where, apart from his contributions, he compiled records by Monod (1956) and Manning & Holthuis (1981) among others. After Türkay's work, Fransen (1991) enumerated or first recorded many decapod species collected in the Cape Verde Islands, and few brachyuran crabs (Türkay, 1986; Manning, 1993, 1996) were first described based on Cape Verdean specimens. González et al. (2004, 2009a, regional reports in Spanish and Portuguese) reported on some decapod species, mainly deep-sea forms from off the Cape Verdes. Also González et al. (2009b) reported the presence of the anomuran *Eumunida bella* de Saint Laurent & Macpherson, 1990 (presently placed within the Eumunididae A. Milne-Edwards & Bouvier, 1900) off the Cape Verde archipelago. The first checklist of brachyuran crabs from the Cape Verde Islands, with a biogeographic comparison with the Canary Islands has been compiled by González et al. (2017).

Within the Aristeidae Wood-Mason, 1891 (Dendrobranchiata), four pantropical benthic species have been reported to occur in waters of the Cape Verde Islands to date: *Cerataspis monstruosus* Gray, 1828 (Bouvier, 1905, as *Plesiopenaeus armatus*, at depths of 3000-3840 m off the Cape Verdes), *Aristeus antennatus* (Risso, 1816) (Bouvier, 1908, 250 m), *Hepomadus tener* Smith, 1884 (Fransen, 1991, as *Hepomades* [sic] *tener*, 3650-3850 m) and *Aristaeopsis edwardsiana* (Johnson, 1867) (González et al., 2004, 301-1000 m, with colour photo on page 31).

Within the Chirostylidae Ortmann, 1892 (Pleocyemata, Anomura), just one eastern Atlantic cold-temperate benthic species, *Uroptychus concolor* (A. Milne-Edwards & Bouvier, 1894) (A. Milne-Edwards & Bouvier, 1900, as *Diptychus nitidus concolor*, 495-618 m), has been reported from the Cape Verdes to date.

Within the Pandalidae Haworth, 1825 (Pleocyemata, Caridea), 14 species have been recorded from the Cape Verde Islands to date. *Heterocarpus grimaldii* A. Milne-Edwards & Bouvier, 1900 (Richard, 1902, Guinean, pelagic, 659-975 m), *Heterocarpus ensifer* A. Milne-Edwards, 1881 (Gurney & Lebour, 1941, amphi-Atlantic of warm affinity, benthic, 104-559 m) and *Heterocarpus laevigatus* Spence Bate, 1888 (Crosnier & Forest, 1973, pantropical, benthic, 790-1060 m).

Bitias stocki Fransen, 1990 (Fransen, 1990, amphi-Atlantic of warm affinity, benthic, 1100-1300 m). *Plesionika acanthonotus* (Smith, 1882) (amphi-Atlantic of warm affinity, benthic, 525 m), *Plesionika rossignoli* Crosnier & Forest, 1968 (Guinean, pelagic, 400-750 m) and *Stylopandalus richardi* (Coutière, 1905) (cosmopolitan, pelagic, 3825-4025 m) were recorded by Fransen (1991). *Plesionika edwardsii* (Brandt, 1851) (66-515 m, with colour photo on page 48), *Plesionika ensis* (A. Milne-Edwards, 1881) (104-426 m, with colour photo on page 31), *Plesionika martia* (A. Milne-Edwards, 1883) (216-805 m, with colour photo on page 50) and *Plesionika williamsi* Forest, 1964 (205-710 m, with colour photo on page 53), all them pantropical benthic species, were reported by González et al. (2004). *Plesionika holthuisi* Crosnier & Forest, 1968 (amphi-Atlantic of warm affinity, 196-364 m) and *Plesionika narval* (Fabricius, 1787) (pantropical, 66-302 m), both benthic, were recorded by González et al. (2009a). Recently, *Plesionika antigai* Zariquiey Álvarez, 1955 (Neves et al., 2016, Atlanto-Mediterranean, benthic, no depth data).

The present account records *Aristeus varidens* Holthuis, 1952 (Aristeidae), *Gastroptychus formosus* (Filhol, 1884) (Chirostylidae) and *Plesionika longicauda* (Rathbun, 1901) (Pandalidae) for the first time from the Cape Verde Islands.

MATERIAL AND METHODS

Six exploratory trapping surveys of the bottom megafauna of the Cape Verde Islands were carried out off the islands of Boa Vista, Santiago, São Vicente, Santa Luzia, Sal and São Nicolau, between 2003 and 2012, at depths down to 1000 m. Collecting operations during the first two cruises (2003 and 2005) covered a depth range between 435 m and 1060 m, in order to search for new living resources off the islands of Boa Vista, which is characterized by a sediment-covered broad shelf and slope, and Santiago, with a narrow shelf and slope dominated by hard substrata. The remaining cruises (2010-2012) were mainly directed to the stock assessment of *P. edwardsii* between 66 m and 458 m depth and covered four additional islands (González et al., 2014). In all cruises bottom traps (BT) and semifloating shrimp traps (SFST, operated around 2.4 m above the seafloor) were used as baited fishing gear (González et al., 1992, 2004, 2014) (fig. 1).

For *P. longicauda* all six preserved ovigerous females were used to estimate fecundity. Attached eggs were removed from pleopods, and egg masses were then placed on 100-mm mesh and washed. A subsample of 20% in weight from each selected female was then counted by means of a dissection microscope. The batch fecundity, defined as the egg production by batch, was estimated by the gravimetric method (Tuset et al., 2011; Triay-Portella et al., 2014, 2016).

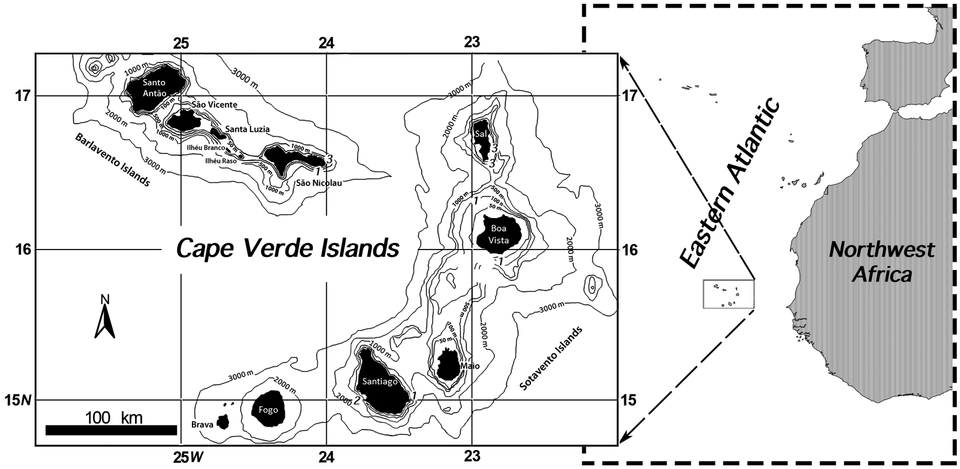

Fig. 1. Map of the study area, the Cape Verde Islands (northeastern Atlantic) with the collection locations: 1, *Aristeus varidens* Holthuis, 1952; 2, *Gastroptychus formosus* (Filhol, 1884); 3, *Plesionika longicauda* (Rathbun, 1901).

Voucher specimens were labelled, curated, data-based and deposited, available for verification (Turney et al., 2015), in the ICCM study collection at the University of Las Palmas de Gran Canaria.

The abbreviations CL and CW stand for carapace length and carapace width, respectively, and are measured with a digital calliper in millimetres. For *G. formosus*, overall body length and cheliped lengths were also taken.

RESULTS

Three decapod species have been newly recorded for the Cape Verde Islands herein.

Systematics

Suborder DENDROBRANCHIATA Spence Bate, 1888

Superfamily PENAEOIDEA Rafinesque, 1815

Family ARISTEIDAE Wood-Mason, 1891

Genus *Aristeus* Duvernoy, 1840

Aristeus varidens Holthuis, 1952

Material examined.— ICCM432, three females, 27.8-30.0 mm CL, cruise Camarão-1, station 4, 15°10′N 23°47′W, off Ponta Água Doce, Santiago Island, 220-258 m, rocks, 19.xi.2011, BT. ICCM433, one female, 31.3 mm CL, cruise Camarão-2, station 1-D3, 16°15′N 23°05′W, off Ponta do Sol, Boa Vista Island, 219-237 m, pebbles, 11.iii.2012, BT. ICCM434, one female, 27.6 mm

CL, cruise Camarão-2, station 18, 15°56′N 22°53′W, East of Ponta Taráfe, Boa Vista Island, 192-236 m, rocks, 14.iii.2012, SFST. ICCM435, one female, 30.7 mm CL, cruise Camarão-3, station 32(9), 16°33′N 24°22′W, off Tarrafal, São Nicolau Island, 426 m, rocks, 25.vii.2012, BT.

Remarks.— The specimens collected agree well with the descriptions and colour pattern given for the species (Lagardère, 1981; Fransen, 2014). A subtropical/tropical Atlantic (Guinean) benthic species. Known from the southwestern of Western Sahara (Rio de Oro, 24°N), Senegal, Guinea, southward to Angola (Cabinda) and south-western Africa (Namibia, 18°S) (Holthuis, 1980; Lagardère, 1981). Young individuals are found at depths of 300 m and below to 1134 m, while adults occur between 400 and 600 m, on muddy bottoms (Holthuis, 1980; Lagardère, 1981; Fransen, 2014). The maximum trawl yields are obtained at night, suggesting that the species may dig into the substrate by day (Lagardère, 1981; Fransen, 2014). Its life span is about 2 years and reproduction begins at the end of the cold season (Lagardère, 1981; Fransen, 2014). Feeds on crustaceans, fishes and polychaete worms (Fransen, 2014). Maximum total length reported up to 12 cm (males) and 20 cm (females) (Holthuis, 1980; Lagardère, 1981; Fransen, 2014). The studied specimens measured up to 31.3 mm CL.

This species seems to be the most abundant of the deep-water shrimps off tropical West Africa, with traditional fishing grounds (commercially bottom trawled) at the continental slopes off Senegal, Guinea and Angola (Holthuis, 1980; Lagardère, 1981; Fransen, 2014). The studied specimens, collected from both windward (São Nicolau) and leeward (Boa Vista and Maio) island chains of the Cape Verdes, were adults caught on (benthic) or over (epibenthic) hard bottoms (rocks, pebbles), between 192 and 426 m of depth, a bathymetric interval shallower than those reported for the African continental slopes.

This is the first record for this species from the Cape Verde Islands, representing the fifth aristeid and the second *Aristeus* species recorded for this archipelago.

Suborder PLEOCYEMATA Burkenroad, 1963
Infraorder ANOMURA MacLeay, 1838
Superfamily CHIROSTYLOIDEA Ortmann, 1892
Family CHIROSTYLIDAE Ortmann, 1892
Genus *Gastroptychus* Caullery, 1896
Gastroptychus formosus (Filhol, 1884)

Material examined.— ICCM431, one male, 8.3/7.4 mm CL/CW, overall body length 22.8/19.7 mm with/without rostrum, cheliped length 79.9/78.0 mm right/left, cruise Cabo Verde 2005-06, station 208/210, 15°02′N 23°46′W, Ponta Covinha, Santiago Island, 525-630 m, mixed substrate, 16.vi.2005, BT.

Remarks.— The collected specimen agrees well with the description and colour pattern given for the species (Filhol, 1884; Zariquiey Álvarez, 1968; Hayward &

Ryland, 1990). An amphi-Atlantic benthic species of wide distribution. Previous records of this species are scarce, although it has been reported across the Atlantic Ocean from Nova Scotia, Canada to Ireland, Scotland, off Rochefort, France, Bay of Biscay and south to the Azores along the Mid-Atlantic Ridge, the Canary Islands (Milne-Edwards & Bouvier, 1900, as *Ptychogaster formosus*; Bouvier, 1922; Zariquiey Álvarez, 1968; González, 1995), and NW Morocco (Hayward & Ryland, 1990; Pohle & Macpherson, 1995; Baba et al., 2008) and south to Cape Bojador, Western Sahara (A. Milne-Edwards & Bouvier, 1900). Reported at depths between 699 and 1786 m (Pohle & Macpherson, 1995; d'Udekem d'Acoz, 1999; Baba et al., 2008), it has been found on corals, sand with rocks, and mixed substrates (González, 1995). This species forms a close association with deep-sea cold-water corals in the North Atlantic; the adults have very specific habitat preferences, being only found on gorgonian and antipatharian corals with strong preference for *Leiopathes* sp. as a host (Le Guilloux et al., 2010). Overall body length 44-52 mm, chelipeds length up to 121 mm (Zariquiey Álvarez, 1968; Hayward & Ryland, 1990). The studied specimens measured 22.8 mm in overall body length (including rostrum) and 79.9 mm in chelipeds length (right).

This is the first record for this species from the Cape Verde Islands and the southernmost one ever recorded, representing the second chirostylid and the first *Gastroptychus* species recorded for this archipelago.

Infraorder CARIDEA Latreille, 1817
Superfamily PANDALOIDEA Haworth, 1825
Family PANDALIDAE Haworth, 1825
Genus *Plesionika* Spence Bate, 1888
Plesionika longicauda (Rathbun, 1901)

Material examined.— ICCM425, three ovigerous females (BT), 16.7-16.9 mm CL, one non-ovigerous female (BT), 14.7 mm CL, ICCM426, two males (SFST), 12.1-15.2 mm CL, cruise Camarão-3, station 19, 16°45′N 22°52′W, off Salão Azul, Sal Island, 105-120 m, rocks, 17.vii.2012. ICCM427, one ovigerous female, 15.6 mm CL, ICCM428, three males, 13.3-13.6 mm CL, cruise Camarão-3, station 22, 16°45′N 22°52′W, off Calhetinha, Sal Island, 125-130 m, rocks, 18.vii.2012, SFST. ICCM429, two ovigerous females (SFST), 16.3-17.4 mm CL, one male (NB), 13.1 mm CL, cruise Camarão-3, station 19-D2, 16°45′N 22°52′W, off Salão Azul, Sal Island, 99-123 m, rocks, 18.vii.2012. ICCM430, one non-ovigerous female, 16.4 mm CL, one male, 9.6 mm CL, cruise Camarão-3, station 25(2), 16°33′N 24°03′W, off Ponta de Leste, São Nicolau Island, 90-135 m, rocks, 23.vii.2012, SFST.

Additional material.— Four individuals caught off Sal Island during cruise Camarão-3 and used for chemical analyses: one 17.0 mm CL ovigerous female, station 19, 16°45′N 22°52′W, off Salão Azul, 105-120 m, rocks, 17.vii.2012, BT; one 15.2 mm CL ovigerous female, station 19-D2, 16°45′N 22°52′W, off Salão Azul, 99-123 m, rocks, 18.vii.2012, BT; one 9.8 mm CL non-ovigerous specimen, station 20, 16°45′N 22°52′W, off Salão Azul, 130-167 m, rocks, 17.vii.2012, BT; one

12.5 mm CL non-ovigerous specimen, station 14-D2, 16°37′N 22°50′W, off Serra Negra, rocks, 126-154 m, 20.vii.2012, BT.

Remarks.— The specimens collected agree well with the description given for the species (Chan & Crosnier, 1991). An amphi-Atlantic benthic species of warm affinity distributed along the West African coast from south of Senegal (16°32′N) to Angola (10°10′S), and the western Atlantic from the Gulf of Mexico, Caribbean Sea to off Suriname, including Bahamas (Chan & Crosnier, 1991). These authors examined material from Senegal, Liberia, Ivory Coast, Gabon, Congo and Angola, but they did not include the Cape Verde Islands in the species' geographical range. However, in the remarks section of their paper they surprisingly wrote "It is interesting that specimens from southern Senegal lack an epipod on maxilliped III but those from Cape Verde Islands and further north all have well-developed epipods". It inhabits depths from 55 to 500 m. This species appears to live in shoals (Chan & Crosnier, 1991). The largest specimen 18 mm CL, the smallest ovigerous female 12 mm CL (Chan & Crosnier, 1991). The studied specimens measured between 9.6 and 17.4 mm CL, the smallest ovigerous female 15.2 mm CL.

Batch fecundity estimate from six ovigerous females (15.6-17.4 mm CL) ranged from 3065 to 6852 eggs; mean value was 5518 ± 1682 eggs, which is consistent with similar values found for *Plesionika* species in the eastern Atlantic (González et al., 1997; Triay-Portella et al., 2016). Also Crosnier & Forest (1973, as *Parapandalus narval*) reported on one 11 mm CL ovigerous female of *P. longicauda* carrying about 5500 small eggs (0.45 × 0.55 mm).

This species has been often confused with *P. narval*, but Chan & Crosnier (1991) cleared its identity and distribution. The studied material was caught in the bathymetric interval of 90-167 m, which is included in the previously known species' vertical distribution. They were equally caught on (benthic) or over (epibenthic) rocky bottoms. Present sporadic catches do not seem to indicate that the species live in shoals. The present material ($n = 19$ individuals) includes 8 ovigerous females (15.2-17.4 mm CL) collected in July.

This is the first documented record for this species from the Cape Verde Islands and the northernmost one ever recorded in the eastern Atlantic, extending its distribution area to 16°45′N. This represents the fourteenth pandalid and the ninth *Plesionika* recorded for this archipelago.

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SOUTHERNMOST RECORD OF *SPONGIOCARIS KOEHLERI* (DECAPODA, STENOPODIDEA, SPONGICOLIDAE) OFF THE CANARY ISLANDS

BY

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Stenopodidean shrimps, including both shallow- and deep-water species widespread in all oceans, play a significant role in trophic webs in benthic ecosystems (e.g., Goy, 2010). Several ecological associations of these shrimps and other invertebrates have been described, i.e., with littoral anemones (Wirtz, 1997), deep sea sponges (Hayashi & Ogawa, 1987; Berggren, 1993; d'Udekem d'Acoz, 1999; Saito et al., 2006; Ortiz et al., 2007; De Grave & Fransen, 2011), comatulid echinoderms (Saito & Fujita, 2009; De Grave & Fransen, 2011), and with deep-water hard corals (Yaldwyn, 1968; Gore, 1981; Goy & Cardoso, 2014). Some stenopodideans display cleaning behaviour on several bony fishes (Limbaugh et al., 1961; Jonasson, 1987; González, 1995; Wicksten, 1998). The behaviour associated with pair formation in several stenopodidean species has also been studied (Yaldwyn, 1964; Johnson, 1969). Many stenopodideans are known only from the type material/locality, and often appear as isolated specimens. Being shallow-water species of ornamental interest, they may be vulnerable to over-collecting (e.g., Calado et al., 2003).

Within the family Spongicolidae Schram, 1986, seven genera with around 45 species are presently recognised worldwide, with a significant number of species recently described (De Grave & Fransen, 2011; Saito & Anker, 2012; Goy & Martin, 2013; Jiang & Li, 2014; Jiang et al., 2015; Komai et al., 2016; Wang et al., 2016). With the exception of *Microprosthema* Stimpson, 1860, genera in the Spongicolidae are associated with deep-sea hexactinellid sponges, and are characterized by reduced body and appendage armature (Saito, 2008). Some members assigned to other spongicolid genera have been transferred to *Spongiocaris* Bruce & Baba, 1973; these species include *Spongicoloides koehleri* (Caullery, 1896) (cf. Saito, 2008).

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Spongiocaris koehleri is a rare eastern Atlantic species, living in the internal cavity of the glass sponge *Regadrella phoenix* Schmidt, 1880 (cf. Zariquiey Álvarez, 1968; d'Udekem d'Acoz, 1999). Here we report on a pair male-female of this species, captured off the Canary Islands, North-eastern Atlantic Ocean, representing the southernmost record of the species ever reported.

MATERIAL AND METHODS

In the frame of a research project on the marine benthic megafauna off the island of Gran Canaria (Canary Islands), a trapping survey was carried out in October 2003, February 2004 and June 2004. The study area is bounded by the 27°57′N and 28°00′N parallels, and the isobaths of 175 and 1275 m. Benthic and semi-floating shrimp traps were used (Carvalho et al., 2006). Decapods were preserved in 70% ethanol and then identified at laboratory. Voucher specimens were labelled, curated, data-based and deposited, available for verification (Turney et al., 2015) in the ICCM study collection, presently at the University of Las Palmas de Gran Canaria. The abbreviation CL stands for carapace length, and is measured with a digital calliper in millimetres.

RESULTS AND DISCUSSION

The following specimens of *Spongiocaris koehleri* (fig. 1) were collected:

ICCM409, one male, 7.21 mm CL, one ovigerous female, 9.38 mm CL, off Taliarte, East of Gran Canaria Island, 27°59′N 15°20′W, 500 m of depth, from a hexactinellid sponge *Regadrella phoenix* (85.20 mm wide) (fig. 1), "Pandcan4" cruise, station 1NB10, 29 Oct. 2004, bottom trap! Specimens of the glass sponge shrimp collected agree well with the descriptions given for the species (Kemp, 1910; Zariquiey Álvarez, 1968; García Raso, 1996).

Up to now, *S. koehleri* was only known from few scattered localities: Bay of Biscay (Caullery, 1896, south side, 1410 m, five specimens; Kemp, 1910, north side, 754 m, 23 specimens), Straits of Gibraltar (Sund, 1920, 1215 m, one specimen), central area of the Gulf of Cadiz (García Raso, 1996, 35°31.3′N 7°26.2′W, muddy bottom with foraminifers and pteropods, 1209-1302 m, one specimen), and north sector of the Moroccan Atlantic (García Raso, 1996, off Kenitra, 34°24.3′N 7°30.3′W, shells with pteropods and foraminifers, 1182 m, two specimens; off Kenitra, 34°22.3′N 7°25.1′W, shells with pteropods and hexactinellid sponges, 948 m, one specimen); all these records well within the South European Atlantic Shelf biogeographic ecoregion of Spalding et al. (2007). The present finding represents the first record of the species from the Canary

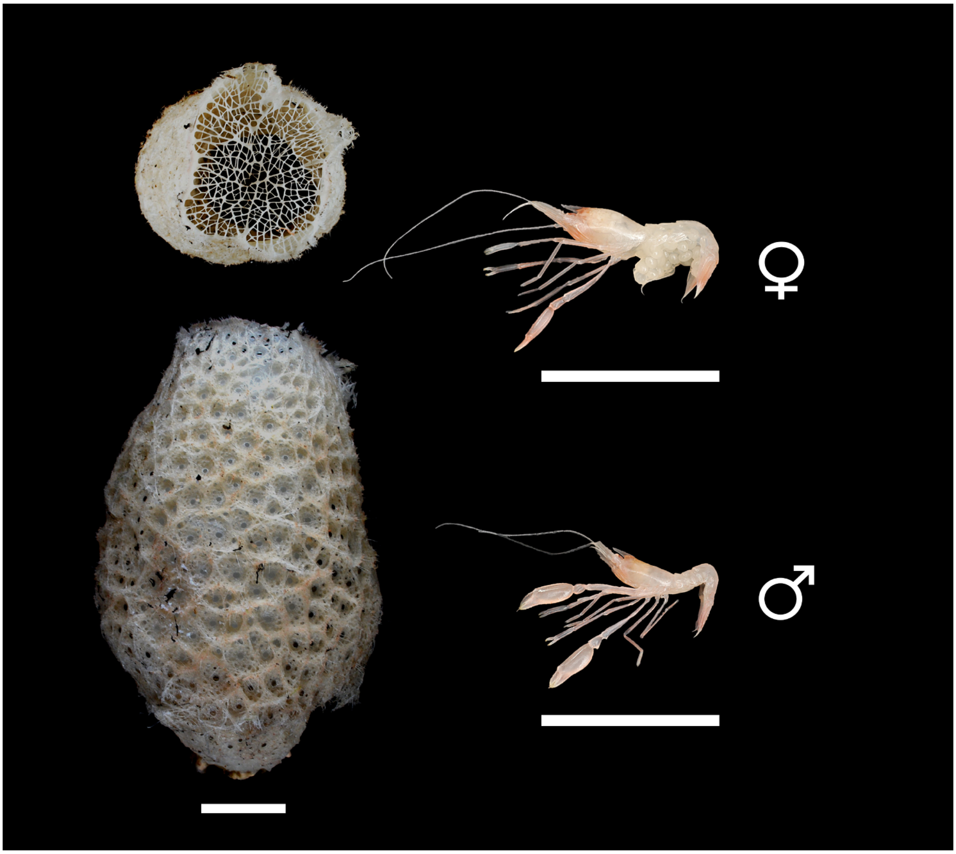

Fig. 1. *Spongiocaris koehleri* (Caullery, 1896), a pair male-female from off the Canary Islands (ICCM409, male, 7.21 mm CL; ovigerous female, 9.38 mm CL) together with their host, the glass sponge *Regadrella phoenix* Schmidt, 1880 (85.20 mm wide) (scale bar = 2.5 cm). This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/15685403.

Islands, as well as the southernmost (27°59′N) and shallowest (500 m) record ever reported for this species. The present record is apparently the first time any member of both the genus and family has been reported in the Azores-Madeira-Canaries ecoregion of Spalding et al. (2007), both ecoregions within the Lusitanian province. Within the four Ibero-Moroccan specimens of García Raso (1996), the largest specimens measured 9.3 mm (female) and 7.5 mm CL (male). The present material has a very similar size: 9.38 mm (female) and 7.21 mm CL (male). Freshly caught, both specimens examined herein were uniformly pale orange. The ovigerous female examined was carrying 25 elongated ellipsoidal eggs, 1.47 mm long and 1.10 mm wide in average, looking like small rugby balls (fig. 1). With the finding of the material examined herein, this species may safely be considered to be established in the Canaries.

The host, *Regadrella phoenix* (fig. 1) is a pantropical species, known from the East Pacific (Chile) and both the West and East Atlantic Oceans (van Soest, 2008), including two records from the Azores based on Topsent (1904, off São Jorge, 38°47′40″N 28°17′5″W, 1022 m) and Topsent (1928, off Santa Maria, 36°58′N 24°58′W, 1330 m). In the literature of Porifera from the Canaries no records exist for this species, apart from *Regadrella* sp. (listed) in the catalogue by Cruz Simó (2002), however that record was not compiled in the subsequent checklist (Cruz Simó et al., 2003). Recently, ROV observations on the deep-sea of the Canary Islands seem to have found several specimens of *Regadrella* sp., as it has been published in the media. So the examined sponge represents the first record for this species from the Canaries. Further research has to be focused on this topic in order to improve the poor knowledge on this interesting commensal association in the Macaronesia.

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The community of deep-sea decapod crustaceans between 175 and 2600 m in submarine canyons of a volcanic oceanic island (central-eastern Atlantic)

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ABSTRACT

The community structure and faunal composition of deep-sea decapod crustaceans in submarine canyons on the slope off Gran Canaria Island (Canary Islands, central-eastern Atlantic) were investigated. Samples were collected during five research cruises (115 stations) at depths between 175 and 2554 m. A total of 26387 decapod specimens, belonging to 24 families and 38 species, were collected with traps. A cluster analysis of the stations showed four distinct assemblages: (i) in the transition area between shelf and slope (175–302 m); (ii) on the upper slope (361–789 m); (iii) on the middle slope (803–1973 m); and iv) on the lower slope (2011–2554 m). The deep-sea decapod fauna of the Canary Islands is dominated by shrimp of the family Pandalidae, which make up more than 23% of the species. Within the Pandalidae, species of the genus *Plesionika* stand out as those of greatest abundance on the island slope. The greatest diversity of species was located on the upper slope. The standardized mean abundance and mean biomass for the transition zone between the shelf and slope and for the upper slope were nearly 5 times greater in abundance and 4 times greater in biomass than those estimated for the middle slope, and nearly 53 and 29 times greater for the lower slope, indicating a lower abundance and biomass at the shallower part of the insular slope. The mean weight per individual showed an increasing pattern with depth and an inverse pattern with the bottom temperature and salinity. The existence of depth boundaries around the Canary Islands is known to be closely linked to oceanographic conditions, determined by the water masses present in this archipelago explaining the discontinuities observed at depths of 800 and 2000 m. The boundary observed inside the bathymetric region of the Eastern North Atlantic Central Water can be related with the transition zone between the shelf and the slope of the island.

1. Introduction

The communities of deep-sea decapod crustaceans on the slope of the eastern-central Atlantic region have rarely been studied by themselves or as part of other broader communities (Rosa et al., 2012), unlike such communities in other zones of the East Atlantic (Cosson et al., 1997; Fariña et al., 1997; Olabarria, 2005; Cartes et al., 2007, 2014; Frutos and Sorbe, 2014; Gunton et al., 2015) and the Mediterranean Sea (Cartes and Sardà, 1993; Cartes et al., 2003; Politou et al., 2004; Fanelli et al., 2007, 2013; Mamouridis et al., 2011; Papiol et al., 2012).

Studies on the bathymetric distribution of faunal communities along slopes have revealed the existence of depth boundaries based on changes in fauna. Those changes seem to be a regular phenomenon in different bathyal ecosystems (Haedrich et al., 1975, 1980; Abelló et al., 1988; Cartes and Sardà, 1993; Fanelli et al., 2007; Frutos and Sorbe, 2014), with a few exceptions (Snelgrove and Haedrich, 1985). It should be noted that depth boundaries, which separate different communities, are the result of biotic or abiotic conditions (Cartes and Sardà, 1993; Maynou and Cartes, 2000; Olabarria, 2005; Cartes et al., 2007, 2008, 2009a, 2011a; Follesa et al., 2009; Fanelli et al., 2013). The faunal discontinuity separating an upper shelf-slope zone of transition is a consequence of the presence of the shelf species extending their distribution down the slope to a deeper bathyal zone (Olabarria, 2005). The deeper discontinuity, located at approximately 2000 m,

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corresponds with the upper limit of the distribution of abyssal species (Maynou and Cartes, 2000), and the presence of other boundaries between communities in the middle slope can frequently be due to hydrographic or trophic conditions (Abelló et al., 1988; Cartes and Sardà, 1993; Olabarria, 2005; Frutos and Sorbe, 2014; Cartes et al., 2015).

In deep-sea communities, many ecological aspects of decapods have been studied, and they depend on both biotic and abiotic factors (Moranta et al., 2004; Olabarria, 2005; Fanelli et al., 2007; Cartes et al., 2009a,b, 2011a). In this respect, the hydrodynamic conditions of the Canary Islands are relevant and variable in depth and may have a remarkable influence over the distribution and abundance of organisms. The Canary Islands are located in the Canary Current System, which is one of the 49 Large Marine Ecosystems of the world, characterized by their singular bathymetry, hydrography and productivity and their ability to support marine populations, which have adapted their feeding, reproductive and growth strategies (Hernández-León et al., 2007). The Canary Islands distinguish the Canary Current System from similar areas because the Canary archipelago extends more than 600 km in a direction perpendicular to the general flow of the current. Therefore, the physical setting observed in the Canary region is quite different to that recorded in other main ocean current systems due to the mesoscale variability imposed by the islands (Barton and Arístegui, 2004; Hernández-León et al., 2007). Hydrologically, these islands are characterized by the presence of four water masses: the Eastern North Atlantic Central Water (ENACW), the Antarctic Intermediate Water (AIW), the Mediterranean Water (MW), and the North Atlantic Deep Water (NADW), which are located at different depths and have characteristic thermohaline properties (Ríos et al., 1992; Hernández-Guerra et al., 2002, 2003). The end of the ENACW and the start of the lower thermocline occur at a depth of approximately 700 m and correspond with values of 11 °C temperature and 35.5 psu in salinity (Hernández-Guerra et al., 2001; Machín et al., 2006). The lower thermocline is characterized by two intermediate water masses, the AIW, detected by its temperature values (7–11 °C), and the MW, with salinity values >35.3 psu (Hernández-Guerra et al., 2001; Machín et al., 2006). The NADW water mass is found at a depth of 2000 m and is characterized by a temperature range of 2–7 °C (Machín et al., 2006). These changes in salinity and mainly in temperature result in the presence of density and thermal barriers that affect the vertical distribution of fauna (Canals et al., 2006). Additionally, the Canary Islands occupy a key position with respect to marine biogeochemical cycles because they are located at the boundary between eutrophic NW African upwelling waters and oligotrophic oceanic North Atlantic subtropical gyre waters (Wilke et al., 2009). The annual average primary production in the oceanic area of the Canary Islands is 200 mg C m^{-2} d^{-1}, reaching values of 800–1000 mg C m^{-2} d^{-1} during the winter bloom (de León and Braun, 1973; Hernández-León et al., 2007). In the coastal areas, the average primary production is 0.81 mg C m^{-3} h^{-1} reaching values of 2.54 mg C m^{-3} h^{-1} in February (Braun et al., 1985; Hernández-León et al., 2007). The coupling of production in the coastal area off Northwest Africa and in the oceanic zone, connected through filaments and eddies topographically formed in the coast or shed by the Canary Islands, promotes a continuous transport of organic matter towards the deep ocean (Hernández León et al., 2007). In the Canary Islands, it is common to observe two layers, one at approximately 400 m and another at 600 m in which diel vertical migrations occur, which move a portion of the epipelagic biomass from 400 to 600 m (Hernández-León et al., 2007). Additionally, a higher amount of dissolved organic carbon and higher ETS activity of bacteria at the 400–600 m depth were observed in the Canaries (Arístegui et al., 2003), suggesting that the excretion and defecation by the deep scattering layers and diel vertical migrations transport carbon downward (Hernández-León et al., 2007). The diel vertical migrations transfer an important fraction of the biological production in the euphotic zone to the deeper layers of the ocean, generating a new cloud of organic material that reaches the lower section of the slope (Hernández-León et al., 2007). Geologically, these islands are characterized by numerous small submarine canyons formed by lateral collapse landslides (Masson et al., 2002; Acosta et al., 2003).

Submarine canyons are complex environments that are rich in nutrients due to both their geomorphology and their material and hydrographic flows (Guerreiro et al., 2009; Pusceddu et al., 2010), which differ from typical slopes because they offer mosaics of habitats and faunal assemblages (Stora et al., 1999; Sabatini et al., 2007; Cartes et al., 2009b; De Leo et al., 2010, 2014). Submarine canyons play an important role in the transfer of organic matter inputs from the shelf to the lower slope, as well as focusing zooplankton and nekton scattering layers and benthic macro- and megafauna (Puig et al., 2001; Canals et al., 2006; De Leo et al., 2010, 2012; Gunton et al., 2015). The broad range of substrate types and complex topography inside submarine canyons can enhance biomass and productivity by providing a higher number of niches, a wider range of resources and an enhanced benthic diversity compared to more homogenous open slope areas (Schlacher et al., 2007; Vetter et al., 2010; Paterson et al., 2011; De Leo et al., 2012, 2014; Leduc et al., 2014). These higher values in the canyons may be restricted in some cases to a depth strata (e.g. De Leo et al., 2012), but in other cases, they are similar to the slopes or higher values can even be found on the slopes compared to adjacent canyons (e.g. Houston and Haedrich, 1984; Soltwedel et al., 2005; Bianchelli et al., 2010; Vetter et al., 2010; Leduc et al., 2014). In canyon systems fueled largely by coast-derived organic detritus, the enhancement of benthic fauna decreases with depth as a consequence of the consumption of organic material downslope (Vetter and Dayton, 1998; De Leo et al., 2012). In large canyons that extend far onto the continental slope, primary production may be enhanced by canyon-hosted eddies, yielding peaks in the abundance of the benthic community at depth in submarine canyons (Duineveld et al., 2001; Escobar-Briones et al., 2008; De Leo et al., 2010, 2012). Other environmental factors, such as the frequency and intensity of disturbance, sediment slumps, water mass properties and the vertical flux of particulate organic carbon, can also have an influence on the differences in benthic invertebrate communities between canyons and slopes (Vetter and Dayton, 1998; Company et al., 2008; Levin and Dayton, 2009; Levin et al., 2010; De Leo et al., 2012; Leduc et al., 2014). Species that live in submarine canyons have greater mobility and are more diverse than those of typical deep-sea assemblages in the same area due to habitat heterogeneity and the input of organic matter (Rowe, 1971; Sabatini et al., 2007; De Leo et al., 2012). Some deep-sea decapods do day-night movements along submarine canyons, possibly for trophic reasons (Sabatini et al., 2007). This movement pattern responds to the ability of deep-water shrimp to adapt their life cycles to the morphology of a canyon (Sabatini et al., 2007). Additionally, this pattern can be related to the predatory character of these animals moving at night to catch prey because decapod shrimp find the canyons to be a suitable place to obtain food and reach different depths in a short distance (Sabatini et al., 2007). This vertical daily migration ability present in the behavior of some decapod shrimp provides them with an important role in the transference of matter and energy to deeper areas (Cartes, 1993). Submarine canyons can also be recruitment areas for various species (Cartes and Sorbe, 1999; Vetter and Dayton, 1999).

Decapods are considered a secondary group in the megabenthic communities of the central Atlantic bathyal ecosystems (Haedrich et al., 1975, 1980; Lampitt et al., 1986). Deep-sea decapods play an important role in deep-sea trophic webs as vectors of organic matter through food webs or as active transporters of food through the water column as a consequence of their prey status for macrofaunal species (Cartes et al., 2001, 2011a). Decapods are detritivores, exploiting the particulate organic matter, or carnivores, feeding on meiofauna and zooplankton (Madurell et al., 2008; Fanelli et al., 2009a,b; Cartes et al., 2011a). Additionally, the biomass of deep-sea decapods depends on the species that exploit the deposits of organic matter generated in the epipelagic layer, and their abundance is dependent on the source of organic material (Fanelli et al., 2011).

Studies on deep-sea decapods of the Canary Islands have been conducted from a systematic, faunistic or fishing perspective (e.g. González, 1995; González and Santana, 1996), and there are no central studies on their abundance, diversity, distribution patterns or species location. For these reasons, the present study examines the community of deep-sea decapod crustaceans along the depth gradient from 175 to 2600 m on the slope of a volcanic oceanic island inside their submarine canyons and analyzes the variations in their distribution, diversity and dominance by depth and their possible connections with the hydrographic characteristics in an area embedded in an oligotrophic ocean. During this study, all populations of the community were unexploited, and all factors affecting population structures were pristine, which allows for an estimation of the characteristics of the community of decapods in the original ecosystem state.

2. Materials and methods

2.1. Study area and sampling procedure

The Canary Islands are a small volcanic ocean archipelago situated to the west of the northwest coast of Africa, consisting of seven islands and few islets. Geologically, the islands are underwater buildings that rise abruptly from the African ocean plate from a depth of 4000 m. The island of Gran Canaria is located in the central part of the archipelago, presenting numerous submarine canyons that formed as a result of lateral collapse landslides (Masson et al., 2002; Acosta et al., 2003). Inside these small submarine canyons (Acosta et al., 2003), the distance between the isobaths of 175 and 2000 m ranges from 4.20 to 5.35 nautical miles (Fig. 1).

Five research cruises were conducted in November 2006 and February, June, September and November 2007 on the slope of six submarine canyons around the island of Gran Canaria (Fig. 1). The samplings were performed around the island and not only on a particular side of it. Due to the abrupt shape of the submarine topography of the island, which was formed by irregular volcanic rocks and escarpments, it was not possible to trawl for samples. Instead, bottom traps were deployed, whose efficiency has been confirmed by their use in commercial fishing and scientific studies on decapods (e.g. McElman and Elner, 1982; Melville-Smith, 1986; Gutiérrez et al., 2011).

The sampling was conducted using semi-floating traps suspended 2.4 m above the bottom (epibenthic) and the equivalent in strings of benthic traps deposited directly on the bottom. The semi-floating trap is a cylinder conical trap, with a 56 × 57 cm^2 base length and a 57 cm height, covered with 15 × 15 mm^2 mesh. Each trap has one tronco conical opening, with a 23 cm outer diameter and 19 cm inner diameter. The benthic trap is a rectangular base tronco pyramidal trap, with a bottom base of 1.15 × 0.80 m^2, a top base of 1.15 × 0.70 m^2 and a 0.50 m height, covered with 15 × 15-mm^2 metallic mesh. Each trap has one tronco conical opening, with a 23 cm outer diameter and 19 cm inner diameter. Ground lines held an average of 10 traps, equally spaced (100 m) along the length of each fishing rope, covering a distance of 1 km. Atlantic chub mackerel (*Somber colias*) was used as bait in both types of traps. All fishing operations were conducted over approximately 24 h to include the entire distribution range of species affected by diel migrations.

Stations ($n = 115$) were conducted covering a bathymetric range between 175 and 2600 m deep and included 40 stations at depths between 175 and 500 m, 30 stations between 501 and 1000 m, 30 stations between 1001 and 2000 m and 15 stations between 2000 and 2600 m (Fig. 1). At each station, data on the salinity and temperature 0.5 m above the seafloor were recorded using a CTD sensor.

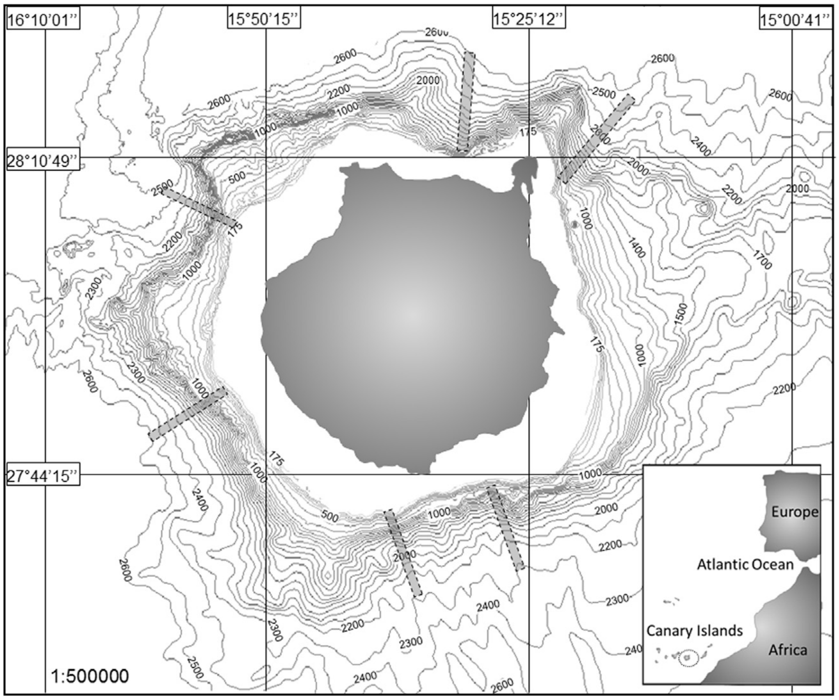

Fig. 1. Sampling areas belonging to the small submarine canyons around Gran Canaria Island.

For each station, the number of specimens and their total weight were recorded. Specimens were identified at the species level. Taxonomical arrangement followed the WoRMS Editorial Board (2015), except for Sergestidae shrimp, which were updated according to Vereshchaka et al. (2014). The combined weight of all of the species that were caught was taken for each station.

2.2. Data analysis

For each station, the species composition and the abundance (expressed as the number of individuals per trap) were estimated by considering each pair of semi-floating and benthic traps jointly as only one data point. The abundance data were analyzed by means of a cluster analysis applied to the stations using the Bray–Curtis index of similarity and the group-average linkage for the dendrogram (Clarke and Warwick, 2001; Clarke and Gorley, 2006) with PRIMER 6.1.13 software (Clarke and Warwick, 1994). To avoid including stations with strings of traps that were not fished by being tangled or misplaced on the bottom by the current, only the stations representing more than 0.05% of the total catch were analyzed. Species with one individual present in all samples were removed from matrices (Fanelli et al., 2007, 2011; Cartes et al., 2014). Standardization and logarithmic transformation were applied prior to the analysis (Clarke and Warwick, 2001). A non-parametric multidimensional scaling ordination (nMDS) was conducted to examine station relationships on a two-dimensional ordination plane using the abundance data (Clarke and Warwick, 2001; Clarke and Gorley, 2006). The significance of the cluster branches was tested using the SIMPROF subroutine within the Primer v.6 software with a significance level of 0.05 (Clarke and Warwick, 2001; Clarke and Gorley, 2006; Clarke et al., 2008). The SIMPROF routine cannot be applied to divide a group consisting of only two samples (Clarke et al., 2008). The Similarity Percentage analysis procedure (SIMPER) was used to identify the species that characterize each assemblage (Clarke and Warwick, 1994, 2001).

Measures of species diversity were assessed for each of the assemblages obtained with the species richness (S), the Shannon–Wiener diversity index (H'), and the Pielou evenness index (J') using the DIVERSE subroutine within the Primer v.6 software. The measures of species diversity were tested for differences among assemblages by an ANOVA test, considering each station as one observation. This analysis was used to evaluate the null hypothesis of equality in means S, H' and J' among the assemblages, with a significance level of 5% ($\alpha=0.05$) and a critical value of $F_{0.05,3,78}=2.74$.

A dominance curve, a plot of percentage cumulative abundance by numbers against the species rank, was applied to investigate changes in species dominance by depth (Clarke, 1990).

The standardized mean biomass (in weight per trap) and mean abundance (in number of individuals per trap) of each station and assemblage obtained were analyzed and tested for differences among the assemblages using an ANOVA test. Trends of weight and the number of individuals per trap were explored as functions of depth. The best relationship was estimated by fitting data to the logistic, exponential, growth, potential, and linear equations using non-linear regression. The trends of the mean weight per individual were also explored as functions of depth. Spearman's correlations between the mean weight per individual and the temperature or salinity were also estimated. To compare the depth distribution of the species with the highest standardized biomass recorded, the Center of Gravity (CoG) (Stefanescu et al., 1992; Cartes et al., 2011b) was calculated by assigning to each individual of each species the depth of their station of capture. The Center of Gravity was tested for differences among species using ANOVA. This analysis was used to evaluate the null hypothesis of equality in the mean depth (Center of Gravity) among species, with a significance level of 5% ($\alpha=0.05$).

A principal components analysis (PCA) was used to examine the relationship among the environmental variables (depth, salinity, and temperature) measured at each station in the bottom and the distribution of species, and a two-dimensional solution plot was used to describe the resulting ordination using the PCA subroutine within the Primer v.6 software (Clarke and Gorley, 2006).

3. Results

The dendrogram of similarities among stations of the cluster analysis and the non-parametric multidimensional scaling ordination (nMDS) analysis showed four distinct groups (confirmed by SIMPROF at $p<0.05$) inside submarine canyons (Figs. 2 and 3): a first assemblage in the transition area between insular shelf and slope (TSS) comprising 25 stations carried out between depths of 175 and 302 m; a second assemblage in the upper part of the slope (US) with 22 stations at depths between 361 and 789 m; a third assemblage in the middle zone of the slope (MS) with 30 stations

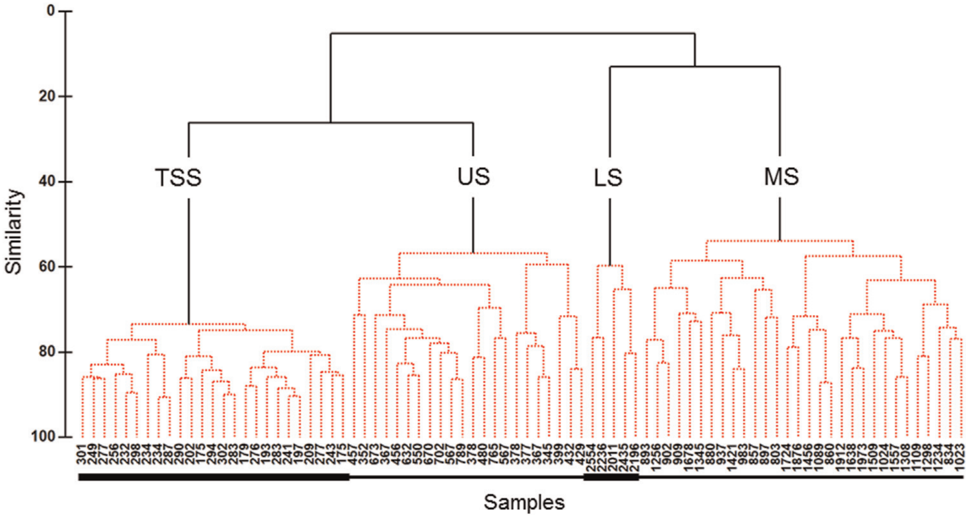

Fig. 2. Dendrogram of the trap stations using group-average clustering from Bray–Curtis similarity of average abundance of decapod crustaceans inside submarine canyons off Gran Canaria. Site groupings based on 54% Bray–Curtis similarity (confirmed by SIMPROF) are indicated. TSS, transitional area between shelf and slope; US, upper slope; MS, middle slope; LS, lower slope.

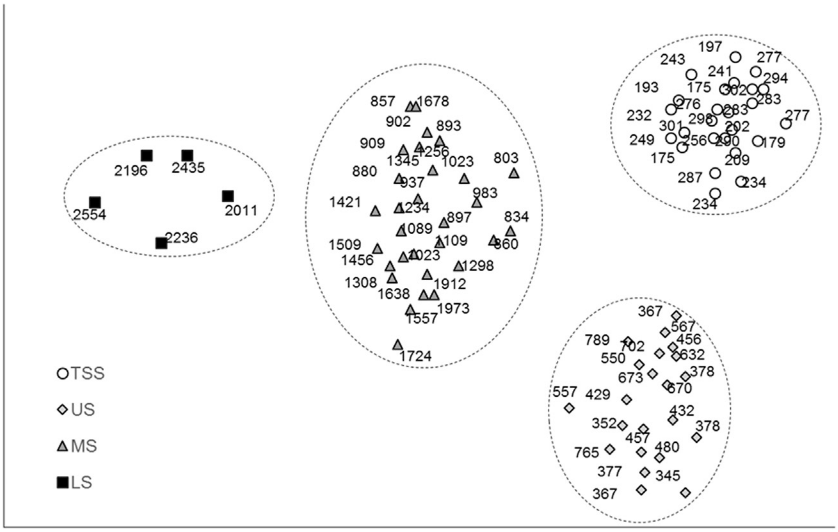

Fig. 3. Non-parametric multidimensional scaling (nMDS) ordination plot of average abundance of decapod crustaceans inside submarine canyons off Gran Canaria. Number indicates the mean depth of each station. TSS, transitional area between shelf and slope; US, upper slope; MS, middle slope; LS, lower slope.

at depths between 803 and 1973 m; and a fourth assemblage in the lower zone of the slope (LS) comprising five stations at depths between 2011 and 2554 m. The nMDS (stress 0.07) showed depth as the first key factor (from right to left).

The results of the similarity percentage analysis procedure (SIMPER) showed that two species of pandalid shrimps, *Plesionika edwardsii* and *Plesionika narval*, showed the major contribution for defining the TSS assemblage (175–302 m). In the US assemblage (361–789 m) the most typifying species were a set of four pandalid shrimp species which contributed 55.58% to the average similarity. The main contributors of the average similarity in the MS assemblage (803–1973 m) were the pandalid shrimps *Heterocarpus grimaldii* and *Heterocarpus laevigatus*, the epialtid crab *Rochinia carpenter*, and the benthesicymid prawn *Benthesicymus bartletti* ($>68\%$). In the LS assemblage (2011 to 2554 m) only two species, the oplophorid shrimp *Oplophorus spinosus* and the geryonid crab *Chaceon inglei,* accounted for more than 93% of the average similarity (Table 1).

By depth strata, the greatest mean species richness (S) was located in the US ($S=15.50\pm1.34$ [± sd]), between 361 and 789 m (Table 2), and the lowest in the LS (3.80 ± 1.92) at depths greater than 2000 m. The ANOVA showed significant differences in the mean species richness among assemblages (ANOVA, $F=55.89>F_{0.05,3,78}=2.74$, $p<0.0001$). The highest diversity (H') was also obtained for the US ($H'=2.29\pm0.22$), decreasing with depth ($H'=1.10\pm0.08$), although the observed value in the shallower TSS was lower ($H'=2.07\pm0.16$). The H' mean values showed differences among the assemblages (ANOVA, $F=20.19>F_{0.05,3,78}=2.74$, $p<0.0001$). Pielou J' indices showed the highest value in the LS ($J'=0.99\pm0.01$), decreasing with the reduction of the depth. J' values showed significant differences among the assemblages (ANOVA, $F=27.29>F_{0.05,3,78}=2.74$, $p<0.001$). Dunnett's *T3* post-hoc test showed significant differences in H', J', and S among all the assemblages ($p<0.05$).

Table 2
Estimates of mean ± s.d. number of individuals (N), species richness (S), Pielou's evenness index (J') and Shannon–Wienner diversity index (H') with respect to the four assemblages identified. TSS, transition zone between shelf and slope; US, upper slope; MS, middle slope; LS, lower slope.

	N	S	J	H'
TSS	48.16 ± 9.46	12.04 ± 2.75	0.77 ± 0.07	2.07 ± 0.16
US	48.18 ± 14.66	15.50 ± 1.34	0.84 ± 0.07	2.29 ± 0.22
MS	21.57 ± 5.46	9.47 ± 2.11	0.90 ± 0.06	1.95 ± 0.20
LS	5.40 ± 2.30	3.80 ± 1.92	0.99 ± 0.01	1.10 ± 0.08

The k-dominance curves for species abundance (Fig. 4) showed that the distribution of the number of individuals among species at TSS differed markedly from US, MS and LS, which were characterized by a higher number of dominant species. The patterns of the dominance curves of US and MS were similar, indicating similar patterns of distribution of individuals among species in

Table 1
Results of the SIMPER routine to analyse the contribution (C, in %) of typifying species (over 3%) to within-group similarity resulting from cluster analysis and nMDS.

Shelf-slope, average similarity: 76.36		Upper slope average similarity: 59.03		Middle slope average similarity: 56.49		Lower slope average similarity: 67.80	
Species	C (%)	Species	C (%)	Species	C (%)	Species	C (%)
P. edwardsii	51.65	*H. ensifer*	32.5	*H. grimaldii*	24.25	*O. spinosus*	47.17
P. narval	11.73	*P. edwardsii*	9.20	*H. laevigatus*	19.29	*C. inglei*	46.71
S. pellucida	7.31	*P. ensis*	7.44	*R. carpenteri*	13.13		
S. macrochelos	6.40	*P. williamsi*	6.44	*B. bartletti*	11.73		
M. goltziana	6.38	*A. edwardsiana*	5.87	*R. robusta*	9.34		
H. barbata	6.19	*P. martia*	5.37	*G. splendens*	7.18		
D. arrosor	5.88	*P. cuvieri*	5.13	*P. typhlops*	3.42		
		B. maravigna	4.97	*N. gracilipes*	3.27		
		P. infirma	4.53				
		E. bella	4.42				
		A. foliacea	3.99				
		C. affinis	3.98				

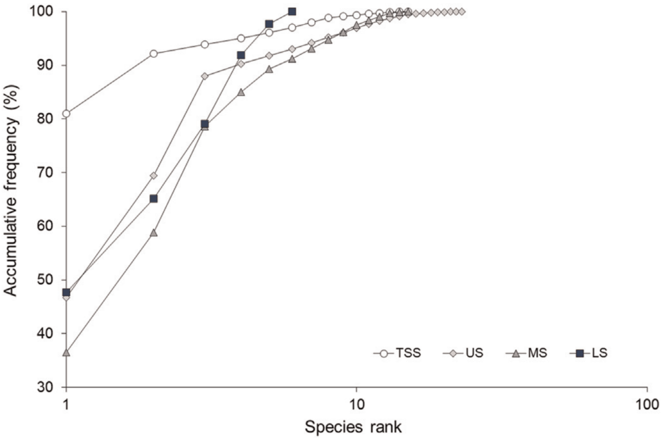

Fig. 4. *k*-dominance curves of the number of individuals by depth inside submarine canyons off Gran Canaria. TSS, transitional area between shelf and slope; US, upper slope; MS, middle slope; LS, lower slope.

these two assemblages with a lower dominance at MS.

The standardized mean abundance (in number of individuals per trap) and mean biomass (in weight per trap) of each of the 38 species of decapod crustaceans collected are presented in Table 3. The standardized mean abundance and the mean biomass (Fig. 5) for the assemblages were significantly different (ANOVA, abundance $F = 24.82 > F_{0.05,3,81} = 2.72$, $p < 0.001$; biomass $F > 24.19 > F_{0.05,3,81} = 2.72$, $p < 0.001$). In both cases, Dunnett's T3 post hoc test identified one homogeneous subset (TSS and US, $p = 0.986$) where the means did not differ within the subset, testing the null hypothesis of equality in the standardized mean abundance and biomass. However, there were significant differences between the MS and LS and each of the other assemblages ($p < 0.001$). The mean values for the TSS and for the US were nearly 5 times higher in abundance and 4 times higher in biomass than that estimated for the MS (Fig. 5). These differences were nearly 53 times higher in abundance and 29 times higher in biomass than those estimated for the LS, indicating a lower abundance and biomass at the shallower part of the insular slope (Fig. 5). The best model to explain the trends between weight or number of individuals per trap and depth was a decreasing exponential model. The linear regression between the mean weight per individual and depth ($R = 0.639$, $p = 0.001$) showed a significantly increasing pattern with depth (Fig. 6). The mean weight per individual showed an inverse pattern to that recorded for the temperature and salinity on the sea bottom (Fig. 6), with a high Spearman's correlation with both variables (temperature $\rho = -0.717$ $p = 0.01$; salinity $\rho = -0.691$, $p = 0.01$). The Center of Gravity (CoG) of the species with high standardized biomass showed that in the TSS assemblage, the shrimp *P. narval* and *P.*

Table 3

List of species arranged, indicating standardized mean abundance (in number of individuals per trap) and standardized mean biomass (in grams per trap) for each species with respect to the four assemblages identified. TSS, transitional area between shelf and slope; US, upper slope; MS, middle slope; LS, lower slope.

Species	Abundance (no. individuals/trap)				Biomass (g/trap)			
	TSS	US	MS	LS	TSS	US	MS	LS
Munida curvimana	0.004				0.05			
Calappa granulata	0.144				7.32			
Plesionika holthuisi	0.052				0.67			
Spinolambrus macrochelos	0.872				16.64			
Dardanus arrosor	0.668	0.004			8.70	0.06		
Homola barbata	0.736	0.048			16.04	1.09		
Maja goltziana	0.804	0.043			12.90	0.73		
Plesionika narval	6.552	0.078			52.42	0.65		
Systellaspis pellucida	0.892	0.030			12.49	0.45		
Plesionika edwardsii	45.672	5.078			555.83	64.61		
Aristaeomorpha foliacea	0.024	0.204			0.60	5.35		
Acanthephyra eximia	0.028	1.770			0.35	22.88		
Paromola cuvieri	0.120	0.548			12.71	60.65		
Aristaeopsis edwardsiana	0.052	0.165	0.013		2.80	9.29	0.72	
Goneplax rhomboides	0.096	0.322	0.000		11.02	38.61	0.00	
Bathynectes maravigna	0.084	0.291	0.010		2.81	10.17	0.33	
Plesionika ensis	0.132	9.126	0.020		1.59	114.59	0.24	
Eumunida bella	0.072	0.248	0.033		0.42	1.53	0.20	
Heterocarpus ensifer	0.188	22.039	0.063		2.64	323.03	0.89	
Plesionika williamsi	0.036	0.691	0.037		0.51	10.27	0.52	
Cancer bellianus	0.052	0.235	0.057		10.21	48.21	11.13	
Plesionika martia	0.008	0.370	0.103		0.11	5.49	1.47	
Chaceon affinis	0.024	0.335	0.230		3.65	53.20	24.96	
Polycheles typhlops		0.035	0.277			0.79	6.03	
Heterocarpus grimaldii		0.004	2.263			0.08	37.82	
Heterocarpus laevigatus		0.122	3.863			1.98	60.11	
Benthesicymus bartletti		0.022	0.460			0.41	8.28	
Ligur ensiferus		0.004				0.06		
Penaeopsis serrata		0.052				0.56		
Hymenopenaeus debilis		0.004				0.03		
Robustosergia robusta		0.013	0.280	0.06		0.19	3.88	0.83
Gardinerosergia splendens			0.213	0.10			2.71	1.27
Homologenus boucheti			0.097	0.02			4.13	0.85
Nematocarcinus gracilipes			0.063	0.04			1.41	0.89
Chaceon inglei			0.003	0.26			0.10	7.63
Oplophorus spinosus			0.003	0.28			0.15	12.84
Rochinia carpenteri			0.387	0.06			4.37	0.68
Psathyrocaris infirma			0.003				0.05	

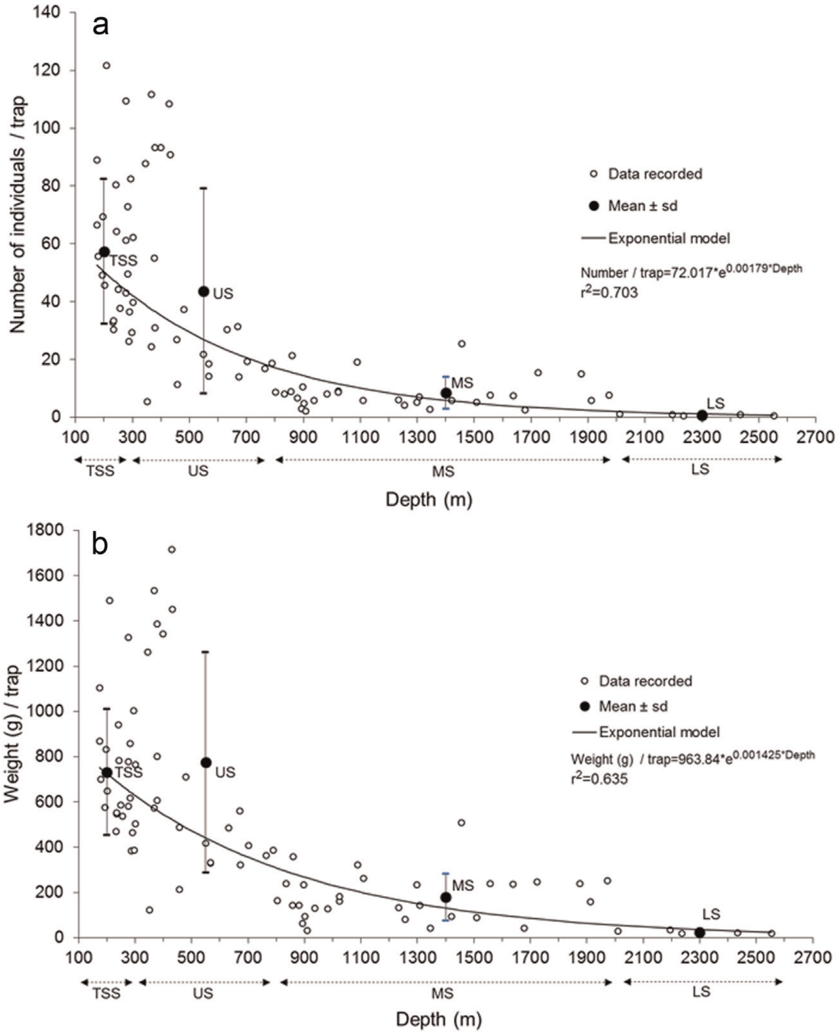

Fig. 5. (a) Standardized mean abundance in terms of number of individual per trap (*N*/trap) and (b) mean biomass in terms of weight in grams per trap (*W*/trap) for each assemblage. Lines are standard deviations. TSS, transitional area between shelf and slope; US, upper slope; MS, middle slope; LS, lower slope.

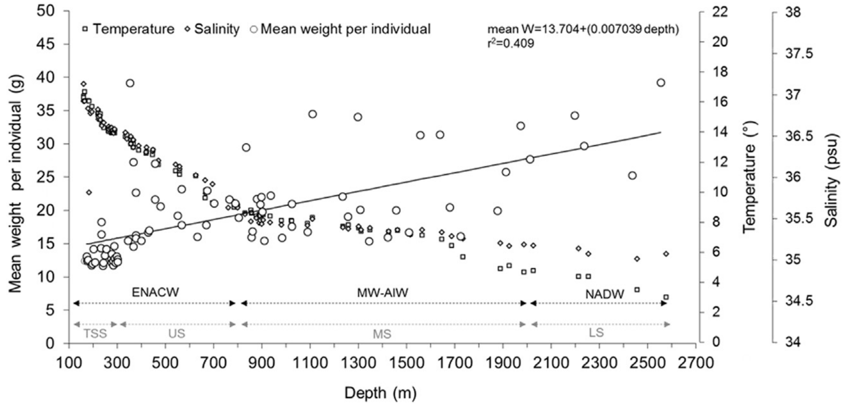

Fig. 6. Mean individual weight (in grams) with depth and data of temperature and salinity in the bottom corresponding to each station. TSS, transitional area between shelf and slope; US, upper slope; MS, middle slope; LS, lower slope. NACW, North Atlantic Central Water; MW-AIW, Mediterranean-Antarctic Intermediate Waters; NADW, North Atlantic Deep Water.

edwardsii have a very similar depth distribution, with less than 25 m in depth between the *CoG* values (Fig. 7). ANOVA did not show significant differences between species in the *CoG* (ANOVA, *P. edwardsii-P. narval* $F = 27.93 > F_{0.05,1,>1000} = 3.84$, $p < 0.001$). In the US assemblage, the large crabs *C. bellianus*, *P. cuvieri*, and *C. affinis* showed a steeper pattern of distribution with depths between consecutive *CoGs* greater than 140 m. ANOVA showed significant differences among species in the *CoG* (ANOVA, *C. bellianus-P. cuvieri-C. affinis* $F = 78.01 > F_{0.05,2,>1000} = 3.00$, $p < 0.0001$). Also in the US assemblage, the shrimp *P. ensis* and *H. ensifer* showed a steeper pattern of distribution, with depths between consecutive *CoGs* greater than 170 m and with a distance with respect to *P. edwardsii* higher than 120 m. ANOVA showed significant differences among species in the Center of Gravity test

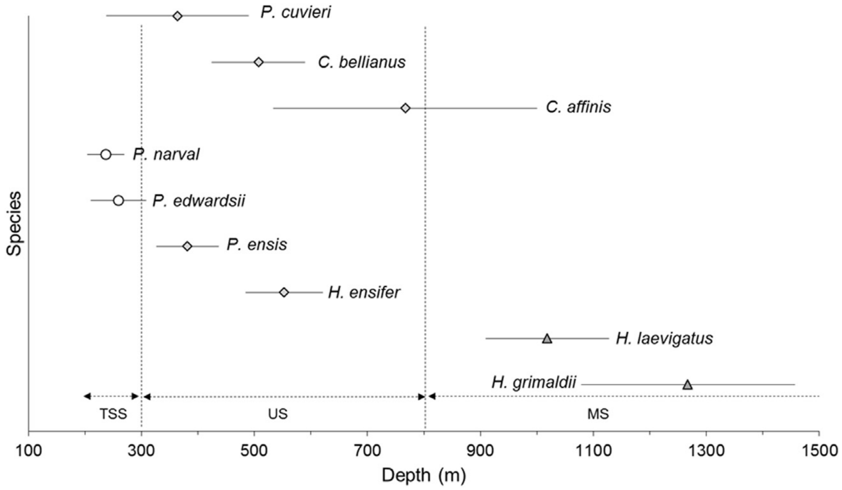

Fig. 7. Distribution of the Center of Gravity with depth of the species with high standardized biomass values. Horizontal lines are standard deviations. TSS, transitional area between shelf and slope; US, upper slope; MS, middle slope.

(ANOVA, *P. edwardsii-P. ensis-H. ensifer* $F=60319>F_{0.05,2,>1000}=3.00$, $p<0.0001$). In the MS, the two deep-water *Heterocarpus* species showed a steeper pattern over more than 250 m of depth (Fig. 7). ANOVA showed significant differences between species in the *CoG* test (ANOVA, *H. grimaldii-H. laevigatus* $F=799.27>F_{0.05,1,>1000}=3.84$, $p<0.0001$).

A PCA analysis between the environmental variables salinity, temperature, and depth data and the distribution of the species allowed the establishment of three different groups (Fig. 8). Dimension 1 separated the species present in the bathymetric region of the Eastern North Atlantic Central Water mass (ENACW, with temperature ranging from 9.2 to 16.8 °C, salinity between 35.65 and 37.15 psu) from that corresponding to the Mediterranean Water (MW)-Antarctic Intermediate Water (AIW) mass (4.78–9.2 °C, salinity > 35.2 psu), and from the North Atlantic Deep Water mass (NADW, 3.1–4.78 °C, salinity < 35.09 psu). Dimension 2 separated the species present in the bathymetric region of the MW-AIW mass from that the NADW. The first of the two subgroups of species present in the bathymetric region of the ENACW were composed of eurybathic shelf species which were introduced into the slope, and of species belonging to the transition area (175–302 m), including *Plesionika holthuisi, P. narval*, *Spinolambrus macrochelos*, *Homola barbata*, *Maja goltziana*, *Dardanus arrosor*, *Calappa granulata*, *P. edwardsii*, and *Systellaspis pellucida.* The second subgroup present in the ENACW was formed by bathyal species which are distributed in the upper part of the slope (361–789 m), including species such as *Plesionika williamsi*, *Plesionika ensis*, *Heterocarpus ensifer*, *Plesionika martia*, *Penaeopsis serrata*, *Goneplax rhomboides*, *Polycheles typhlops*, *Eumunida bella*, *Aristaeomorpha foliacea*, *C. bellianus*, *Bathynectes maravigna*, and *P. cuvieri.* The group present in the bathymetric region of the MW-AIW mass comprised species from the middle zone of the slope (803–1973 m), including *Robustosergia robusta*, *Gardinerosergia splendens*, *Aristaeopsis edwardsiana*, *R. carpenteri*, *Homologenus boucheti*, *Psathyrocaris infirma*, *H. laevigatus*, and *H. grimaldii.* The group present in the bathymetric region of the NADW mass comprised species from the lower part of the slope (2011–2554 m), including species such as *C. inglei* and *O. spinosus.* In the graph, species closely bound to determine areas, and other species widely distributed across areas such as *C. affinis* and *B. bartletti* were observed (Fig. 8).

4. Discussion

The deep-sea decapod fauna found in the submarine canyons of Gran Canaria (Canary Islands) were composed of 38 species that varied with depth, which was the main factor affecting the

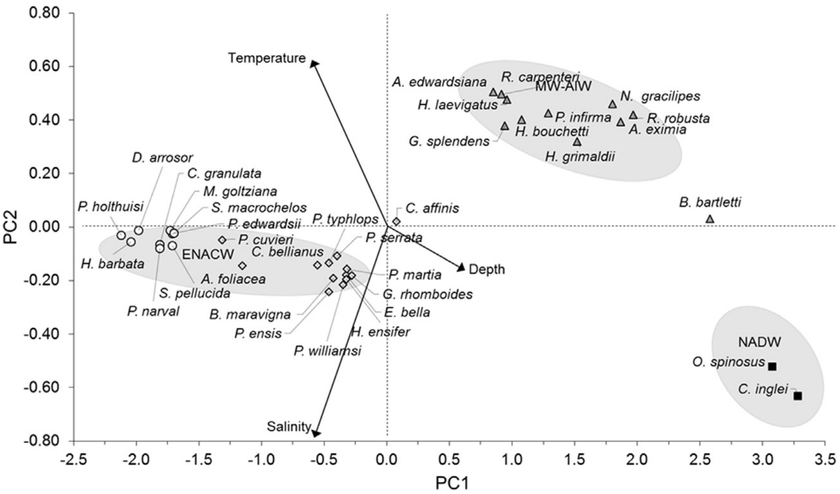

Fig. 8. Principal components analysis between oceanographic parameters (temperature, salinity and depth) corresponding to each station and bathymetric distribution of the species. NACW, North Atlantic Central Water; MW-AIW, Mediterranean-Antarctic Intermediate Waters; NADW, North Atlantic Deep Water.

distribution of benthic species (Haedrich et al., 1975; Abelló et al., 1988; Cartes et al., 1994; Maynou and Cartes, 2000). In terms of number of species, the deep-sea decapod fauna is dominated by the family Pandalidae, which composed more than 23% of the collected species. Within the pandalid shrimp, the species of genus *Plesionika* stand out as those of greatest abundance on the upper slope of the island. Although the sampling method used in this study (i.e., traps) can enhance the dominance of pandalids over other sampling methods such as trawl, biomass estimates made in the Canary Islands by means of experiences of depletion of *P. edwardsii* and *Chaceon affinis* showed higher abundances and biomasses for the former (González et al., 1998), confirming the differences in abundance obtained in this study. Muñoz et al. (2012) used trawl data and also found the dominance of the pandalid species off the western African coast. This dominance pattern of *Plesionika* species at depth has also been observed in the southwestern Mediterranean (Maynou and Cartes, 2000), an area in which decapod crustaceans show the greatest affinity for the eastern Atlantic decapod fauna (Cartes and Sardà, 1993). The number of species found in the Canaries is less than the 67 species of decapod found over the Galicia Bank by Cartes et al. (2015). This differences could be related to the high diversity of species present over the Galicia Bank, which is formed by a number of rare biogeographic species of southern distribution and a high number of species of northern origin.

The analyzed community of decapods consists of four assemblages separated by depth with discontinuities located at depths of 300, 800, and 2000 m, which correspond to the transition between shelf and slope, the upper part of the slope, middle slope, and deep slope. This pattern with discontinuities located in different parts of the slope has been described for deep-sea decapods in the western Mediterranean (Cartes and Sardà, 1993; Maynou and Cartes, 2000; Follesa et al., 2009; Fanelli et al., 2013) and in the Atlantic Ocean (Wenner and Boesch, 1979; Markle et al., 1988; Cartes et al., 2014). The variations in the depths of the discontinuities among regions are probably related to the environmental conditions or to the food resources available for the deep-sea decapod species, which show different response patterns to a depth gradient among geographic regions (Maynou and Cartes, 2000). The recorded dominance of the pandalid species of *Plesionika* at depths between 200 and 1000 m has also been observed in the Mediterranean by Maynou and Cartes (2000), who reported the dominance of the non-migrator macroplankton feeder mainly composed of species of *Plesionika*. Due to their abundance and trophic characteristics, species of *Plesionika* play an important ecological role in the megabenthic communities that transfer energy to the next trophic levels as part of the macroinvertebrate and fish diets (Vafidis et al., 2005).

The dominant species of the TSS assemblage, the pandalid shrimp *P. edwardsii* and *P. narval*, had similar depth distributions of *CoGs* calculated for the standardized abundance, ecological niches and biological characteristics (González et al., 1997; Santana et al., 1997; Vafidis et al., 2005) and showed high differences in their abundance. Both species have been described as active predators on macroplankton and can be considered as generalized feeders (Burukovskij, 1992; Cartes, 1993; Cartes et al., 2002; Kitsos et al., 2008). These species also used benthic resources, such as epibenthic and endobenthic invertebrates, as a secondary component in their diet and have been described as scavengers (Burukovskij, 1992; Cartes, 1993; Kitsos et al., 2008). In this study, only one of these two species had high levels of abundance, suggesting that there is direct competition for space or resources. However, these differences in abundance can also be explained by depth because in the Canaries, *P. narval* has its maximum abundance (> 90%) in depths shallower than 175 m (González et al., 1997). Additionally, for the different size ranges of both species (> 25% carapace length), trophic partitioning among these species can occur, causing them to feed on a different size range of prey (Cartes, 1993). In the assemblage found on the upper slope, the pandalid shrimp *P. ensis* and *P. edwardsii* have similar biological characteristics with a *CoG* of distribution of the standardized abundance at depths significantly separate by more than 120 m, and both species have high abundance levels, although they have similar diets. Both species have been described as predators on macroplankton and are considered generalized feeders, preying on decapods and on benthic resources, such as epibenthic and endobenthic invertebrates, and scavenging on benthic macroinvertebrates as a secondary activity in their feeding habits (Cartes, 1993; Labropoulou and Kostika, 1999; Fanelli and Cartes, 2004). No evidence exists of trophic partitioning among these *Plesionika* species, which appear to prefer similar prey in different areas along their wide geographical range, as has been indicated by Labropoulou and Kostika (1999) and Kitsos et al. (2008). The relatively high overlap between their diets, the high trophic level occupied by these pandalids, and the observed pattern of rapid succession with depth may be consistent with a bathymetric displacement of *CoG* between these species (Cartes, 1993; Rex, 1977), with *P. ensis* having a deeper habitat than *P. edwardsii.* This bathymetric displacement allows both species to have a high level of abundance given that there is no direct competition for space or resources. Additionally, the dominant species in this assemblage, the pandalid shrimp *H. ensifer*, has a *CoG* of the standardized abundance located deeper than those estimated for *P. ensis* or *P. edwardsii*, which is the probable reason that the three species, *P. edwardsii*, *P. ensis*, and *H. ensifer*, can co-exist in high numbers given that they do not directly compete with one another. This pattern of stepper distribution among *Plesionika* and/or *Heterocarpus* species was also observed on the African coast (Muñoz et al., 2012) as well as in Mediterranean waters, where these species are distributed in a stepped form to avoid competition for space and resources (Cartes, 1993). Vafidis et al. (2005) indicated that as a general pattern, *Plesionika* species are segregated by depth, showing a divided bathymetric space, where each species has a preferred depth range. Cartes (1998), Labropoulou and Kostika (1999), and Fanelli et al. (2004) noted an intraspecific segregation by depth among *Plesionika* species with high dietary overlap in the areas where they coexist, with competitive trophic interactions responsible for the low overlap in the bathymetrical distribution of the species. A similar pattern of stepped distribution has been observed in this study for the large crabs *C. bellianus*, *P. cuvieri*, and *C. affinis*. In this case, the steeper distribution is linked to an aggressive behavior exhibited for these species, as has been indicated by Triay-Portella et al. (2014) and Biscoito et al. (2015).

The greatest mean species richness and diversity were located on the upper slope, and the species richness and diversity decreased when the depth increased or decreased. The pattern found in the Canaries was also described in the neighboring area of the Madeira Archipelago by Rosa et al. (2012), who found an exponential decline in richness from shallow to abyssal depths. This pattern is probably linked to various factors, such as temperature, heterogeneity of habitats or food availability, that simultaneously influence the species richness and diversity. Rosa et al. (2012) suggested a relationship between decapod diversity and temperature, with decreasing richness with decreasing temperature, while Paterson and Lambshead (1995), Rex et al. (2005), and Rosa et al. (2012) suggested a reduction in species richness with depth as a consequence of the reduction in food availability. As a general pattern among benthic macrofauna, the greatest richness of species has been observed in the middle bathyal zone (Maynou and Cartes, 2000; Moranta et al., 2004; Muñoz et al., 2012; Fanelli et al., 2013), generating a bell-shaped distribution of species richness with depth (Gage and Tyler, 1991; Maynou and Cartes, 2000; Muñoz et al., 2012). In this regard, Gage and Tyler (1991) and Maynou and Cartes (2000) indicated that the intermediated disturbance hypothesis is used to explain this pattern as a mechanism combining production and competition dynamics and varying-frequency disturbances. As Maynou and Cartes (2000) noted, the high disturbance of the shelf may explain the low species richness found in the shallower area, and the low species richness on the lower slope can be best explained by a decrease in the food supply, enhancing competition and species exclusion. A reduction in diversity following a downslope gradient from the upper to the lower slope has been described as a common feature in the deep Atlantic (Gage and Tyler, 1991) as well as in the Mediterranean (Fanelli et al., 2013). In the Mediterranean, Fanelli et al. (2013) found greater decapod biomass and diversity in the upper slope zone, coinciding with minimum values of O_2. However, in the Canaries, the lowest values of dissolved oxygen are found in the MW-AIW area (Machín et al., 2006) with lower biomass and diversity than on the upper slope, suggesting that other factors are responsible for this diversity pattern.

The maximum values of standardized abundance were observed in the transition zone between shelf and slope (TSS) assemblage, while the biomass in the upper slope (US) showed an exponential decreasing pattern with depth. A similar decreasing pattern with low values of abundances and biomasses recorded with depth has been described in the Atlantic (Haedrich et al., 1975; Wenner and Boesch, 1979; Markle et al., 1988; Cartes et al., 2007) as well as in the Mediterranean (Follesa et al., 2009; Fanelli et al., 2013). Although of a marked oligotrophic character (Schmoker et al., 2012, 2014), the Canary archipelago shows certain oceanographic events, such as areas of geostrophic eddies and wind-shear (island mass effect), which can generate notable differences between shallow and deep waters in relation to biomass (Arístegui and Montero, 2005; Hernández-León et al., 2007). The depth of the greatest biomass coincides with the zone of highest zooplankton biomass in the area. In this respect, more than 50% of the planktonic biomass is located in the first 200 m, and the macrozooplankton, which form a deep scattering layer, prey on this planktonic biomass (Hays, 1996; Hernández-León et al., 2007) and enable macroplankton feeders, such as the pandalid shrimp *Plesionika* and *Heterocarpus*, to receive a greater supply of material and consequently possess greater biomass.

The smallest mean weight per individual and the highest biomass were observed in the TSS and US areas associated with an abundance of small swimmer decapods such as *P. narval*, *P. martia* or *P. edwardsii*. This coincides with the observed k-dominance curves that are characterized by a few species widely dominating the assemblage. However, the mean weight per individual increases with depth, probably reflecting the high abundance of the small decapods on the upper slope. The high concentration of small-sized/weighted species with high renewal rates is associated with high productivity. In the Canaries, there is a shock phenomenon (island mass effect) of wind and of the eastern boundary current in the surface zone against the islands that generates concentrations of nutrients, productivity and biomass of mesozooplankton that are higher than those in the oceanic waters of the archipelago (Hernández-León et al., 2007). Furthermore, in the surface zone, geostrophic eddies act to drain organic matter, favoring the development of biomass on the upper part of the slope and establishing levels of productivity that are greater than in deep waters in which the water masses are oligotrophic in character and have very low levels of productivity (Arístegui et al., 1994; Arístegui and Montero, 2005; Hernández-León et al., 2007). Under these oligotrophic conditions in the LS, biomass is distributed more homogeneously among different size/weight classes or is increasing in the largest sizes/weights (Saiz-Salinas and Ramos, 1999). The same pattern of increase in range size with depth has also been described in Madeira (Rosa et al., 2012). The opposite pattern has been described in the Mediterranean with a downward trend in mean size/weight of the dominant species with depth (Sardà and Cartes, 1993; Fanelli et al., 2013). These differences may be due to the oligotrophic character of the deep Mediterranean and to metabolic rates, which decrease as temperature decreases with depth. Moreover, temperature remains constant at around 13 °C below approximately 200 m in the Mediterranean, which is different from the Canaries (Childress et al., 1990).

The causes of zonation can be attributed to changes in environmental parameters with depth, which affect the biology and physiology of organisms (Rex, 1976; Yeh and Drazen, 2009). The bathymetric partitioning observed in the distribution of the deep-sea decapod community in the small submarine canyons of the Canaries responds to changes in these parameters, and it is a phenomenon described throughout the world's oceans (Haedrich et al., 1980; Yeh and Drazen, 2009).

In the Canaries, the existence of depth boundaries inside the submarine canyons is closely linked to oceanographic conditions, as has been found in other areas (Snelgrove and Haedrich, 1985; Olabarria, 2005; Fanelli et al., 2013; Cartes et al., 2014). These discontinuities coincide with the transition zone between the insular shelf and slope, as well as with the transition between the ENACW and MW-AIW, and between the MW-AIW and NADW water masses located at depths of approximately 700 and 2000 m, respectively (Hernández-Guerra et al., 2002; Hernández-León et al., 2007). In this regard, the values found in this study (9.2 °C and 35.65 psu in salinity between the ENACW and MW-AIW masses) are in agreement with those given by Hernández-Guerra et al. (2001) and Machín et al. (2006), who indicated that the end of the ENACW occurred at approximately 11 °C and 35.5 psu in salinity (Fig. 6). The values recorded in this study for the NADW mass in areas deeper than 2000 m (3.1–4.78 °C and less than 35.09 psu in salinity) also coincide with the characteristics of the NADW mass indicated by Machín et al. (2006) (Fig. 6). These changes in salinity and mainly in temperature result in the presence of density and thermal barriers for the vertical distribution of fauna (Canals et al., 2006). Olabarria (2005) and Cartes et al. (2007, 2014) also noted the existence of boundaries in the NE Atlantic related to the structure of water masses. The first depth boundary observed inside the submarine canyons is located at a depth of 300 m, inside the ENACW mass, which reaches a depth of approximately 700 m and is far from the influence of the surface mixed layer, which reaches no more than 100–150 m deep (Hernández-Guerra et al., 2002; Hernández-León et al., 2007). This boundary is formed as a consequence of the penetration of the eurybathic species of the shelf into the first 100 m of the transition zone between shelf and slope, marking this depth their limit (Cartes et al., 2003) or of species characteristic of this ecotone, such as *D. arrosor*, *P. narval* or *P. macrochelos*. A faunal discontinuity in the Atlantic separating an upper shelf-slope zone of transition, where shelf species extend their distribution down the slope, from a deeper bathyal zone has also been indicated by Markle et al. (1988), Olabarria (2005), and Frutos and Sorbe (2014). At a depth of approximately 2000 m, the MW-AIW mass is replaced by the NADW mass (Hernández-Guerra et al., 2002; Hernández-León et al., 2007), which, along with the upper limit of the distribution of abyssal species, marks the final discontinuity (Maynou and Cartes, 2000). The deepest discontinuity that separates the assemblages located in the middle and deep sections of the slope has been established in all areas studied (e.g. Cartes et al., 2003, 2014; Follesa et al., 2009; Fanelli et al., 2013). The presence of assemblages of decapods along the slope in the Atlantic Ocean, with faunal boundaries associated with water masses, has also been described by Fariña et al. (1997) and by Cartes et al. (2007, 2014). Fanelli et al. (2013) suggested that environmental variables, such as temperature, salinity and O_2 that are related to water mass characteristics, and their change with depth are fundamental in the bathymetric distribution, biomass and assemblage structure of deep-sea decapod species. Cartes et al. (2014), studying a seamount in the NE Atlantic between depths of 744 and 1800 m, found two assemblages: one influenced by Mediterranean outflow waters and another in the deep slope related to the Labrador Sea Water. In the former instance, these authors found coincident species with those observed in the Canaries associated with the MW mass such as *R. robusta*, *C. affinis*, and *P. typhlops* and with the ENACW mass such as *C. bellianus*, *P. martia*, and *B. maravigna*, although some of these species have also been found in the Canaries at depths of the MW mass. The existence of a boundary between the upper and middle zones of the slope inside the submarine canyons can frequently be due to hydrographic conditions as a consequence of the Levantine Intermediate Water or seasonal changes that the Mediterranean Intermediate Water mass undergoes, as has been extensively described in the Mediterranean (Abelló et al., 1988; Cartes and Sardà, 1993; Papiol et al., 2012). In the Mediterranean, the existence of other boundaries between communities in the middle zone of the slope corresponds to trophic conditions that rely on the stability of oceanographic conditions, i.e., temperature and salinity, over the middle slope (Cartes and Sardà, 1993; Cartes et al., 2015), in spite of some long-term changes in temperature, salinity and dissolved oxygen that were recently evidenced (Cartes et al., 2015). However, there is no such stability in the water column in the Canaries, which brings into focus the fact that the discontinuity observed in the middle area of the slope is a consequence of a change in the water masses present, which are the principal cause of limits between communities.

Data regarding the individual distribution of each species support the importance of water masses in the Canaries. Thus, the sergestid prawn *R. robusta* and the Oplophoroidea shrimp *A. eximia* can show a deeper limit of distribution in the Mediterranean, down to 3300 m (Company et al., 2004). In the Canaries, the depth of these species is likely limited by the appearance of the NADW mass, which generates a sharp change in temperature at a depth of 2000 m, creating a different thermal stability to that observed in the Mediterranean water mass (Williams, 1998; Skliris and Lascaratos, 2004). The distribution of the giant red shrimp *A. foliacea* in the Canary Islands is mainly found above 600 m. However, this species reaches depths of 700 m in the western Mediterranean and 1100 m in the eastern Mediterranean (Abelló et al., 1988; Cartes et al., 1994; Company et al., 2004; Politou et al., 2004). *A. foliacea* is a species that is considered much more closely tied to warm water masses than other deep-water decapods (Politou et al., 2004). This agrees with the fact that temperature and salinity data recorded are considerably higher in the ENACW mass than in other deep water masses, which explains the more limited depth range in the Canaries.

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Ichthyological note – *Note ichtyologique*

On the presence of *Trachinus pellegrini* (Trachinidae) in the Canary and Cape Verde Islands (north-eastern Atlantic)

by

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Résumé. - Présence de *Trachinus pellegrini* (Trachinidae) aux îles Canaries et aux îles du Cap-Vert (Atlantique nord-est).

Trachinus pellegrini Cadenat, 1937 est signalée pour la première fois aux îles Canaries, ce qui représente sa limite de répartition la plus septentrionale. Les différences morphologiques entre adultes et juvéniles sont également présentées. La présence de cette espèce aux îles du Cap-Vert est aussi confirmée.

Key words. – Trachinidae - *Trachinus pellegrini* - Canary Islands - Cape Verde Islands - Eastern Atlantic - New record.

Trachinids (Perciformes) are small to medium-sized fishes (45 cm total length maximum) living, as often burrowers, on sandy or muddy bottoms in littoral areas and on the upper part of continental shelf of the eastern Atlantic Ocean (including the Mediterranean and Black seas), rarely down to 150 or 200 m of depth. Their gill cover spine and spines on first dorsal fin bear venomous glands. Weeverfishes are usually caught in bottom trawls and also in various artisanal fishing gears. They are not of great commercial importance, but they are esteemed as foodfishes in many localities (Roux, 1981; Bauchot, 1987; Nelson, 2006).

Up to date, the family Trachinidae was represented in the Canary Islands (Fig. 1) by two genera and three species: *Echiichthys vipera* (Cuvier, 1829), *Trachinus draco* Linnaeus, 1758, and *Trachinus radiatus* Cuvier, 1829 (Brito *et al*., 2002; Brito and Sancho, 2003) and in the Cape Verde Islands (Fig. 1) by a single genus with three species: *Trachinus armatus* Bleeker, 1861, *Trachinus collignoni* Roux, 1957, and *Trachinus pellegrini* Cadenat, 1937 (Wirtz *et al*., 2013).

Trachinus araneus Cuvier, 1829 was recorded from the Canaries by Steindachner (1867) and Brito (1991), but Brito *et al*. (2002) did not find any evidence of its presence, postulating a probable misidentification with *T. radiatus*. The authors have also found no evidence of this species.

Reiner (1996, 2005) recorded *T. araneus* from the Cape Verde, but Wirtz *et al*. (2013) pointed out that it is not a valid record, because no proof of existence is given. *T. collignoni* was also recorded from the Cape Verde by Cadenat and Roux (1964) and subsequently compiled by Reiner (1996, 2005), but according to Wirtz *et al*. (2013), this record needs confirmation, on the basis of the uncertainty expressed by Cadenat and Roux (1964).

Following a series of surveys off the Canary Islands, *T. pellegrini* (Fig. 2A) was caught for the first time from this archipelago. An in-depth morphological comparison has resulted in the identification of *Trachinus* sp. from the Cape Verde Islands (see González *et al*., 2014) as *T. pellegrini* (Fig. 2B). The present morphometric and meristic study will contribute to enrich the morphology data of this poorly known species.

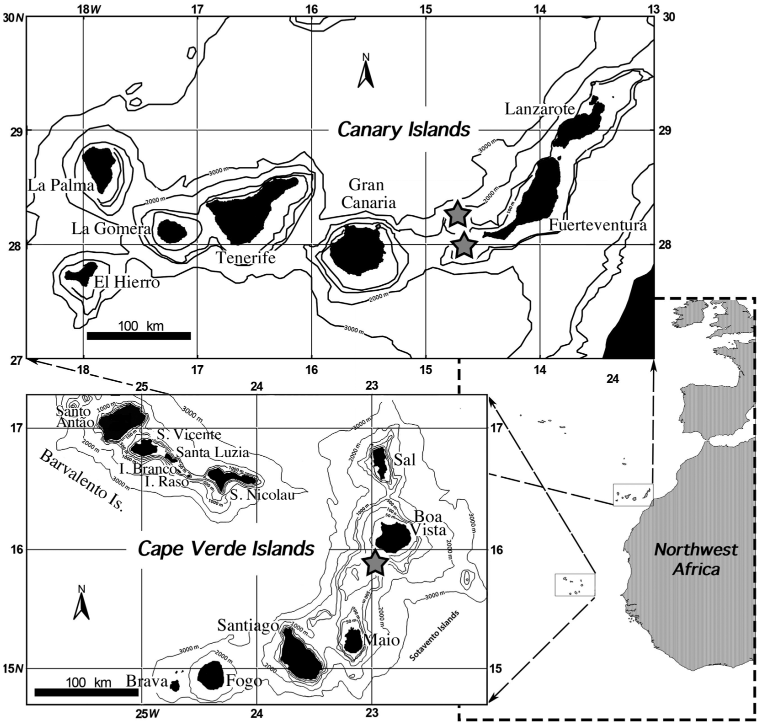

Figure 1. - The Canary and Cape Verde Islands. Collection locations for *Trachinus pellegrini* (★).

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Figure 2. - *Trachinus pellegrini*. **A**: Juvenile from the Canary Islands (TFMC-VP/1947, 68.0 mm TL, 59.6 mm SL); **B**: Subadult from the Cape Verde Islands (MMF42285, 119 mm TL, 101 mm SL). Scale bars = 25 mm.

MATERIAL AND METHODS

All specimens studied herein were caught during experimental fishing cruises on board Spanish research vessels around the Canary and the Cape Verde Islands. Cruises Infueco-0710 and Infueco-0611 took place around the Canaries on board the R/Vs *Emma Bardán* and *Miguel Oliver*, respectively. Cruise Camarão-2 was done around the Cape Verde on board the R/V *Prof. Ignacio Lozano*.

Canarian specimens examined were caught with dredge and small-scale bottom trawl off submarine banks nearby Fuerteventura Island (Fig. 1). The Cape Verdean specimen was collected in a bottom fish trap off Boa Vista Island (Fig. 1).

The present paper follows the best practice approach to overcome unverified and unverifiable "first records" as proposed by Bello *et al*. (2014).

Voucher specimens were deposited in the collections of the 'Museo de Ciencias Naturales de Tenerife' (TFMC) and the 'Museu de História Natural do Funchal' (MMF). Muscle tissue samples taken from specimens were stored at ICCM ('Iniciativa de Colecciones de Ciencias Marinas') from the Biology Department of the University of Las Palmas de Gran Canaria.

Meristic and morphometric measurements (in mm) were made following Hubbs and Lagler (1958). Other counts and terminology follow Cadenat (1937, 1938) and Roux (1981). Due to the high number of morphometric (23, including total length TL) and meristic (13) variables considered, as well as many body proportions (6), we have opted to explain abbreviations in table I.

RESULTS

Trachinus pellegrini Cadenat, 1937 (Figs 2A, B)

Material examined. - Canary Islands: MMF44358, one subadult, 93.6 mm TL, 79.7 mm SL, 28°16.7'N 14°46'W, Banco de Amanay, South-west of Fuerteventura Island, 114 m of depth, cruise Infueco-0710, sta. BV2, soft substrate, 6 Jul. 2010, small-scale bottom trawl; TFMC-VP/1946, one subadult, 113.1 mm TL, 95.0 mm SL, 28º03'N 14º39'W, El Banquete, South of Fuerteventura Island, 188 m of depth, cruise Infueco-0710, sta. DR6, rocky bottom with sand, 10 Jul. 2010, dredge; TFMC-VP/1947 (Fig. 2A), one juvenile, 68.0 mm TL, 59.6 mm SL, 28º15'N 14º48.5'W, Banco de Amanay, South-west of Fuerteventura Island, 141 m of depth, cruise Infueco-0611, sta. BV4, soft substrate, 11 Jun. 2011, small-scale bottom trawl. Cape Verde Islands: MMF42285 (Fig. 2B), one subadult, 119 mm TL, 101 mm SL, 15º55'N 22º56'W, Ponta Lacacão, Boa Vista Island, 122-137 m of depth, cruise Camarão-2, sta. 15, rocky bottom with sand, 7 Mar. 2012, bottom fish trap.

Selected body proportions and meristics of the specimens studied are shown in table I and compared with the scarce morphology data available from the literature (Cadenat, 1937, 1938).

Regarding body proportions, data from the specimens examined herein agree in all respects with published data (Tab. I). Our specimens extend, above or below, the proportions IOD in %EDh, TL/Bdepth, TL/HL, EDh/SnL, PsOL/SnL and HL/EDh. In our specimens, pectoral fin length (PL) seems to show a tendency to decrease with size. The opposite seems to occur with least depth of caudal peduncle (CPHt) and also with caudal peduncle length (CPL) (taken at ventral profile). Also, inter-orbital distance (IOD) seems to increase with size (Tab. I).

When comparing with the holotype, meristics of the specimens examined herein agree in almost all respects, except for some minor differences (Tab. I), e.g. in second dorsal fin rays (one ray less), anal fin rays (one more ray), pectoral fin rays (14-16 vs 17) and caudal fin rays (two more rays). Our adult and subadult specimens bear six spines in the first-dorsal fin, except for the juvenile individual, which has only five spines. Lower gill rakers on the 1st arch coincide with the holotype. There is no published information on upper gill rakers to compare with our data. Lateral line scales ranged from 74 to 82 in our specimens, thus establishing a range that was not previously known. Antero-supraorbital spines in our material ranged from two to three, with one juvenile specimen bearing two on the right side and three on the left. Adult and subadult

Table I. - Selected counts, morphometrics and body proportions of *Trachinus pellegrini*.

	MMF42285 1 specimen 119 mm TL Cape Verde Islands Present study			TFMC/VP1946 1 specimen 113 mm TL Canary Islands Present study			MMF44358 1 specimen 94 mm TL Canary Islands Present study			TFMC/VP1947 1 specimen 68 mm TL Canary Islands Present study			Cadenat (1937, 1938) 2 spec., 137-140 mm TL Cape Verde Islands holotype, 215 mm TL Guinea-Conakry	
	mm	in %SL	in %HL	mm	in %SL	in %HL	mm	in %SL	in %HL	mm	in %SL	in %HL	in %SL	in %HL
Morphometrics and body proportions														
Standard length, SL	101.0	–	–	95.0	–	–	80.0	–	–	60.0	–	–	–	–
Pre-first dorsal length, PD1L	26.0	25.7	–	21.0	22.5	–	19.0	23.5	–	16.0	26.1	–	no data	–
Pre-second dorsal length, PD2L	39.0	38.6	–	35.0	36.8	–	28.0	35.1	–	21.0	35.8	–	no data	–
Preanal length, PAL	41.0	40.6	–	35.0	37.2	–	28.0	34.8	–	25.0	42.7	–	no data	–
Pre-anus length, PAnL	39.0	38.6	–	33.0	34.4	–	27.0	33.7	–	25.0	41.6	–	no data	–
Prepectoral length, PPL	32.0	31.7	–	26.0	26.9	–	21.0	26.4	–	18.0	30.2	–	no data	–
Pectoral fin length, PL	18.0	17.8	–	18.0	19.3	–	16.0	20.3	–	15.0	25.9	–	no data	–
Head length, HL	31.0	30.7	–	27.0	28.7	–	23.0	28.9	–	20.0	32.7	–	no data	–
Head height at posterior border of orbit, HHt	19.0	18.8	–	15.0	16.1	–	12.0	15.4	–	11.0	19.0	–	no data	–
Preopercular length, POpL	20.0	19.8	–	21.0	22.1	–	17.0	20.8	–	14.0	23.3	–	no data	–
Maximum body depth, Bdepth (at anus level)	25.0	24.8	–	21.0	21.7	–	18.0	22.4	–	15.0	24.5	–	no data	–
Least depth of caudal peduncle, CPHt	8.0	7.9	–	7.0	7.4	–	6.0	7.1	–	4.0	6.7	–	no data	–
Caudal peduncle length, CPL (at ventral profile)	7.0	6.9	–	4.0	4.2	–	2.5	3.1	–	2.0	3.1	–	no data	–
Snout length, SnL (until mid level of eye)	5.0	–	16.1	3.5	–	12.8	3.3	–	14.3	2.6	–	13.1	–	no data
Eye diameter, EDh (horizontal)	8.5	–	27.4	6.5	–	23.7	6.2	–	26.8	5.7	–	29.4	–	26.7-28.6
Eye diameter, EDv (vertical)	7.0	–	22.6	5.0	–	18.4	5.3	–	23.0	5.0	–	25.6	–	no data
Inter-orbital distance, IOD	2.5	–	8.1	2.0	–	7.3	1.3	–	5.5	1.0	–	5.0	–	no data
Post-orbital length, PsOL	19.0	–	61.3	18.0	–	66.0	14.0	–	60.9	12.0	–	60.4	–	no data
Upper jaw length, UpJL	14.0	–	45.2	13.0	–	48.3	11.0	–	46.0	9.0	–	47.2	–	no data
Gape length, GL	11.0	–	35.5	11.0	–	40.6	9.0	–	38.2	7.0	–	37.8	–	no data
Length of longest dorsal–fin ray (4th)	8.0	7.9	25.8	broken	13.1+	45.7+	14.8	18.6	64.5	6.8	11.4	34.9	no data	no data
Length of longest anal–fin ray	8.0	7.9	25.8	6.7	7.0	24.5	5.3	6.6	22.9	5.5	9.2	28.2	no data	no data
IOD in %EDh	29.4			30.9			20.6			17.1			25.0	
TL/Bdepth	4.76			5.48			5.25			4.64			4.75-5.00	
TL/HL	3.84			4.15			4.07			3.49			3.75- 4.05	
EDh/SnL	0.59			0.54			0.53			0.45			0.50	
PsOL/SnL	3.80			5.14			4.24			4.60			4.90	
HL/EDh	3.65			4.21			3.73			3.40			3.50-3.75	

Table I; - Continued.

Meristics	MMF42285	TFMC/VP1946	MMF44358	TFMC/VP1947	Cadenat (1937, 1938)
					from holotype
First dorsal–fin spines	6	6	6	5	6
Second dorsal–fin rays	26	27	27	27	27-28
Anal fin rays	28	29	30	28	29-30
Pectoral fin rays	15	16	16	14	17
Caudal fin rays (segmented)	15	14	14	15	13
Branchiostegal rays	6	6	6	6	6
Upper gill rakers (1st arch)	7	1 tubercle + 5	1 tubercle + 5	6	no data
Lower gill rakers (1st arch)	12 + 1 tubercle	12 + 2 tubercles	12 + 2 tubercles	12	12 + 2 tubercles
Total developed gill rakers	19	17	17	18	no data
Scales in lateral line	74	79	79	76	82
Antero–superior orbital spines (right/left)	2	3	3	2 / 3	2
Preopercular spines	absent	absent	absent	4 small spines on inferior edge	absent

specimens examined have no preopercular spines. The juvenile has four small spines on the lower edge of preopercle (Tab. I).

Anal-fin rays are fleshy and their segmentation is hardly visible in adult or subadult specimens (ranging 94-119 mm TL), while they are not fleshy and segmentation is well visible in the juvenile specimen examined (68 mm TL).

Like in Roux (1981), our four specimens have the first dorsal-fin bluish grey. On the comparative table in Cadenat (1938), the author says the first dorsal fin is entirely transparent. However, in the text describing the species, Cadenat (1937, 1938) clarified that first dorsal-fin of type material is light bluish grey, bordered excessively pale yellow and with no trace of black spots, as found in other species.

Regarding the extraordinary development of the second-dorsal rays, Cadenat (1938) says that it is a minor character, manifesting perhaps at the time of reproduction, or is only a secondary sexual character in males.

The maximum published length for the species is 200 mm TL, common length 150 mm TL (Roux, 1990). Our material ranges from 68 to 119 mm TL, most probably corresponding to juvenile to subadult individuals.

Remarks. - *T. pellegrini* is an eastern Atlantic species, ranging from Mauritania (Froese and Pauly, 2015, FishBase) and Senegal to Nigeria, including the Cape Verde Islands (Roux, 1990). Previous records from the Canary Islands by Roux (1981, 1990) could not be confirmed. Its presence around the Cape Verde Islands was confirmed by Menezes *et al*. (2004).

This is a tropical demersal species, inhabiting rock and sand bottoms (Roux, 1981), to a maximum depth of 188 m [previously 150 m (Roux, 1981; Schneider, 1990)]. The specimens examined herein were collected on rocky bottom with sand and on soft substrata, at depths between 122 and 137 m (Cape Verdes) and from 114 to 188 m (Canaries). The upper limit of its vertical distribution remains unknown. According to Roux (1981) it feeds mainly on crustaceans.

Trachinus pellegrini is recorded for the first time from the Canary Islands waters fixing now the northernmost limit (28°16.7’N) of the species distribution. Although the species was known with certainty from the Senegalese coasts (Roux, 1990), Roux (1981) had already pointed out “possibly ranging further north” and it has been recently found in Mauritania (Froese and Pauly, 2015, FishBase). Moreover, *T. pellegrini* is, up to date, the only *Trachinus* species inhabiting both the Canary and Cape Verde Islands.

In the last thirty years, sea surface temperature in the area of the Canary Islands has shown and increasing trend (Santos *et al*., 2012), with records over 24°C. In this scenario, the appearance of *T. pellegrini* in the Canary Islands waters would not be surprising, and its presence could be one more evidence of the changes in the distribution of species due to warming in the Atlantic. This phenomenon (‘tropicalization’) has been observed in the Canaries even for species with low dispersal ability (Falcón *et al*., 2002; Brito *et al*., 2005).

Another hypothesis explaining the present record of *T. pellegrini* in the Canaries could be its misidentification with *T. radiatus*, since both species have radiating bony crests on top of head behind eyes. Possibly the species is also present in the Atlantic Moroccan and Saharan neighboring coasts and has passed unnoticed. If this is the case, we are in the presence of a eurythermal species, occurring both in tropical waters (Cape Verdes) and in temperate waters (Fuerteventura banks, Canaries).

Finally, it would be worth mentioning the possibility of transport in ballast waters, discarded close to or in the surroundings of main harbours (see Brito *et al*., 2011). Over the last five years, transits of oil platforms between Africa and major ports of the Canaries for repair and maintenance have greatly increased. Although remote, this hypothesis should not be ruled out as these enormous floating structures come mostly from the coast of central Africa, e.g. off Nigeria, within the known distribution of *T. pellegrini*.

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Sex-structure, depth distribution, intermoult period and reproductive pattern of the deep-sea red crab *Chaceon affinis* (Brachyura, Geryonidae) in two populations in the north-eastern Atlantic

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ABSTRACT

This work investigated the biology of *Chaceon affinis* in two isolated populations of the Atlantic Ocean, including depth distribution, sexual structure, reproductive patterns and intermoult period. Males were larger and heavier than females. Mean size decreased with depth for both males and females. The highest abundance was found at 600–799 m of depth for males and at 800–999 m depth stratum for females. The highest abundance of ovigerous females was found at the 800–999 m depth stratum. Of the different ovaries' colour or colour shades recorded, only six categories were histologically characterized. The presence of spermatophores in the spermatheca of females in carapace stages II and III suggests that spermatophores are viable and used during the intermoult period. The size at sexual maturity in females was estimated at 104.4–104.7 mm carapace width (CW) in Madeira, and 109.3–110.5 mm CW in the Canary Islands. Only three categories of testes were identified. Mature testes consisted in a large mass, with highly coiled vasa deferentia visible to the naked eye. The size at sexual maturity in males was estimated at 113.8 mm CW in Madeira and 118.9 mm CW in the Canaries. The relative growth of males showed significant changes along the ontogeny and size at which allometric growth changes, as an indicator of morphometric maturity, occurred between 103.2 and 103.6 mm CW in Madeira and between 111.4 and 113.1 mm CW in the Canaries. In females, size at which allometric growth changes was found for maximum width of fifth abdominal somite (AS5W) at 98.2 mm CW in Madeira and 103.0 mm CW in the Canaries. The size at maturity obtained for *C. affinis* indicates that the minimum landing size (MLS) should not be set smaller than 125 mm CW in Madeira and 130 mm CW in the Canaries. This conservative MLS, higher than length at functional maturity, would safeguard immature individuals until they reach the size at which they can contribute to the reproductive capacity of the population. Ovigerous females were observed from October to April in Madeira, and in all months in the Canaries. Moreover, the observation of berried females in the last developmental stage in all quarters of the year suggests that gonad maturation and release of larvae are asynchronous throughout the spawning season. A total of 138 crabs with CW between 96 and 154 mm were tagged off Madeira. Of these, nine were recovered in the same area, more than 900 days after tagging. Eight of the recaptures were females with a wide range of CW confirming intermoult periods exceeding three years with expected growth per moult of less than 20 mm CW.

1. Introduction

Crabs of the family Geryonidae are widely distributed on continental slopes of the world ocean, and one of the major members of the slope megafauna, accounting for 50% or more of bathyal megafaunal biomass in some areas (Haedrich et al., 1975, 1980; Erdman et al., 1991; Hastie, 1995). They play an important role in the trophic structure of the bathyal ecosystems (Haedrich et al., 1980; Merrett and Haedrich, 1997; Biscoito and Saldanha, 2000; Cartes and Carrassón, 2004; Mantelatto et al., 2014) and a growing demand for human consumption is leading to an increasing commercial exploitation of these crabs (Hilário and Cunha, 2013).

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The genus *Chaceon* Manning & Holthuis, 1989 contains thirty-four medium to large sized commercial species (Groeneveld et al., 2013; Davie, 2014). One of them, the deep-sea red crab *Chaceon affinis* (Milne-Edwards & Bouvier, 1894), the largest species in the family, has been commercially harvested since 1990 and is currently caught in different parts of the northeast Atlantic without regulation or control (Sampedro et al., 2001; Robinson, 2008) including in the Madeira and Canary archipelagos where an artisanal fishery started in recent years. *C. affinis* is distributed from Iceland to Senegal, around all the Macaronesian archipelagos and oceanic seamounts throughout the eastern Atlantic Ocean (Manning and Holthuis, 1981, 1989; d'Udekem d'Acoz, 1999). It has also been found in the vicinity of hydrothermal vent sites on the Mid-Atlantic Ridge (Biscoito and Saldanha, 2000). Although recorded between 130 and 2047 m of depth, it is most commonly found between 500 and 1200 m depth and separate populations are present in each of the three Macaronesian archipelagos (Azores, Madeira and Canaries).

C. affinis is expected to be highly vulnerable to overexploitation for their high economic value and *k*-strategy life-traits (Erdman and Blake, 1988; Robinson, 2008; Pezzuto and Sant'Ana, 2009). For these reasons, in order to assure its sustainability, fishing and biological regulations are needed. This work investigates the sex structure, distribution and reproductive patterns and intermoult period of *C. affinis* in two archipelagos of the Northeast Atlantic. It also addresses some questions about its life cycle and, from a precautionary approach, recommends several measures to harvest this species within biologically safe limits. Although there are previous studies on this species in the Canary Islands, the information given is limited by the small number of individuals studied (Castro et al., 2010) and low geographical representation (Fernández-Vergaz et al., 2000; López-Abellán et al., 2002).

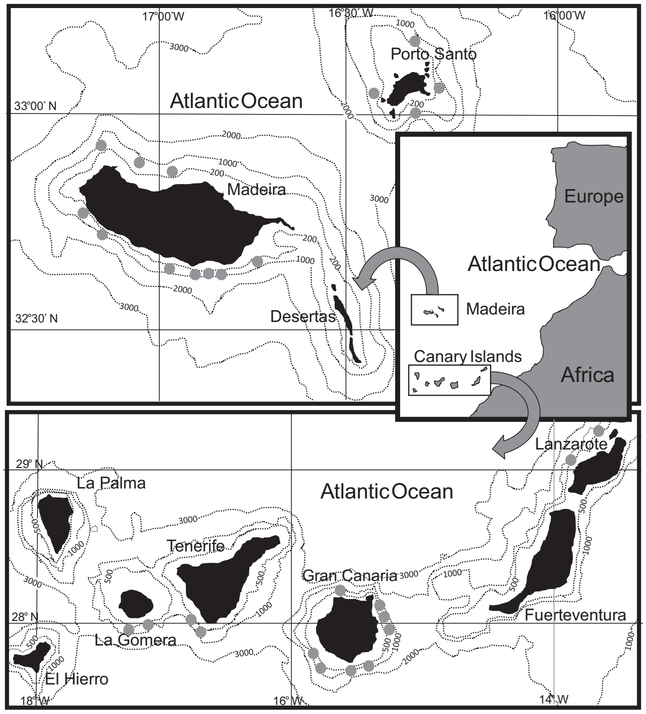

Fig. 1. Location of the sampling sites off the Madeira and Canary archipelagos.

2. Materials and methods

2.1. Sampling and data collection

A total of 8389 individuals of *C. affinis* caught around Madeira and the Canary archipelagos between 2005 and 2011 were studied. Forty seven research cruises using bottom traps were carried out. The work areas were randomly prospected from 400 to 1300 m (Fig. 1). The sampled locations varied from trip to trip and the sampling effort, across the bathymetric range, was equally distributed at 200 m intervals, with a total of four strata prospected: 400–599, 600–799, 800–999, and ≥ 1000 m of depth. For each depth stratum, 120 traps were deployed on the sea ground, covering sandy, muddy and rocky bottoms, with a total of 480 traps used.

Crabs were captured with square metallic traps, with 80 × 50 cm base length and 50 cm in height, covered with 15 × 15 mm mesh. Each trap had one troncoconical opening, with a 23-cm outer diameter and a 19-cm inner diameter (Biscoito, 1993). Atlantic chub mackerel (*Somber colias*) was used as bait and immersion times ranged from 30 to 36 h.

Measurements were taken following Attrill et al. (1991): carapace width (CW), carapace length (CL), right/left cheliped length (R/LCHL) and width of fifth abdominal somite (AS5W) in females. These measurements were defined as follows: CW, the maximum transversal diameter at the midline of the carapace, excluding the fifth dorsolateral spines; CL, the longitudinal diameter from the diastema between the rostral teeth to the posterior carapace margin; R/LCHL, the distance from the more distal point on the palm base to the dactyl tip; AS5W, the maximum width of the fifth abdominal segment. CW and CL were taken on the upper side on the crab, in the left-right and anterior-posterior direction respectively; R/LCHL on the upper external margin of the chelipeds, in the distal-basal direction; AS5W on the underside and in the left-right direction. All measurements were taken to the nearest mm. Individuals with regenerated, damaged or missing parts were excluded from statistical analysis, as well as those parasitized with *Sacculina* sp.

Carapace conservation stage, sex (based on abdomen morphology) and ovigerous condition (based on the presence of external or remaining eggs on the pleopods) were also recorded. The carapace conservation was macroscopically classified as follows: stage I, carapace with neither barnacles nor lesions produced by chitinolytic bacteria; stage II, carapace with a low level of lesions and barnacle infestation; III, carapace with a high level of lesions and barnacles (Pinho et al., 2001a). Total wet weight (TW) and gonad weight (GW) were recorded to the nearest 0.1 g.

Colour of the ovaries was recorded using the chromatic scale proposed by González et al. (1998) and used by Pinho et al. (2001a). A six-stage maturity scale modified from Erdman and Blake (1988) and based on size, shape and condition of ovaries was used. Stage I: immature; ovaries translucent, small (less than 2 mm in diameter), very thin and tubular, without pronounced lobules. Stage II: early developed; ovaries small and easily seen, with four thin lobules and a thick ovarian wall. Stage III: developing (if before first maturity)/resting (after first maturity); ovaries characterised by moderately thick lobules, but without pronounced lobation and less compact than in further stages. Stage IV: advanced; ovaries swollen and with pronounced lobation that becomes noticeable in this stage. Stage V: mature; ovaries forming large masses occupying nearly all the abdominal cavity, greatly swollen and lobed, with oocytes visible to the naked eye. Stage VI: post-spawning; ovaries forming very flaccid masses, with a thin ovarian wall, and unspawned oocytes visible to the naked eye.

Samples from each maturity stage were fixed and preserved in 4% buffered formaldehyde, and subsequently processed for histological analyses.

A three-stage maturity scale based on shape, size and colour of testes was used for males. Stage I: I, immature (colourless), with vasa deferentia not morphologically differentiated; Stage II: advanced (white), with vasa deferentia morphologically differentiated and partially filled with sperm or spermatophores, low coiled visible to the naked eye. Stage III: mature (milk-white), with highly coiled vasa deferentia, visible to the naked eye and swollen testes. Macroscopic mature stages were validated histologically.

A subsample of female spermathecae collected in each maturity and carapace stage was also histologically examined for presence of sperm or spermatophores (Haefner, 1977). For histology, fixed tissues were dehydrated in a series of ethanol solutions (70, 96, 100%), cleared in Panreac isoparafine H, and then embedded in paraffin Paraplast in a vacuum chamber. Blocks were cut in 5 μm sections which were stained with Harris haematoxylin followed by eosin counterstaining.

The vulval condition was used as evidence of copulation in females: gonopores closed meaning immature animals, gonopores open meaning copulated animals. In the latter, abrasion marks were also observed (Hartnoll, 1969; Haefner, 1977).

2.2. Relationships between main variables and sex ratio

The CW–TW and CW–CL relationships were estimated for males and females by means of a power equation and a linear function, respectively. Relationships between CW and CL were calculated to facilitate the comparison with CL-based biological parameters previously reported. The equality of the two CW–TW regressions estimated for both males and females, as well as the two CW–CL regressions, was tested using *F*-test (Sachs, 1982). This test evaluated the null hypothesis of equality of two regression estimated by sexes with a significance level of 5% ($\alpha=0.05$) and a critical value of $F_{0.05,\ 1,\ >200}=3.89$ (Sachs, 1982; Sokal and Rohlf, 2012). Differences between the expected value from isometric growth and values of the regression coefficient (b) were compared by a *t*-test (Sachs, 1982). This test evaluated the null hypothesis H_0: $b=1$ in CW–CL relationship and H_0: $b=3$ in CW–TW relationship between sexes with a significance level of 5% ($\alpha=0.05$) and a critical value of $t_{0.05,\ >200}=1.97$ (Sachs, 1982; Sokal and Rohlf, 2012).

The sex ratio was estimated for the total sample and by size intervals. The Pearson chi-square goodness-of-fit test was used to evaluate the null hypothesis of equality of frequencies between sexes (H_0:1:1 ratio) with a significance level of 5% ($\alpha=0.05$) and a critical value of $\chi^2_{0.05,1}=3.84$ (Sachs, 1982; Sokal and Rohlf, 2012). The Student *t*-test was used to evaluate the null hypothesis of equality in mean CW and equality in mean TW between sexes (H_0: $\mu_1=\mu_2$) with a significance level of 5% ($\alpha=0.05$) and a critical value of $t_{0.05,\ >200}=1.97$. Differences in CW distribution between males and females were analysed using the Kolmogorov–Smirnov non-parametric *Z*-test. This test evaluated the null hypothesis of equality in CW distribution between sexes (H_0: $F_1(x)=F_2(x)$) with a significance level of 5% ($\alpha=0.05$) and a critical value of $Z_{0.05}=1.96$ (Sachs, 1982; Sokal and Rohlf, 2012). The mean CW values among depth strata were compared with ANOVA. This analysis was used to evaluate the null hypothesis of equality in mean CW among depth strata (H_0: $\mu_1=\mu_2=\ldots=\mu_n$), with a significance level of 5% ($\alpha=0.05$) and a critical value of $F_{0.05,3,\ >200}=2.65$. Once the null hypothesis was rejected, Dunnett's *T3* post-hoc test was applied to determine which strata differed. The post hoc test identifies homogeneous subsets where means that do not differ within each subset, testing the null hypothesis of equality in mean CW with a significance level of 5% ($\alpha=0.05$) (Sokal and Rohlf, 2012).

2.3. Spawning period and maturity

To assess the reproductive period, the monthly relative proportion of *C. affinis* in each sexual maturity stage (both sexes) and its ovigerous condition (females) were determined. The gonadosomatic index (GSI) of female specimens was also calculated by dividing GW by TW and referred by month.

Sexual maturity was calculated as the relative proportion of mature females by size classes: physiologically in IV to VI maturity stages; and morphologically with open vulvae and blackened vulval margins (Melville-Smith, 1987). Sexual maturity for males was estimated as the proportion of mature males by size classes (stage III). Size at sexual maturity was estimated by fitting data to the logistic equation $P=100/1+\exp(-r(\mathrm{CW}-\mathrm{CW}_{50})$ by non-linear regression; where, CW_{50} is the size at 50% maturity, P the proportion of morphologically or physiologically mature crabs in each size class, and r is the model parameter. The mean CW values among maturity stages were compared with ANOVA. This analysis was used to evaluate the null hypothesis of equality in mean CW among maturity stages (H_0: $\mu_1=\mu_2=\ldots=\mu_n$), with a significance level of 5% ($\alpha=0.05$) and a critical value of $F_{0.05,5,\ >200}=2.26$. Once the null hypothesis was rejected, Dunnett's *T3* post-hoc test was applied to determine which maturity stages differed. The post hoc test identifies homogeneous subsets of means that do not differ from each other, testing the null hypothesis of equality in mean CW with a significance level of 5% ($\alpha=0.05$) (Sokal and Rohlf, 2012). The absence of differences in mean CW among maturity stages identified with Dunnett's *T3* test was verified with ANOVA. This analysis evaluated the null hypothesis of equality in mean CW among maturity stages (H_0: $\mu_1=\mu_2=\ldots=\mu_n$), in the homogeneous subsets identified, with a significance level of 5% ($\alpha=0.05$) and a critical value of $F_{0.05,2,\ >150}=3.06$).

The relative reproductive potential (RRP) was estimated for *C. affinis* by means of the equation $\mathrm{RRP}_i=M_i\times F_i\times C_i$, where RRP_i is the relative reproductive potential for size class i, M_i the proportion of mature females in size-class i, F_i the mean individual fecundity of size-class i and C_i the proportion of size class i in the sample (Goñi et al., 2003). The RRP estimates the size class of spawning females that makes the greatest contribution to egg production in a population (Goñi et al., 2003). Mean fecundity at size estimated by Tuset et al. (2011), the maturity-size give and the size structure of the female population from October to April in Madeira and all year round in the Canaries were used to calculate RRP.

In females, AS5W was plotted against CW, as well as, in both sexes, length of chelae in order to determine possible changes associated to the pubertal moult (Somerton, 1980; Attrill et al., 1991). A power equation was fitted to the data by non-linear regression for the values for which the data could be separated into two groups. Size at which allometric growth changes, as an indicator of morphometric maturity, was iteratively searched by increments of 0.1 mm CW (Somerton, 1980). A *T*-test based on the difference between the residual sums of squares was estimated following Somerton (1980). This test evaluated the null hypothesis of equality of the sums of squares of the two subsets and of the simple model with a critical value of $F_{0.05,2,\ >200}=3.80$ (Somerton, 1980). ANCOVA and *F*-test were also calculated to test differences between the two regressions, corresponding to the pre- and post-pubertal growth phases. These tests evaluated the null hypothesis of equality of two regression estimated by sexes with a significance level of 5% ($\alpha=0.05$) and a critical value of $F_{0.05,1,\ >200}=3.89$ (Sachs, 1982; Sokal and Rohlf, 2012). The relative growth pattern of the AS5W and chelae length in pre- and post-pubertal phases were analysed by means of *t*-test (Sachs, 1982). This test evaluated the null hypothesis of equality of the regression coefficient (H_0: $b_1=b_2$), with a significance level of 5% ($\alpha=0.05$) and a critical value of $t_{0.05,\ >200}=1.97$ (Sachs, 1982; Sokal and Rohlf, 2012).

2.4. Mark-recapture experiment

In the Bay of Funchal, Madeira, a small-scale mark-recapture experiment was done in order to estimate the intermoult period and short-term movements in *C. affinis*. A total of 138 crabs were marked using plastic tags, which were attached around the articulation between the coxa and the ischium of the 5th right walking leg. In case of moulting, these tags remain with the exuviae. For each tagged crab, a record was made with its position and depth, tag number, carapace width, sex, carapace state and, in case of females, the ovigerous and vulvae condition. Tagging occurred at night in order to prevent crab's eye damage due to direct sun light exposure, as combined bright light and elevated temperature proved to cause severe progressive and irreversible eye membrane disintegrations in crustaceans (Meyer-Rochow, 2001).

On the third day of mark-and-recapture experiment, eight crabs, which were marked in first day were recaptured and therefore excluded of the experiment.

3. Results

3.1. Size-structure

A total of 8389 individuals of *C. affinis* were collected (4187 in Madeira and 4202 in the Canary archipelagos) (Table 1). In both archipelagos males were larger and heavier than females (Table 1). In Madeira the difference between sexes in maximum size and weight was 26.8 mm (14.5%) in CW and 813.9 g (44.2%) in TW, respectively. In Canaries the difference was 18.0 mm (9.6%) in CW and 840 g (39.1%) in TW. In both areas, the Student *t*-test indicated that null hypothesis was rejected for equality in mean CW or for equality in mean TW between sexes (Madeira CW $t = 16.02 > t_{0.05,4185} = 1.97$, $p < 0.0001$; TW $t = 20.18 > t_{0.05,4185} = 1.97$, $p < 0.0001$; Canaries CW $t = 12.26 > t_{0.05,4200} = 1.97$, $p < 0.0001$; TW $t = 12.15 > t_{\ 0.05,4200} = 1.97$, $p < 0.0001$), and therefore there were differences in mean CW and TW between both sexes. The higher length and weight were recorded in the Canaries. The Kolmogorov–Smirnov non-parametric *Z*-test showed that null hypothesis of equality in CW distribution between sexes was rejected (Madeira $Z = 10.98 > Z_{0.05} = 1.96$, $p < 0.0001$; Canaries $Z = 8.23 > Z_{0.05} = 1.96$, $p < 0.0001$) (Fig. 2).

The *F*-test for CW–TW relationship between sexes in both archipelagos indicated that null hypothesis of equality of two regressions estimated was rejected (Madeira $F = 6.12 > F_{0.05,1,4183} = 3.89$, $p < 0.0001$; Canaries $F = 6.43 > F_{0.05,1,4198} = 3.89$, $p < 0.0001$). This relationship was higher in Madeira than in the Canaries, *t*-test showing that null hypothesis of equality in the regression coefficient H_0: $b = 3$ was rejected in Madeira for males (allometric positive) and for females (allometric negative). In the Canaries null hypothesis was retained for males (isometry) and rejected for females (allometric negative) (Table 2). The *F*-test for CW–TW relationship of males between the two areas indicated that null hypothesis of equality of two regressions estimated was rejected ($F = 7.42 > F_{0.05,1,4288} = 3.89$, $p < 0.0001$). The *F*-test for CW–CL relationship between sexes in both archipelagos showed that null hypothesis of equality of two regressions estimated was retained (Madeira $F = 1.04 < F_{0.05,1,4183} = 3.89$, $p > 0.05$; Canaries $F = 1.01 < F_{t\ 0.05,1,4198} = 3.89$, $p > 0.05$), *t*-test showing that null hypothesis of equality in the regression coefficient (isometry) was retained in all cases (Table 2).

Table 1
Carapace width (CW in mm) and total wet weight (TW in g) values for males and females of *Chaceon affinis*. *min*, minimum; *max*, maximum; *n*, number of specimens; *mean*, mean value followed by ± standard deviation.

Area/sex	CW			TW			
	Min	Max	Mean	Min	Max	Mean	*n*
Madeira							
Males	38.0	184.8	124.0 ± 27.2	10.3	1842.0	629.9 ± 358.8	2131
Females	35.1	158.0	112.0 ± 20.1	10.4	1028.1	419.4 ± 185.3	2056
Canaries							
Males	42.0	187.0	125.1 ± 29.3	28.0	2150.0	689.1 ± 441.7	2161
Females	44.0	169.1	115.4 ± 21.7	28.1	1310.2	470.9 ± 233.5	2041

3.2. Sex ratio

The obtained sex ratio was similar in the two areas (Madeira 1:0.96; Canaries 1:0.94), and the Pearson chi-square goodness-of-fit test indicated that null hypothesis of equality of frequencies between sexes was retained (Madeira $\chi^2 = 1.343 < \chi^2_{0.05,1} = 3.84$, $p > 0.246$; Canaries $\chi^2 = 3.427 < \chi^2_{0.05,1} = 3.84$, $p > 0.064$), and therefore there were no differences between the frequencies observed from the expected 1:1 ratio. Females were significantly more abundant than males within 110–130 mm CW size classes in Madeira ($\chi^2 \geq 21.7 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$). The same pattern was observed within 110–140 mm CW size classes in the Canaries ($\chi^2 \geq 6.64 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$). However, males were significantly dominant in size classes larger than 140 mm CW in Madeira ($\chi^2 \geq 50.13 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$) and 150 mm CW in the Canary Islands ($\chi^2 \geq 58.7 > \chi^2_{0.05,1} = 3.84$ $p < 0.0001$) (Fig. 2).

Mean size decreased with depth for males and females in both areas (Fig. 3). ANOVA analysis on mean CW by sex among the different depth strata indicated that null hypothesis of equality in mean CW among depth strata was rejected (Madeira: males $F = 197.10 > F_{0.05,3,>200} = 2.65$, $p < 0.0001$; females $F = 173.47 > F_{0.05,3,>200} = 2.65$, $p < 0.0001$; Canaries: males $F = 29.24 > F_{0.05,3,>200} = 2.65$, $p < 0.0001$; females $F = 21.57 > F_{0.05,3,>200} = 2.65$, $p < 0.0001$). Dunnett's *T3* post-hoc test showed significant differences in CW among all strata in both areas ($p < 0.05$).

Few individuals were caught at the >1000 m depth stratum, and the highest abundance in both areas was found at 600–799 m and 800–999 m depth stratum. The Pearson chi-square goodness-of-fit test indicated that null hypothesis of equality of frequencies between sexes in both areas was rejected at depth stratum of 600–799 m ($\chi^2 \geq 77.32 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$) with males more abundant than females (1: ≥0.68), and at 800–999 m ($\chi^2 \geq 46.89 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$) with females more abundant than males

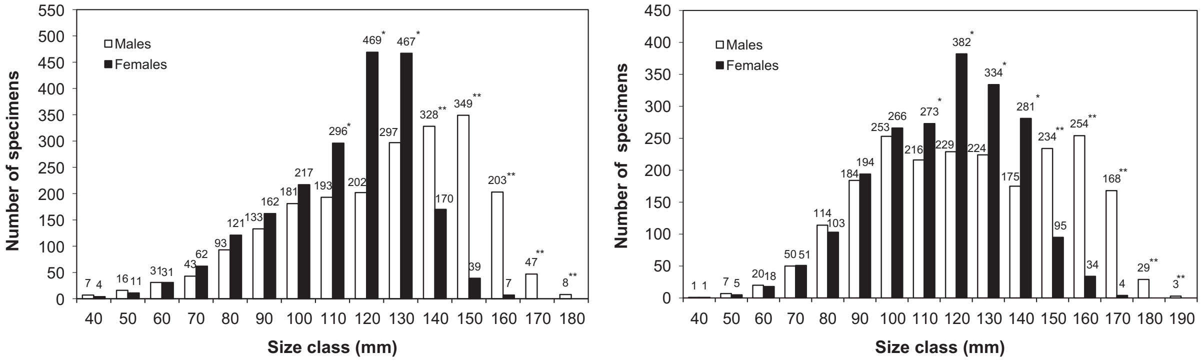

Fig. 2. Number of specimens of males and females of *Chaceon affinis* in Madeira (left) and the Canaries (right). Numbers correspond to individuals for each size class of 10 mm carapace width. ⁎ indicate sex ratios different from 1:1 in favour of females and ⁎⁎ in favour of males.

(1: ≤ 1.67) (Fig. 4). The highest abundance of ovigerous females was found at the 800–999 m depth stratum.

3.3. Sexual maturity

In *C. affinis*, ovary location is similar to that reported for other species in the genus by Haefner (1977), Melville-Smith (1987) and Erdman and Blake (1988), i.e., H-shaped in form and spermatheca extending ventrally to vulvae (gonopores) which open on the sixth thoracic somite. Of the different ovaries' colour or colour shades recorded, only six categories were histologically characterized (Fig. 5). Immature ovaries (stage I), colourless, presented the germ strand surrounded by fibrous connective tissue with oogonia close to it. Early developed ovaries (stage II), ivory or various orange shades, were characterized in having oocytes in various stages of early pre-vitellogenesis. Resting ovaries (stage III), various shades of grey or brown, were characterized by the presence of advanced pre-vitellogenic oocytes and abundant fibrous connective tissue. Advanced ovaries (stage IV), colour varying from various shades of orange to various shades of brown, lilac, violet or grey, were characterized by the presence of oocytes from early to late phases of vitellogenesis, exhibiting a granular texture in result of the accumulation of yolk globules. Mature ovaries (stage V), various shades of purple, lilac, grey or brown, were dominated by mature oocytes, granular in appearance due to high concentration of yolk globules, the vitellogenesis being complete at this stage. Post-spawning ovaries (stage VI), various shades of purple, brown or grey, consisting in a very flaccid mass with a thin ovarian wall. Histologically, this stage was characterized by the presence of unspawned oocytes undergoing reabsorption, which are often surrounded by phagocytes (Fig. 6).

Table 2
Parameters of CW–TW (TW = a CW^b) and CW–CL relationship (CL = a + b CW) for males, females and all crabs of *Chaceon affinis*.

Relationship	Sex	*a*	*b*	S.E.(b)	r^2	*n*	*t*
Madeira							
CW–TW	Males	0.00013	3.164	0.016	0.968	2131	10.2[a]
CW–TW	Females	0.00064	2.814	0.019	0.941	2056	9.5[a]
CW–TW	All crabs	0.00009	3.231	0.012	0.961	4187	19.5[a]
CW–CL	Males	-0.728	0.833	0.002	0.998	2131	83.5[a]
CW–CL	Females	-0.298	0.838	0.003	0.994	2056	54.1[a]
CW–CL	All crabs	0.082	0.830	0.002	0.992	4187	85.0[a]
Canaries							
CW–TW	Males	0.00029	3.009	0.017	0.962	2161	0.5
CW–TW	Females	0.00089	2.759	0.023	0.902	2041	10.2[a]
CW–TW	All crabs	0.00019	3.085	0.013	0.944	4202	6.3[a]
CW–CL	Males	0.638	0.827	0.002	0.992	2161	86.5[a]
CW–CL	Females	0.629	0.830	0.002	0.989	2041	85.0[a]
CW–CL	All crabs	0.588	0.830	0.002	0.990	4202	85.0[a]

a, intercept; *b*, regression coefficient (allometric coefficient); S.E., standard error; r^2, determination coefficient. *n*, number of specimens; *t*, *t*-test value.

[a] Null hypothesis of isometric growth rejected at significance level $\alpha = 0.05$ ($t > t_{0.05, >200} = 1.97$).

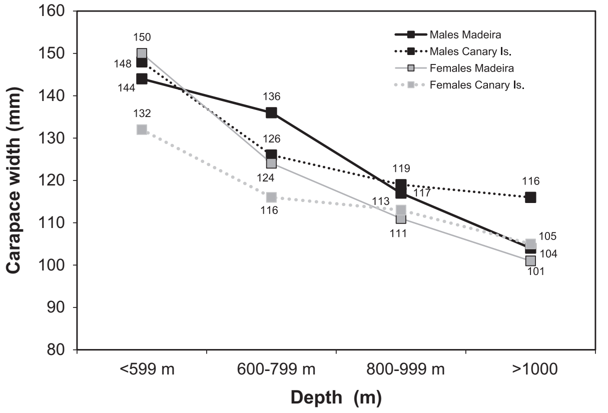

Fig. 3. Variation of the mean size with depth for males and females of *Chaceonaffinis* in Madeira and the Canaries. Numbers correspond to mean carapace width in mm.

In the analysed spermathecae, 83% contained spermatophores inside, in the same development stage that was observed in the tests of males (Fig. 6). Three forms of spermathecae were observed: turgid, half full, and empty. Turgid spermathecae were found in females who had their carapaces ranked in conservation stage I. Half full spermathecae were observed in females with their carapaces ranked in conservation stages II or III. Empty spermathecae were found in immature females or in some females with their carapaces ranked in conservation stage III.

The sample from Madeira contained 342 females with immature ovaries (mean ± s.d.: 97.1 ± 10.0 mm CW), 396 with early ovaries (114.3 ± 12.7 mm CW), 350 with intermediate/resting ovaries (113.6 ± 8.7 mm CW), 331 with advanced ovaries (124.1 ± 10.80 mm CW), 546 with mature ovaries (125.7 ± 8.9 mm CW), and 91 with post-spawning ovaries (124.6 ± 11.3 mm CW). The Canary Islands sample contained 775 females with immature ovaries (mean ± s.d.: 102.3 ± 19.5 mm CW), 108 with early ovaries (117.3 ± 23.1 mm CW), 223 with intermediate/resting ovaries (119.2 ± 12.8 mm CW), 271 with advanced ovaries (133.1 ± 13.4 mm CW), 317 with mature ovaries (132.8 ± 14.7 mm CW), and 337 with post-spawning ovaries (134.9 ± 19.7 mm CW). Females showed different mean CW among the different stages of ovarian development. ANOVA analysis indicated that null hypothesis was rejected (Madeira $F = 26.03 > F_{0.05,5,>200} = 2.26$, $p < 0.0001$; Canaries: $F = 28.14 > F_{0.05,5,>200} = 2.26$, $p < 0.0001$). Dunnett's *T3* post-hoc test identified two homogeneous

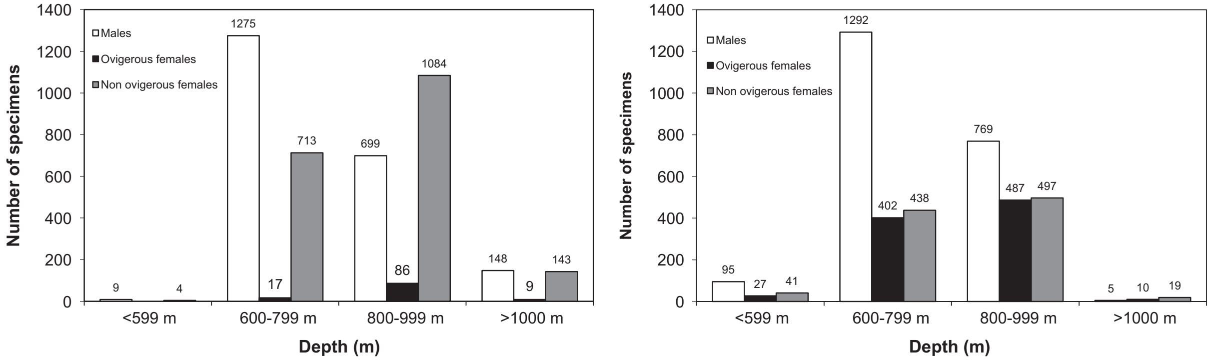

Fig. 4. Number of males and females (in ovigerous or non ovigerous condition) of *Chaceon affinis* by depth stratum in Madeira (left) and the Canary (right) archipelagos. Numbers correspond to individuals for each depth stratum.

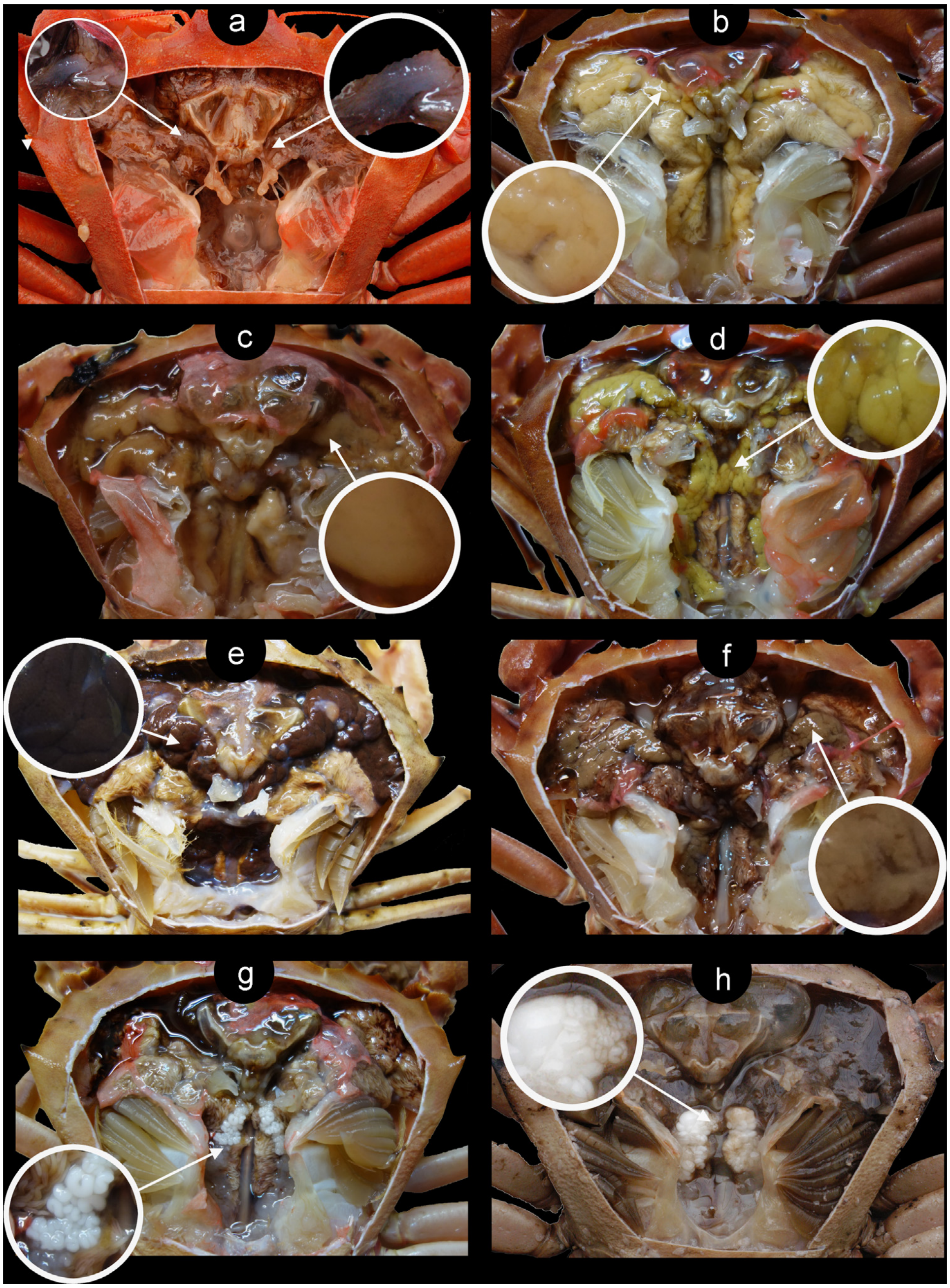

Fig. 5. Macroscopic scale of sexual maturity stages in *Chaceon affinis*. Females: (a) I, immature; (b) II, early developed; (c) III, resting; (d) IV, advanced; (e) V, mature; (f) VI, post-spawning. Males: (g) II, advanced; (h) III, mature.

subsets of ovarian stages (maturity stages II–III and IV–VI, $p > 0.128$) where means that do not differ within each subset, testing the null hypothesis of equality in mean CW. However, there were significant differences between stage I and each one of the other stages, and also between each stage II–III and each stage from IV to VI ($p < 0.05$). ANOVA analysis on mean CW among ovarian stages of the homogeneous subsets (stage IV–VI) indicated that null hypothesis was retained (Madeira $F = 0.46 < F_{0.05,2,>150} = 3.06$, $p > 0.05$; Canaries $F = 0.38 < F_{0.05,2,>150} = 3.06$, $p > 0.05$).

The smallest female with open vulvae measured 79.6 mm CW in Madeira and 74.0 mm CW in the Canaries and the largest 158 mm CW in Madeira and 169 mm CW in the Canaries (Fig. 7). Student *t*-test showed that null hypothesis of equality in mean CW of females with open vulvae (mean ± s.d.: Madeira, 124.10 ± 11.01 mm; Canaries, 133.2 ± 16.02 mm) and closed vulvae (Madeira, 91.62 ± 17.25 mm; Canaries, 101.45 ± 21.55 mm) was rejected (Madeira, $t = 43.74 > t_{0.05,2054} = 1.97$, $p < 0.0001$; Canaries, $t = 19.66 > t_{0.05,2039} = 1.97$, $p < 0.0001$) in both areas. Student *t*-test between areas also showed that null hypothesis of equality in mean CW of females with open vulvae ($t = 8.57 > t_{0.05,1500} = 1.97$, $p < 0.0001$) and closed vulvae ($t = 5.63 > t_{0.05,2593} = 1.97$, $p < 0.0001$) was rejected. The size at sexual maturity CW_{50}, based on maturity stages and vulvae condition, was estimated at 104.7 and 104.4 mm CW respectively, in Madeira, and 110.5 and 109.3 mm CW respectively, in the Canary Islands (Fig. 8).

Three categories of testes were identified: I, immature (translucent); II, advanced (white); and III, mature (milky white) (Fig. 7). Immature testes (stage I) had vasa deferentia morphologically not differentiated. Advanced testes (stage II) had vasa deferentia morphologically differentiated and partially filled with sperm, weakly coiled and barely visible to the naked eye. Mature testes (stage III) consisted

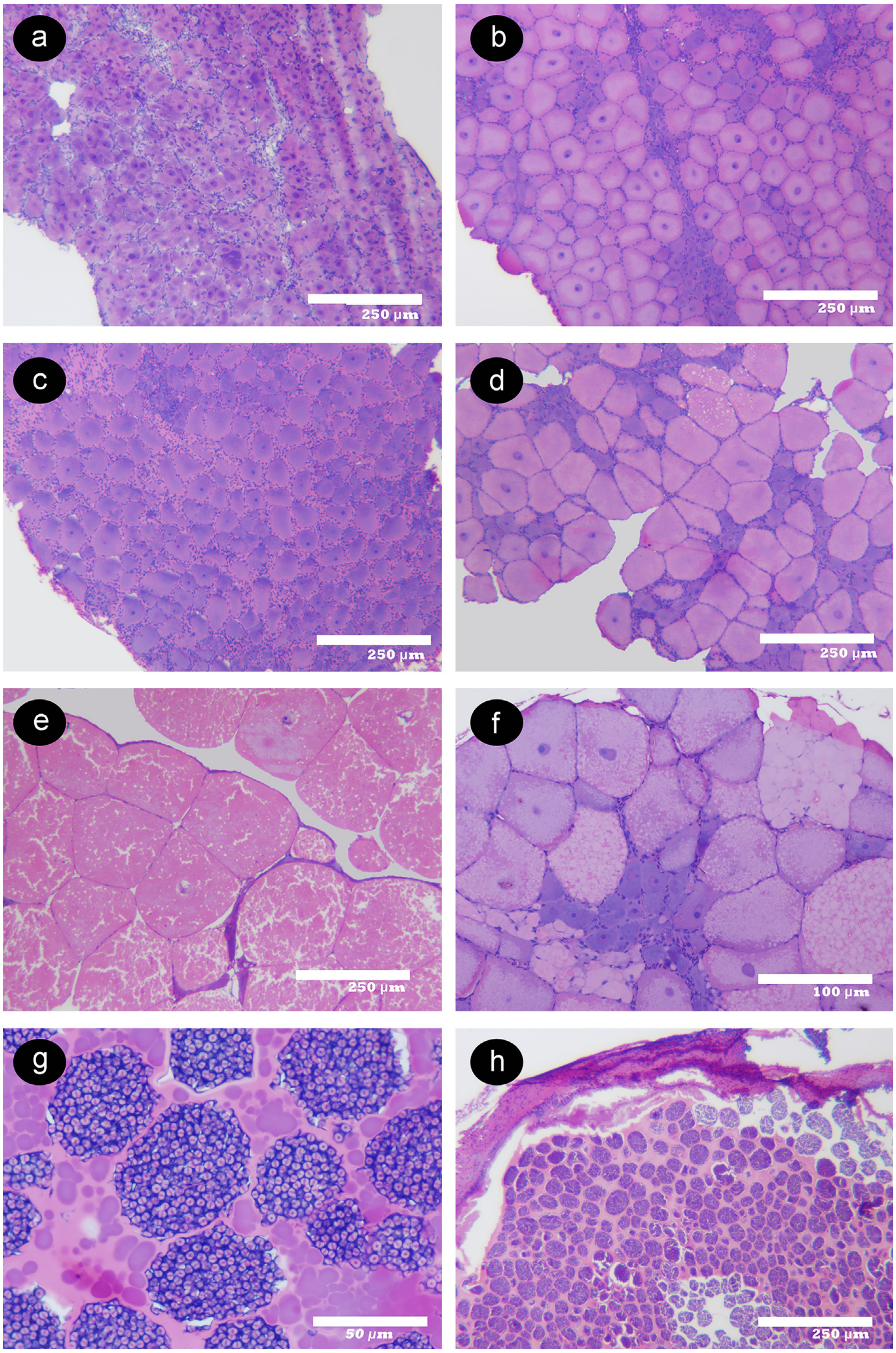

Fig. 6. Histological sections illustrating *Chaceon affinis* (a) Immature ovary with the germ strand surrounded by fibrous connective tissue, (b) Early developed ovary with oocytes in various stages of early pre-vitellogenesis, (c) Resting ovary with advanced pre-vitellogenic oocytes and fibrous connective tissue, (d) Advanced, with oocytes in vitellogenesis, (e) Mature ovary dominated by mature oocytes, (f) Post-spawning ovary with unspawned oocytes undergoing reabsorption, (g) Advanced teste, (h) Spermatheca.

in a large mass, with highly coiled vasa deferentia visible to the naked eye.

Males showed different mean CW among gonadal development stages. ANOVA analysis indicated that null hypothesis of equality in mean CW among gonadal development stages was rejected (Madeira $F=6.37>F_{0.05,2,>200}=3.04$, $p<0.001$; Canaries: $F=3.62>F_{0.05,2,>200}=3.04$, $p<0.05$). Dunnett's *T3* post-hoc test showed significant differences in CW among the stages ($p<0.05$). The size at onset of sexual maturity in males (CW_{50}), based on gonadal development, was estimated at 113.8 mm CW in Madeira and 118.9 mm CW in the Canaries (Fig. 9).

3.4. Spawning period

The size of ovigerous females ranged from 99.4 to 142.2 mm CW in Madeira (5.8% of the total females), and from 74 to 169 mm CW in the Canaries (42.3%). Ovigerous females were observed from

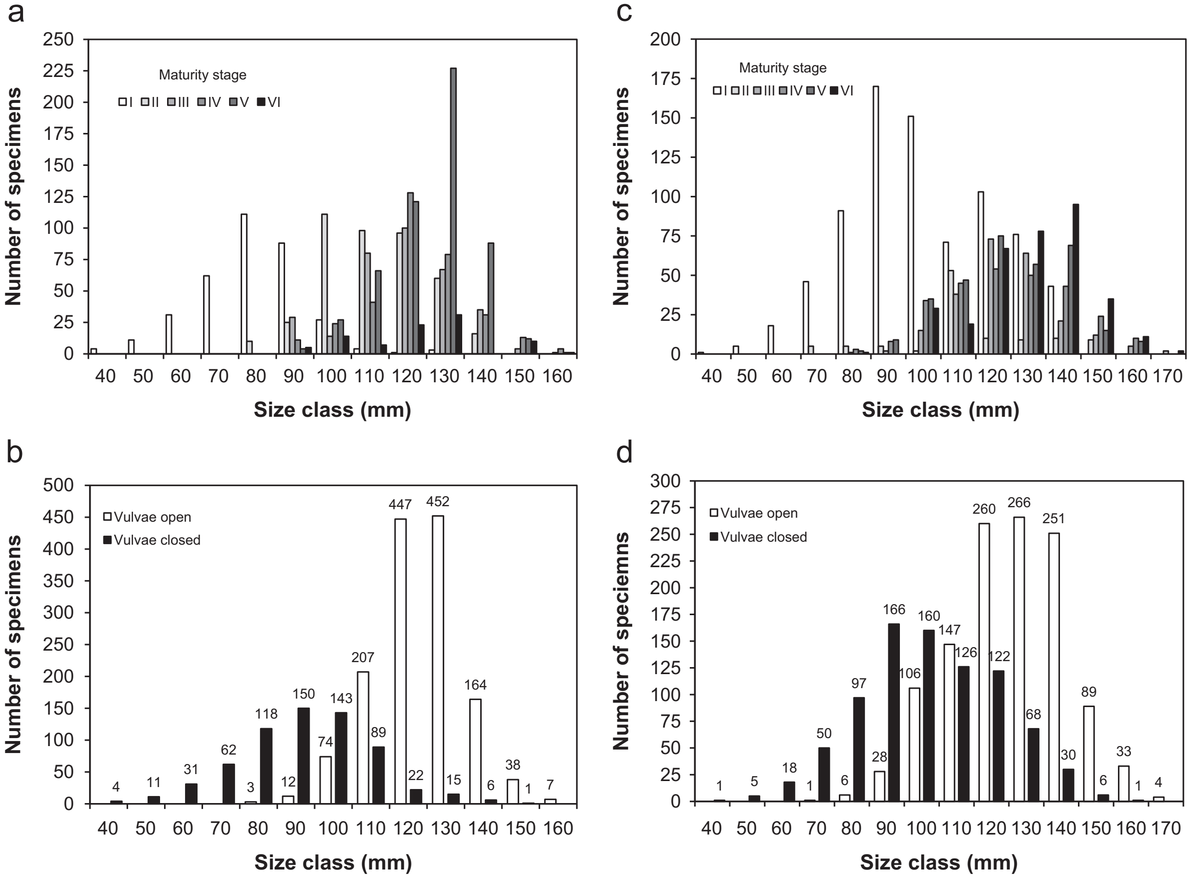

Fig. 7. Number of females by (a and c) maturity stages and (b and d) vulval condition for *Chaceon affinis* in Madeira (left) and the Canaries (right). Numbers correspond to individuals for each size class of 10 mm.

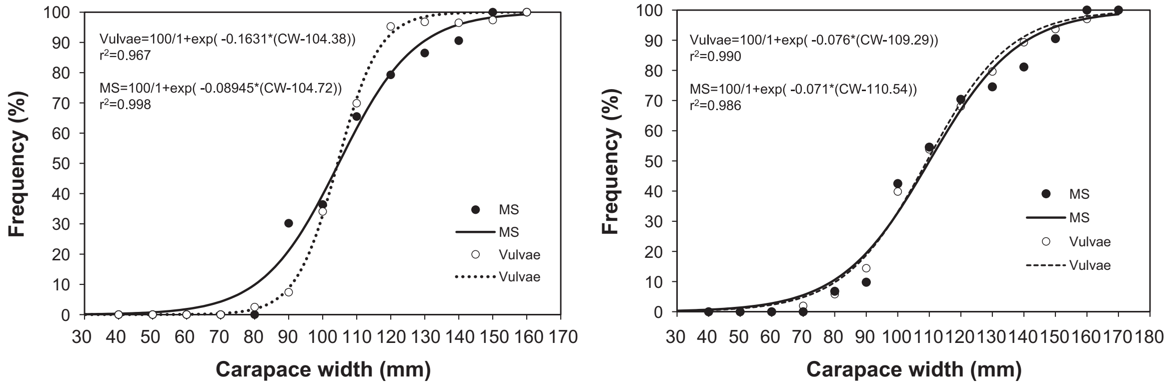

Fig. 8. Ogives of size at first maturity, based on maturity stage (MS) and open vulval condition (vulvae), for females of *Chaceon affinis* in Madeira (left) and the Canaries (right). r^2, determination coefficient.

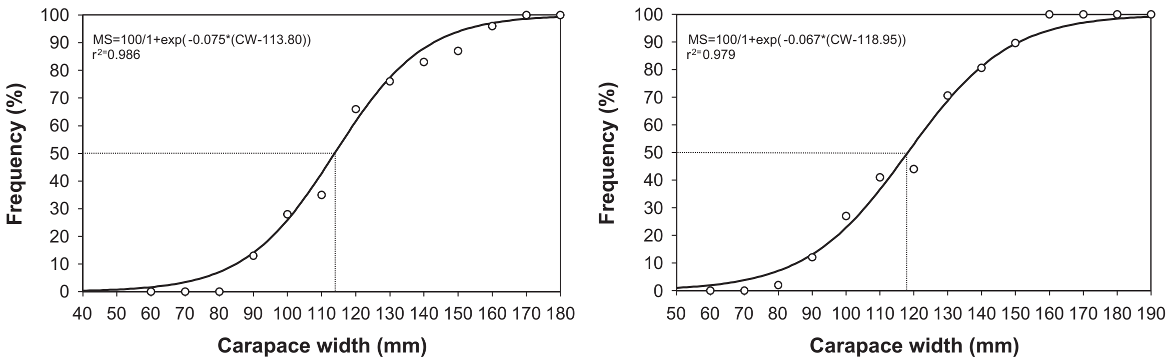

Fig. 9. Ogives of size at first maturity, based on maturity stage (MS), for males of *Chaceon affinis* in Madeira (left) and the Canaries (right). r^2, determination coefficient.

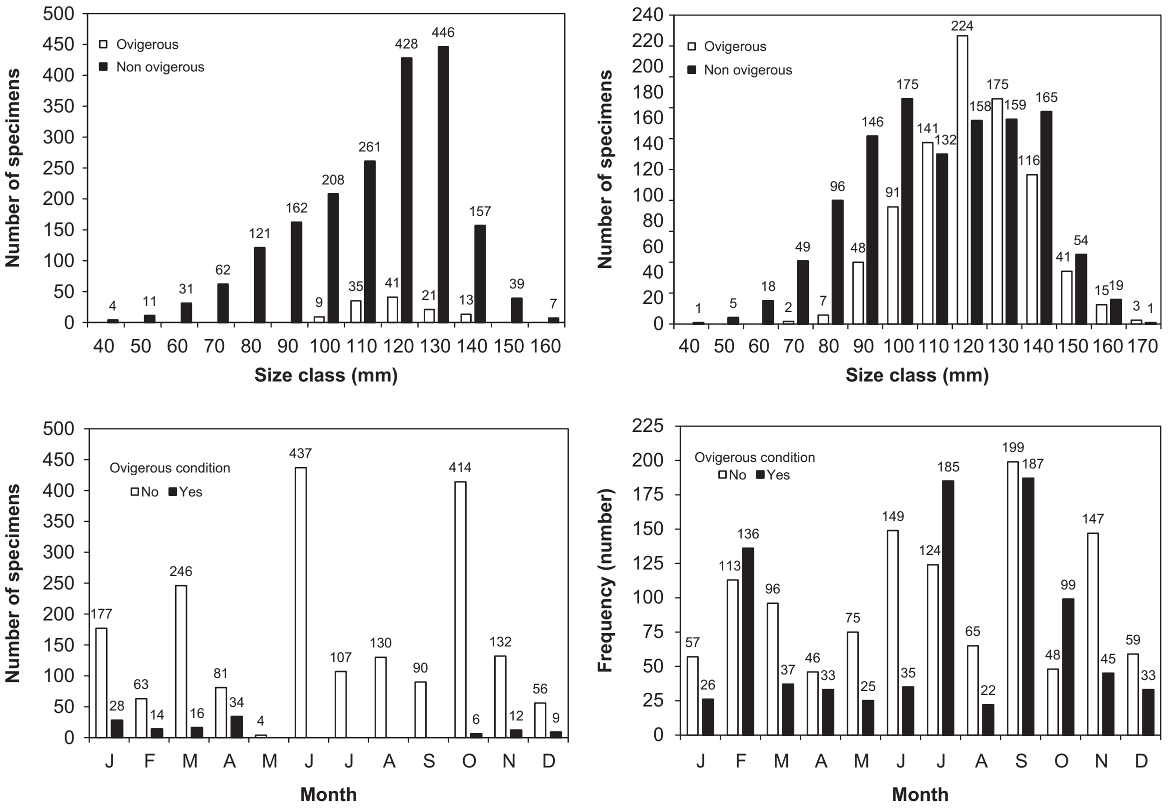

Fig. 10. Number of females of *Chaceon affinis* by ovigerous condition by size group (up) and month (below) in Madeira (left) and the Canaries (right). Numbers correspond to individuals for each size class of 10 mm.

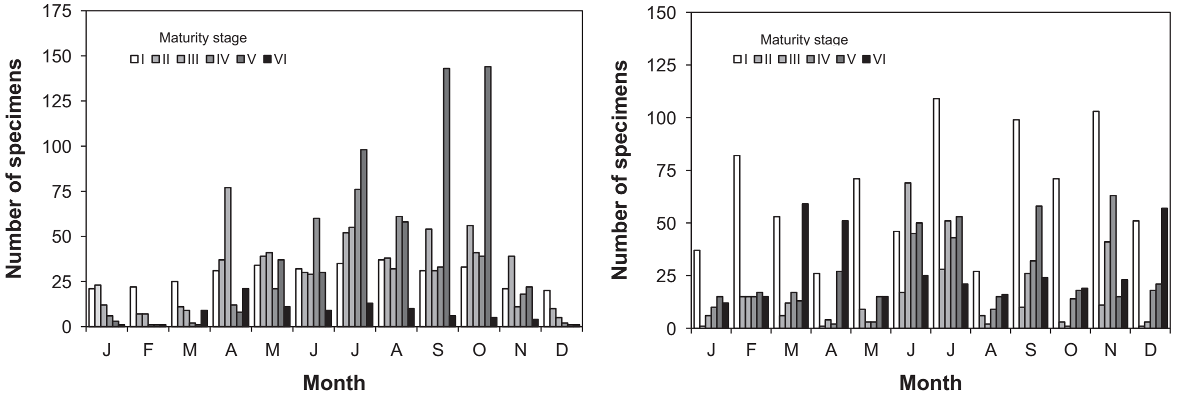

Fig. 11. Number of females specimens of *Chaceon affinis* in each maturity stage by month in Madeira (left) and the Canaries (right).

October to April in Madeira, and in all months in the Canaries (Fig. 10).

Females with ovaries in advanced, mature or post-spawning stages ranged from 89.4 to 158.0 mm CW in Madeira (47.1% of the total females), and from 82.7 to 169.0 mm CW in the Canaries (45.3%). Females with advanced, mature or post-spawning ovaries stages were observed mainly from July to October in Madeira and mainly from March to December in the Canaries (Fig. 11).

Gonadosomatic index (GSI) in females showed highest values from April to November in Madeira and all year round in the Canaries (Fig. 12). The mean GSI showed differences among months in Madeira. ANOVA analysis showed that null hypothesis of equality in GSI among months was rejected ($F=22.1>F_{0.05,11,>200}=1.86$, $p<0.001$). Dunnett's *T3* post-hoc test identified two homogeneous subsets of months with no differences in mean GSI values (December–March, $p>0.05$; April–November, $p>0.05$), but with significant differences among months within each group ($p<0.05$).

The modal size class of egg production in Madeira was 110–130 mm CW, which yielded 79.13% of the population egg production (Fig. 13). Crabs smaller than 100 mm CW comprised 29.78% of the population and produced 4.84% of the eggs. In the Canaries, modal size class of egg production was 120–140 mm CW, which yielded 66.28% of the population egg production. Females smaller than 110 mm CW comprised 44.63% of the population and produced 21.96% of the eggs (Fig. 13).

3.5. Morphometric maturity

Right/left cheliped length for both sexes, as well as maximum width of fifth abdominal somite (AS5W) in females, were plotted

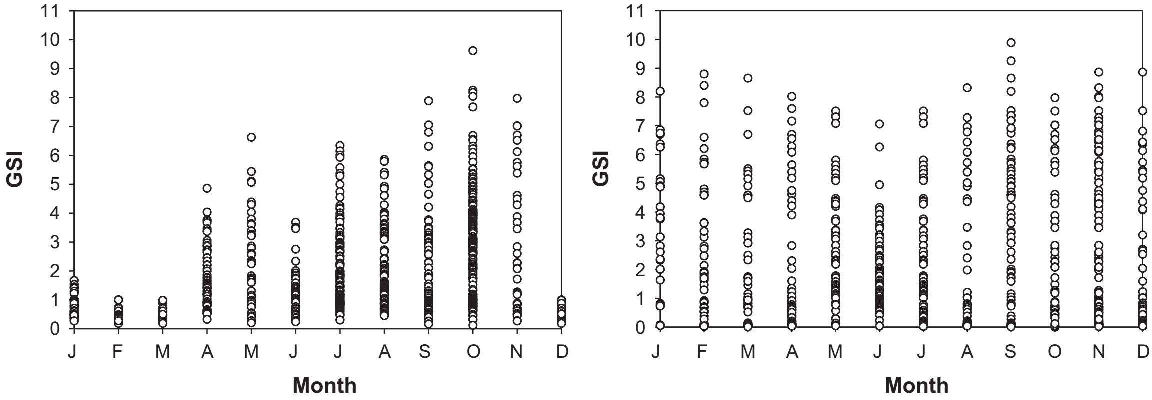

Fig. 12. Monthly GSI values for females of *Chaceon affinis* in Madeira (left) and the Canaries (right).

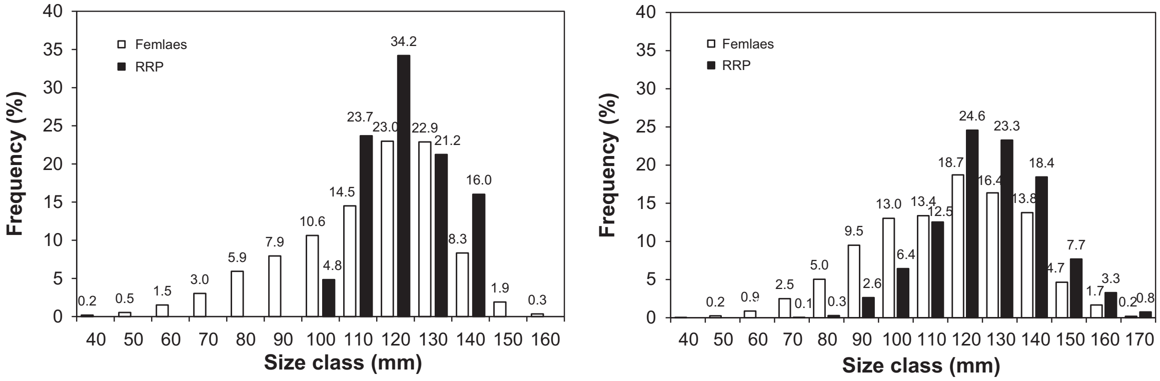

Fig. 13. Frequency-size distribution of females of *Chaceon affinis* in Madeira (left) and the Canaries (right) and its relative reproductive potential (RRP). Numbers correspond to frequency for each size class of 10 mm.

against CW and revealed changes in relative growth associated to the pubertal moult (Fig. 14). The relative growth of males showed changes along the ontogeny for all selected measurements. Size at which allometric growth changes as an indicator of morphometric maturity occurred between 103.2 and 103.6 mm CW in Madeira and between 111.4 and 113.1 mm CW in the Canaries ($T \geq 4.37 > F_{0.05,2,>200} = 3.80$). ANCOVA and *F*-test showed that null hypothesis of equality of the two regressions, corresponding to the pre- and post-pubertal growth phases, was rejected in all cases (ANCOVA, $F \geq 5.32 > F_{0.05,1,>200} = 3.89$, $p < 0.05$; *F*-test, $F \geq 7.94 > F_{0.05,1,>200} = 3.89$, $p < 0.001$). The *t*-test on the growth of the male chelae showed that null hypothesis of equality of the regression coefficient was rejected in all cases ($t \geq 2.65 > t_{0.05,>200} = 1.97$, $p < 0.0001$). Allometry in the growth of the chelae was always positive irrespective of subset considered (pre- or post-pubertal phase) or area. However, Student *t*-test also indicated in both areas that null hypothesis of equality of the regression coefficient between subsets considered was rejected ($t \geq 6.77 > t_{0.05,>2000} = 1.97$, $p < 0.001$). The function calculated for males larger than size at which allometric growth changes showed a significant increase in their slopes.

As no evident discontinuities were observed in the relative growth of both chelae for females along its ontogeny, all points were used for the calculation of regressions (Fig. 14). The *t*-test on the growth of the female chelae in both areas showed that null hypothesis of equality of the regression coefficient was rejected ($t \geq 4.21 > t_{0.05,>2000} = 1.97$, $p < 0.001$), showing an allometric negative growth. Moreover, *F*-test showed that null hypothesis of equality of the two regressions, corresponding to the right and left chela in length, was retained in all cases (*F*-test, $F \leq 0.97 < F_{0.05,1,>200} = 3.89$, $p > 0.05$). Size at which allometric growth changes as an indicator of morphometric maturity for AS5W was found at 98.2 mm CW in Madeira and at 103.0 mm CW in the Canaries (Fig. 14). ANCOVA and *F*-test showed that null hypothesis of equality of the two regressions, corresponding to the pre- and post-pubertal growth phases, was rejected in all cases (ANCOVA, $F \geq 4.02 > F_{0.05,1,>200} = 3.89$, $p < 0.05$; *F*-test, $F \geq 4.93 > F_{0.05,1,>200} = 3.89$, $p < 0.05$). Allometry in the growth of the AS5W was always positive irrespective of subset considered (pre- or post-pubertal phase) or area. However, Student *t*-test also indicated that the null hypothesis of equality of the regression coefficient between subset considered was rejected in both areas ($t \geq 14.52 > t_{0.05,>2000} = 1.97$, $p < 0.0001$). The function calculated for females larger than size at which allometric growth changes showed a significant decrease in their slopes.

3.6. Carapace stage and moult

Number of males and females with carapace in stage I decreased with increasing CW in both areas. The reverse was noted in crabs not having recently moulted (stage II or III) (Fig. 15). Number of ovigerous females decreased with increasing carapace stage in the Canaries (Fig. 16). Female crabs in stages II or III showed a high frequency of maturity stages 3–5 (Fig. 17).

3.7. Mark and recapture

Only 9 out of 138 tagged and released crabs (96–154 mm CW) in Madeira were recovered in the same area, more than 900 days after tagging (Fig. 18). No changes in carapace width and, in case of females, in the ovigerous and vulvae condition were observed. The carapace state of conservation changed in all individuals from stage I or II to a higher state.

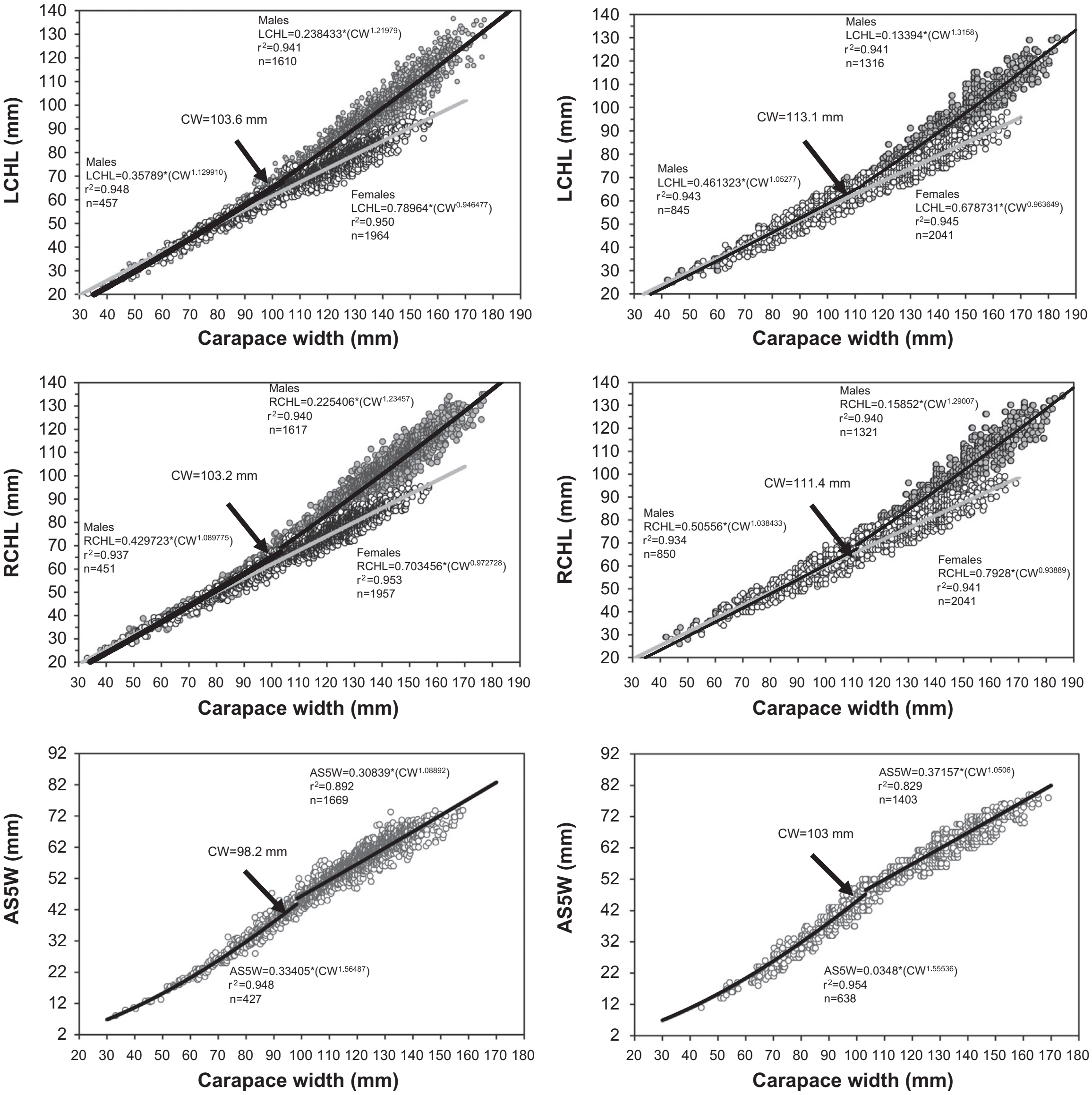

Fig. 14. Right and left chela length (R/LCHL) and maximum width of the fifth abdominal somite (AS5W) plotted against carapace width (CW) of females of *Chaceon affinis* in Madeira (left) and the Canaries (right). *n*, number of crabs. r^2, determination coefficient. Lines fitted correspond to each potential model estimated. Arrows indicate the size at which allometric growth changes as an indicator of morphological maturity.

4. Discussion

4.1. Size frequency distributions and moulting

The size distribution found was similar to that observed in studies on *C. affinis* off the Azores (Pinho et al., 2001a), the Canary Islands (López-Abellán et al., 2002) and Irish waters (Robinson, 2008). The shape of the size frequency distribution is typical of a long-lived K-strategist crab in that, after maturity, growth becomes so slow and/or variable that as crabs in the smaller size classes grow, they gradually merge into the larger size classes (Hartnoll, 1974, 1978; Robinson, 2008).

The size frequency distribution of *C. affinis* obtained was characterized by the scarcity of small crabs. The absence of specimens smaller than 40 mm CW is a constant in all samples collected for this species from Ireland to the Canary Islands waters (Fernández-Vergaz et al., 2000; Pinho et al., 2001a; López-Abellán et al., 2002; Robinson, 2008; Castro et al., 2010). Pinho et al. (2001a) and Robinson (2008) pointed out that this scarcity could be related to trap selectivity, or to competition for food. An example of this could be a size-dominant behaviour around traps where the presence of larger conspecifics in traps could deter smaller crabs from entering and result in commercial catches being unrepresentative of the true population size structure. Another possible cause for the absence of these small sizes could be related to hiddenness strategies during the moulting and hardening of the carapace in the pre-pubertal stage. In this regard, it is noted that more than 98% of small size specimens sampled in this study in both archipelagos, as well those analysed by Pinho et al. (2001a) in the Azorean waters, showed signs of a recent moult, which may mean that moulting is highly frequent in small individuals. Melville-Smith (1989) reported a total of 9 moults before 40 mm CW in *Chaceon maritae* (Manning & Holthuis, 1981). Mori and Manconi (1990) indicated that, in pre-puberty deep crabs with several moults, their exoskeletons are unstable substrata that can be colonised only by rapidly growing species. The presence of a richer and more diversified epizoitic assemblage on post-puberty individuals implies that their exoskeletons provide a more stable substratum indicating greater stability and a lower moulting frequency. The absence of small specimens can also be due to a different pattern of depth distribution between recruits/juveniles and adult specimens as it is suggested in Fig. 3, with mean

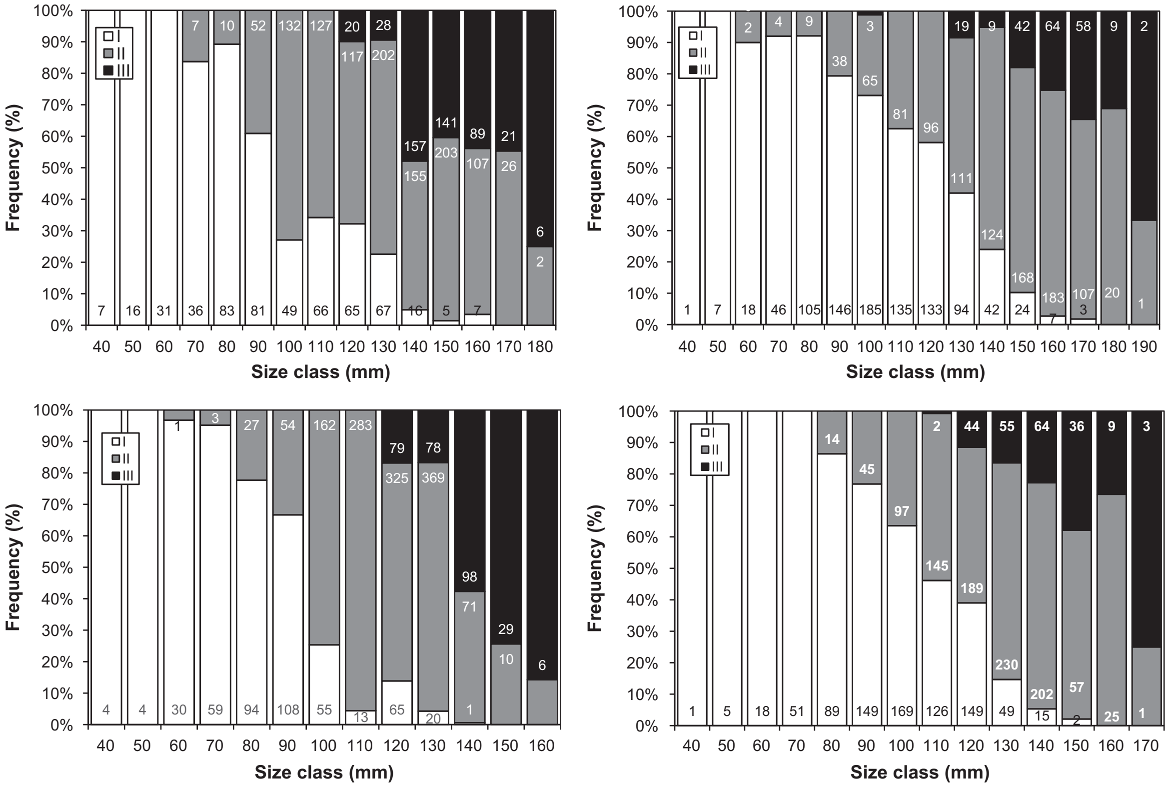

Fig. 15. Frequency of carapace conservation stages by size classes for males (up) and females (below) of *Chaceon affinis* in Madeira (left) and the Canaries (right). The number of individuals is indicated for each size class and stage. I, carapace with neither barnacles nor lesions; II, carapace with low levels of barnacle infestation and lesions; III, carapace with high levels of barnacles and lesions.

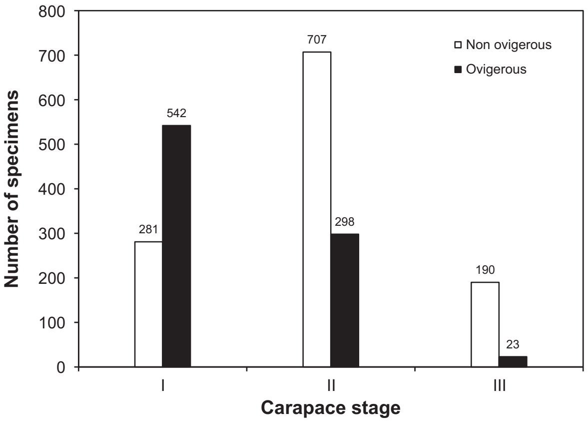

Fig. 16. Frequency of carapace conservation stages by ovigerous condition of *Chaceon affinis* in the Canaries. The number of individuals is indicated for each carapace stage and ovigerous condition. I, carapace with neither barnacles nor lesions; II, carapace with low levels of barnacle infestation and lesions; III, carapace with high levels of barnacles and lesions.

size decreasing with depth. In this sense, Hastie (1995) indicated that recruits and juveniles of geryonid crabs are generally distributed on deeper waters.

The observed differences in the size frequency distributions between both sexes of *C. affinis* reflect a common pattern for deep-sea crabs. Melville-Smith (1989) attributed these differences to the different moulting processes for each sex, stating that the unimodal structure could be the result of similar intermoult periods in both immature males and females, and of different elapsed periods of time between moults after maturity, being less frequent in females. In *C. affinis* an intermoult period shorter for males than for females may be due to sex distribution by depth. Males dominate 600–800 m depth stratum, while females tend to be found in deeper waters down to 800–1000 m. Temperatures at these depth strata differ by 2–4 °C and, since temperature is the most important extrinsic factor affecting intermoult period (Hartnoll, 1982), one would expect growth to be slower for an animal in deeper water. Melville-Smith (1989) also explained the differences in size between sexes as a consequence of females making a higher reproductive investment and consequently having a lower growth rate, and therefore undergoing smaller size increments per moult than males.

The maximum size observed in Irish waters, Azores, Madeira and the Canary Islands (Pinho et al., 2001a; López-Abellán et al., 2002; Robinson, 2008) was very similar and ranged between 185 and 190 mm CW for males and 155–160 mm CW for females. These sizes may indicate the maximum size the species can attain as a result of large intermoult periods, which exceed its lifespan. The low frequency of crabs larger than at sexual maturity with carapace in stage I, may be a result from the increase of the intermoult period with age or size. In this sense, several authors pointed out, for this species and other congeneric species, to the existence of moult processes after sexual maturity, but with large intermoult periods, in some cases as large as 3–7 years (Lux et al., 1982; Melville-Smith, 1989; Pinho et al., 2001a; Pezzuto and Sant'Ana, 2009). The mark-and-recapture data from eight females within a wide range of CW (37.9 mm, 107.8–145.7 mm, equivalent to 23.9% of females' maximum size) suggested the existence of several moulting processes (with a very low moulting frequencies and intermoult periods exceeding three years) due to an expected a growth per moult lower than 20 mm CW, as in other *Chaceon* species. Considering tags remain with exuviae after ecdysis, the tagged crabs recovered after 3 years provide a direct evidence of long intermoult periods, despite the small numbers of individuals recaptured. Melville-Smith (1989) indicated for *Chaceon quinquedens* (Smith, 1879) and *C. maritae* a growth per moult lower than

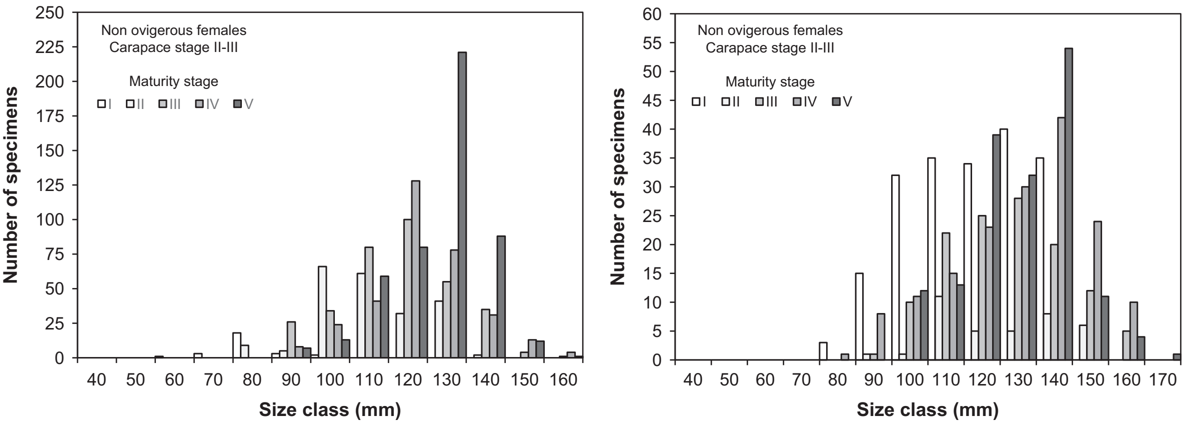

Fig. 17. Frequency of maturity stages for females with carapace conservation stages II-III of *Chaceon affinis* in Madeira (left) and the Canaries (right).

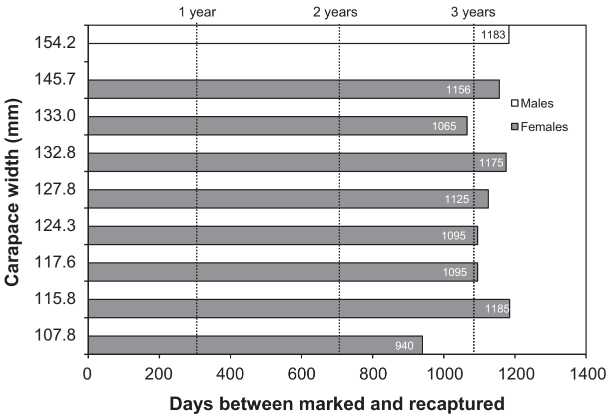

Fig. 18. Elapsed time period (in days) between marked and recaptured for one male and eight females of *Chaceon affinis*. The size of marked-and-recaptured crabs not changed.

20 mm CW with maximum intermoult periods between 4 and 5 years. Related with this, exoskeletons of *C. affinis* that have not recently moulted are blackened or discoloured in abraded or damaged areas, and they are usually infested with lepadid barnacles (Pinho et al., 2001a). The association of lepadids and discolouration serves as an indicator of the time lapse since the last moult, although the exact time span cannot presently be determined (Haefner, 1977). The best confirmation of the growth pattern in a species is by observation of moulting (Attrill et al., 1991). However, several features of the samples of *C. affinis* offer clues to the nature of its growth pattern. The presence of a normal size distribution of males and females with a tail of surviving and still moulting larger individuals could indicate a population with indeterminate growth (Attrill et al., 1991). However, this supposition must be confirmed by further studies.

4.2. Length-weight relationship and sex ratio

The allometric pattern of the CW–TW relationship found in Madeira and the Canaries, is similar to the one found by Pinho et al. (2001a) in the Azores, and seems to be a characteristic of the species. Although differences in growth pattern between sexes were similar to those found by Fernández-Vergaz et al. (2000) and Pinho et al. (2001a), the samples size may be too small to adequately explain these relationships, as pointed out by Castro et al. (2010). Males and females have different weight at a given size. This may be due to chelae weight in males not being compensated by the weights of egg mass and mature ovaries in females (Robinson, 2008).

In *C. affinis*, sex ratio seems to be linked to depth, with males located mainly at 600–800 m of depth and females at 800–1000 m. In the Azorean waters Pinho et al. (2001a) also found that male abundance decreased significantly with depth, but females maintained a constant number and were even more abundant than males below 900 m of depth. The predominance of males observed by López-Abellán et al. (2002) may have been due to different sampling effort along the bathymetric interval. This effort was higher on the upper slope where the number of males is significantly greater than females, which in turn were most abundant at deeper strata.

The upper limit of the vertical distribution of *C. affinis* (600 m) may be a consequence of the presence of large quantities of the crabs *Cancer bellianus* Johnson, 1861 (Cancridae) and *P. cuvieri* (Homolidae), which inhabit chiefly at 400–700 m thus creating a competition border (Pinho et al., 2001a, b; Triay-Portella et al., 2014). The presence of these large predators may also be responsible for the size by depth stratification found in *C. affinis*, with smaller animals being found at greater depths (Quiles et al., 2001; Triay-Portella et al., 2014). This pattern has been observed previously in *C. affinis* (Robinson, 2008), as well as in other decapod species (Sardà and Cartes, 1993; Triay-Portella et al., 2014).

The presence of females in higher numbers in deeper areas may be a consequence of seasonal downward movements of ovigerous females. This pattern do not follow that observed in many geryonids in which crabs move to shallower areas of the slope in order to spawn. This can be due to a combination of the oceanographic conditions and to the presence of competitors. As pointed out by López-Abellán et al. (2002), these seasonal displacements could be related to strategies to diminish competition with other aggressive crabs such as *C. bellianus* and, to a much lesser extent *P. cuvieri*, particularly in the upper limit of *C. affinis* vertical distribution. Erdman et al. (1991) found a different distribution for the same species in two areas with different oceanographic conditions. In a portion of their geographic range *C. fenneri* inhabits in the deep slope and in other, it inhabits the upper slope. In *C. fenneri* and *C. quinquedens*, Erdman et al. (1991) found a modification of typical shallow-water brachyuran reproductive tactics that have led to the successful colonization of the continental slope habitat. Hilário and Cunha (2013) found individuals of *C. affinis* in precopulatory embrace in waters deeper (mainly at 1200–2400 m) than mentioned in previous studies, as a consequence of a mating-related migration. These authors indicated that the presence of distinct water masses may create suitable conditions for competitors of *C. affinis* can live deeper than in other locations, and therefore shifting both species' distributions downwards. In Madeira and the Canaries the presence of distinct water masses creates suitable conditions for *C. bellianus* and *P. cuvieri*, and therefore *C. affinis* requiring a deeper distribution during reproduction to avoid competition for space and food.

4.3. Spawning season and reproductive pattern

Ovigerous females were observed all year round off the Canary Islands, whereas off Madeira they were only found during a seven-month period. In the Azores, this period was even shorter (October to March) (Pinho et al., 2001a). This may be due to differences in latitude and consequently temperature among areas and its influence on the development of the eggs. Previous studies on the reproduction of *Chaceon* have reported both continuous and annual reproduction cycles for the same species in different areas (Haefner, 1977, 1978; Melville-Smith, 1987; Erdman and Blake, 1988; Erdman et al., 1991). Moreover, the observation of berried females in the last developmental stage described by Tuset et al. (2011) in all quarters of the year in the Canaries suggests that gonad maturation and release of larvae are asynchronous throughout the spawning season. Related with this, Haefner (1977, 1978), Melville-Smith (1987), Erdman and Blake (1988) and Erdman et al. (1991) suggested that eggs were carried for nine months before hatching. Additionally, the presence of ovigerous females on early development gonadal stages and the relative high percentage of non-ovigerous females with low gonadal development, suggest that the time lapse between hatching and a new egg mass can be large. Hartnoll (1969) and Elner et al. (1987) pointed out, for *Chaceon* species, that mating comprises a prolonged courtship followed by copulation shortly after ecdysis, while the female is being protected by the male, and that the process of gonadal maturation and release of the eggs encompasses a period of about two years. This broad period has been interpreted as a consequence of the food-limited characteristic of the deep-water environment (Erdman and Blake, 1988; Erdman et al., 1991; Pinho et al., 2001a; Pezzuto and Sant'Ana, 2009).

The present results on reproduction and intermoult period provide greater support for a biennial individual reproduction cycle, as it has been suggested by Pinho et al. (2001a) and Hilário and Cunha (2013) for *C. affinis* and by Erdman and Blake (1988) for other species of this genus. The large intermoult period and the high incidence of non-ovigerous intermoult females observed in this species during the breeding season may indicate that potential energy restraints have led to a low frequency of reproduction (Bull and Shine, 1979). This low frequency has been found in *Chaceon fenneri* (Manning & Holthuis, 1984), *Chaceon quinquedens* and *Chaceon ramosae* (Manning, Tavares & Albuquerque, 1989) (Lux et al., 1982; Erdman and Blake, 1988; Erdman et al., 1991; Pezzuto and Sant'Ana, 2009) and suggested by Pinho et al. (2001a) and Hilário and Cunha (2013) for *C. affinis*. In this sense, Erdman and Blake (1988) and Erdman et al. (1991) suggest that a long breeding season, together with null or low number of moulting females and high incidence of intermoult non-ovigerous females, may cause a slow growth rate and biennial reproduction.

Histological analysis of the gonads did not validate the sexual maturity colour scale proposed by González et al. (1998), since several colours occurred simultaneously in several phases, proving it inadequate as maturity scale. The maturity scale based on the morphology of the gonads was histologically confirmed.

The presence of spermatophores in the spermatheca of crabs in carapace stages II and III, suggests that spermatophores are viable and used during the intermoult period. This is corroborated by Hilário and Cunha (2013) who pointed out that, as geryonid crabs have a long intermoult period, the reproductive cycle of *C. affinis* females can be as long as 7 years, the intermoult period being as a consequence of spermatophore storage. This capacity of spermatophore storage and posterior fertilization of the oocytes has been observed in other species of geryonid crabs (Hinsch, 1988). In this sense, Lux et al. (1982) in a mark-and-recapture experiment found that some *C. quinquedens* females were recaptured as ovigerous, mostly up to three years after being released. These authors concluded that sperm stored since the last moult remained viable for several years.

A low frequency of reproduction may increase adult survival; a low frequency of moulting would reduce moult-associated risks, while biennial reproduction would increase the period for accumulation of energy reserves necessary to reproduce (Somerton and MacIntosh, 1985). A long life, with alternate periods of growth and reproduction, may also insure reproductive success in a slope environment where population densities are low and mates may be difficult to find (Erdman et al., 1991). A longer cycle will result in a decrease in the reproductive output of the species and render the stock more vulnerable to fishing (Hilário and Cunha, 2013).

4.4. Estimates of size at maturity

In females the allometric pattern of AS5W growth and the frequency distribution of the vulvae condition indicated that the size at sexual maturity (<8 mm CW) is similar both morphologically and physiologically, suggesting that both occur in a short period of time. This pattern was also evident in males (<9 mm CW). In both cases, crabs reach, firstly, morphological maturation and subsequently the physiological maturity, and there is a first investment of energy in body growth to later derive this energy to gonadal development. Males do not acquire the ability to fertilize females until they reach the right size to compete and mate. For females, since copulation and fertilization occurs after moulting, hopefully morphological maturity occurs first and then the physiological one, considering that the sperm is deposited in the spermatheca of the females and they can subsequently self-fertilize (Elner et al., 1987). Pezzuto and Sant'Ana (2009) also concluded that morphometric maturity is attained before individuals of both sexes are functionally mature. Elner et al. (1987), based in experimental observation in tanks, indicated that egg extrusion occurs after nine months of mating event.

In almost all cases examined, females of *C. affinis* showed evidence of mating on their vulval margins. Abrasion marks around the vulvae margins have been considered as signs of copulation in many species of crabs as a result of abrasive activity of male pleopods during mating (Haefner, 1977). The significant differences between size of immature and mature females of *C. affinis* allowed the validation of the vulvae condition as a good external indicator of sexual maturity, as it has been considered in many brachyuran crabs (e.g. Hartnoll, 1969), including *Chaceon notialis* Manning & Holthuis, 1989 (Delgado and Defeo, 2004).

Many previous studies have identified discontinuities in the relative growth rate of deep-sea crab body parts, such as abdomen width in females and chelae size in males, which have been considered as indicators of morphological size of maturity (e.g. Hartnoll, 1974, 1982; Hall et al., 2006). In this work, positive allometry in chelae length was observed in males over the entire size range of animals sampled, with a marked increase in relative growth rate after 103–111 mm CW, whilst females appeared to have a negative relative growth rate of chelae over the entire size-range. The change in the slope in the allometric growth of the chelae observed in males of *C. affinis* represents the transition from immature to mature crabs. These two stages of development are probably separated by a moult to maturity, which can be reached over a wide range of sizes for distinct individuals.

Similarly, Hartnoll (1974, 1982), Clayton (1990) and Claverie and Smith (2009) indicated that the increased relative growth of chelae in males after puberty is common in crabs. The allometric change observed can be controlled by behavioural (Conan and Comeau, 1986; Comeau and Conan, 1992) and/or hormonal changes (Comeau and Conan, 1992; Cormier et al., 1992). In *C. affinis*, it coincides with differentiation of primary sexual characteristics (gonads). In many species, the growth of the chelae is required by males to efficiently mate with females as an adaptation to hold the female during the pre-copulatory embrace (Hartnoll, 1982; Conan and Comeau, 1986; Comeau and Conan, 1992). Mating in this species and in other *Chaceon* species is a relatively long process, where the male protect the female while it moults, and then males place females with the chelae into the position for mating (Mori and Relini, 1982; Elner et al., 1987; Attrill et al., 1991; Hilário and Cunha, 2013). For this purpose, the male needs a large chela to manipulate the female and a large body size to facilitate enclosing and protecting female prior to mating. This make that males must be larger than females to provide the necessary courtship protection and to be able to achieve the mechanics of copulation (Attrill et al., 1991; Hilário and Cunha, 2013). Negative allometry recorded in female chelae suggests that no intraspecific competition for food or shelter exists in this species (Hartnoll, 1974; Claverie and Smith, 2009). This requirement correlates well with the different size range observed between sexes and with the size at maturity estimated for each sex, and this sexual dimorphism in size is similar to that recorded by Pinho et al. (2001a), López-Abellán et al. (2002) and Robinson (2008) in the North Atlantic.

Positive allometry in abdomen width was found before 98–103 mm CW, but with a decrease in relative growth rate after this length. The high change in female abdomen allometry with carapace width suggests that the morphological size of maturity is well defined in the sampled females. The allometric patterns observed may be interpreted as a redistribution of energy demanded after maturation, leading to variation in growth rate due to different demands among developing organs (Nijhout and Emlen, 1998; Claverie and Smith, 2009). The size range in which relative growth of fifth abdominal segment changes seems to be clearly associated with maturation of the vulvae, copulation and insemination, gonad development, and extrusion of eggs. In this sense, females become sexually mature within the size range of 80–90 mm CW. Most females >110 mm CW showed signs of copulation, and their ovaries were in advanced to mature stages of development. Additionally, few females <110 mm CW from the Canaries were ovigerous. Mature females with broader abdomens are presumably able to carry more eggs (Hartnoll, 1974; Claverie and Smith, 2009). After maturation, energy is needed to produce eggs and the abdomen may already be wide enough to effectively carry all the eggs produced by the female; consequently, the allometric abdominal growth rate can be slowed for older females. The change in the morphological growth pattern observed in chelae and abdominal somite width differs among areas and it is considered to be associated with a transition between immature and mature life history phases. This dissimilarity observed among areas indicates that the size dependency of this life history event is not preserved among the populations and can be considered as it is regulated under local conditions. Also it can be a consequence of the reduced food supply characteristic of the slope (Rowe, 1983) and its potential effect on growth and reproduction.

The size at maturity obtained for *C. affinis* supports that the minimum landing size (MLS) should not be set smaller than 115 mm CW in Madeira and 120 mm CW in the Canaries. This conservative MLS, higher than length at functional maturity, would safeguard immature individuals until they reach the size at which they can contribute to the reproductive capacity of the population. In a precautionary approach, Tallack (2007) and Robinson (2008) suggested that the size at maturity, as an estimation of a functional size at maturity, is recommended as a biological support to establish a legal size.

Considering the newness of this fishery, the absence of landing statistics, and a lack of knowledge pertaining to population biomass, an initial precautionary MLS of 125–130 mm CW would seem worthy of consideration by regulatory bodies. A fishery regulated on the basis of a MLS of 125–130 mm CW and a low rate of females in the catches could be sufficient to preserve the reproductive potential of the species. A MLS of 125–130 mm CW is larger than the size at which females yield the greatest contribution to egg production, and the average size of females caught is below this MLS. However, given that the species is not regulated by means of a catch limit, if a male-fishery is established with a MLS close to the size at maturity adopted (125–130 mm CW), the exploitation of males might result in a reduction of the number of dominant males able to fertilise females (Sainte-Marie et al., 1997; Orensanz et al., 1998). These circumstances suggest the need to implement additional management measures. Consequently, the validity of the MLS proposed for the fishery must be reviewed to ensure a management strategy that would avoid the possible future overfishing of the species. Alternative management measures could be implemented, such as the establishment of closed areas to protect the spawning females and/or a catch prohibition on females carrying eggs, which could contribute to preserving the breeding stock prior to extrusion of eggs. Further, considering that *C. affinis* is captured only with baited traps, control of gear selectivity, using escape vents to avoid capture of individuals under 125–130 mm CW, could be a more suitable option to protect the species' reproductive potential (Tallack, 2007). Although trap escape vents are a better option considering the depths involved and the fact that crabs may be preyed upon on their way back to the seabed, crabs less than 125–130 mm CW could be discarded alive and intact from vessels. In this sense, during the mark-and-recapture experiment in Madeira the marked deep-sea crabs returned uninjured to the seabed, and were recaptured in the same area and depth 72 h latter without horizontal displacements.

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Reproductive pattern and egg development of the deep-sea crab *Paromola cuvieri* (*Brachyura*, Homolidae) around the Canary Islands (NE Atlantic)

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Epibionts
Canary Islands

ABSTRACT

This work investigated the biology of *Paromola cuvieri* in the Atlantic Ocean, including reproductive patterns, sex structure, depth distribution and egg development. Females were more abundant than males, mainly at depths greater than 600 m. Males were dominant in size classes larger than 110 mm carapace width (CW), especially over 120 mm, for which only males were observed. The mean length of both sexes decreased with depth. *P. cuvieri* appears to have continuous reproduction throughout the year. Large females tend to spawn mainly between summer and winter, but smaller females spawn during the summer. Four maturity categories were identified based on the ovary colour, and these categories were histologically validated. Three categories of testes were identified according to their colour and morphology. Sexual maturity was estimated at sizes between 71.6 and 74.0 mm CW for females and at 91.0 mm CW for males. The relative growth showed changes along the ontogeny, at 73.6 mm CW (females) and 91.3–92.2 mm CW (males). Egg development appears to not be completely synchronous, and two colour patterns can be observed simultaneously. Four stages of egg development were found: eggs undivided and fully filled with yolk in orange egg masses; eggs with a free region of yolk visible in orange or red egg masses; embryos with slightly pigmented, crescent-shaped eyes in brown egg masses; and embryos with visible pigmented structures, enlarged eyes, segmented appendages and abdomen in brown egg masses. The mean number of external eggs carried by females in stage I was estimated to be 315,753 ± 19,267. Three species of barnacle were observed on the exoskeleton: *Poecilasma aurantia*, *Poecilasma crassa* and *Heteralepas microstoma* (*Cirripedia*, Thoracica).

1. Introduction

Decapods are amongst the most abundant invertebrates on continental slopes worldwide, playing an important role in the distinctive bathyal ecosystems of these depths (Haedrich et al., 1980; Merrett and Haedrich, 1997; Cartes and Carrason, 2004; Fanelli et al., 2007). The structure of the bathyal decapod crustacean populations on the upper slope in the eastern Atlantic Ocean and the Mediterranean is relatively well known (Stora et al., 1999; Cartes and Carrason, 2004). Although some species are confined to restricted depth ranges, other eurybathic species are found in many different habitats, including muddy bottoms, coral gardens, deep-sea hydrothermal vents, and sea sponge aggregations (Stora et al., 1999; Cartes and Carrason, 2004; Desbruyères et al., 2006; Follesa et al., 2009; Muñoz et al., 2012). However, despite the increasing interest in the study of these habitats in the last decades, many aspects of the biology of some of the main species remain almost unknown. In this sense, most research has been concentrated on a few species due to the commercial fishing activity on certain crab species, such as *Chaceon affinis* (A. Milne-Edwards and Bouvier, 1894) or *Cancer bellianus* Johnson, 1861 (Quiles et al., 2001; Tuset et al., 2011). However, the ecology of the species *Paromola cuvieri* (Risso, 1816), in particular, along with that of the entire family Homolidae, remains largely unknown despite

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its relative relevance in terms of biomass (Follesa et al., 2009; Muñoz et al., 2012).

P. cuvieri is a deep-water homolid decapod crustacean. It has been found throughout the eastern Atlantic, from the Hebrides and southern Scandinavia to off Namibia, including the Macaronesian archipelagos and the Mediterranean (Kensley, 1980; Manning and Holthuis, 1981; Guinot and Richer de Forges, 1995). It is present at depths between 10 and 1212 m but generally occurs beyond shelf depths (Manning and Holthuis, 1981; Guinot and Richer de Forges, 1995; Follesa et al., 2009). *P. cuvieri* occurs in a wide variety of habitats, including muddy bottoms (Manning and Holthuis, 1981; Cartes and Sardà, 1992; Follesa et al., 2009; Muñoz et al., 2012), coral gardens (Freiwald et al., 2009; Weaver et al., 2009; Capezzuto et al., 2012), deep-sea sponge aggregations (Braga-Henriques et al., 2012) and deep-sea hydrothermal vents (Biscoito, 1997), some of which have been identified as priority habitats for conservation (Braga-Henriques et al., 2012).

P. cuvieri is one of the most unknown of the relatively abundant species of the assemblages in the continental slope of the eastern Atlantic and the Mediterranean. Some aspects of its distribution, size range, reproduction, and feeding behaviour were studied by Mori (1986), based on a limited number of individuals ($n=137$), many of them acquired from fish markets. The aim of this work is to provide information on the reproductive pattern and egg development of *P. cuvieri*, including size–depth distribution, fecundity and the epizoites associated with this species in an unexploited population from the Canary Islands. This paper can help extend the presently limited knowledge of this species' life history. Additionally, because this species constitutes a fraction of the total discards generated by the fisheries in the East Atlantic and Mediterranean, the present data can be used to implement adequate management measures to ensure the conservation of this resource as a by-catch of deep-sea fisheries in various areas (Sánchez et al., 2004; Massutí and Reñones, 2005; Maynou and Cartes, 2012).

2. Materials and methods

2.1. Sampling and biological data collection

Four research cruises using traps were carried out during 2010 and 2011: spring (May–June 2010), summer (September 2010), autumn (November 2010), and winter (February–March 2011) on board the R/V *Prof. I. Lozano*, around the island of Gran Canaria, Canary Islands (Central-east Atlantic), as part of a larger study on the entire assemblages of deep-sea pandalid shrimp and brachyuran crabs. The work area (27°41′–28°09′ N and 15°18′–15°41′ W) was randomly prospected from 100 to 1000 m. The sampled locations varied from trip to trip, and the sampling effort, across the bathymetric range, was equally distributed at 100 m depth intervals, with a total of nine depth strata prospected. For each depth stratum, 120 traps were deployed on the sea ground, covering sandy, muddy and rocky bottoms, with a total of 1080 traps used.

Specimens of *P. cuvieri* were captured in square metallic traps, with 100 × 100 cm base length and 50 cm in height, covered with 19 × 19-mm mesh. Traps were baited with mackerel (*Scomber colias*) and deployed on the sea bottom, with immersion times ranging from 30 to 36 h. Each trap had one flexible troncoconical opening with a 24-cm outer diameter and a 17-cm inner diameter.

At the laboratory, several measurements were recorded for each crab using a digital calliper and rounding to the nearest mm (Fig. 1). Measurements of the body: carapace width (CW) (maximum transverse diameter, excluding spines) and carapace length (CL) (midline distance from the diastema, below the central tooth of the frontal margin, to the posterior carapace edge). Measurements of the chela and abdomen were carried out following Fernández-Vergaz et al. (2000) and Quiles et al. (2001): width of right/left chela (R/LCHW) (maximum diameter of the propodus at level of its jointure with the dactyl), right/left hand-length (R/LCHL) (propodus + dactyl), and maximum width of the fifth abdominal somite (AS5W) in females. Individuals with missing or regenerated appendages were excluded from statistical analysis.

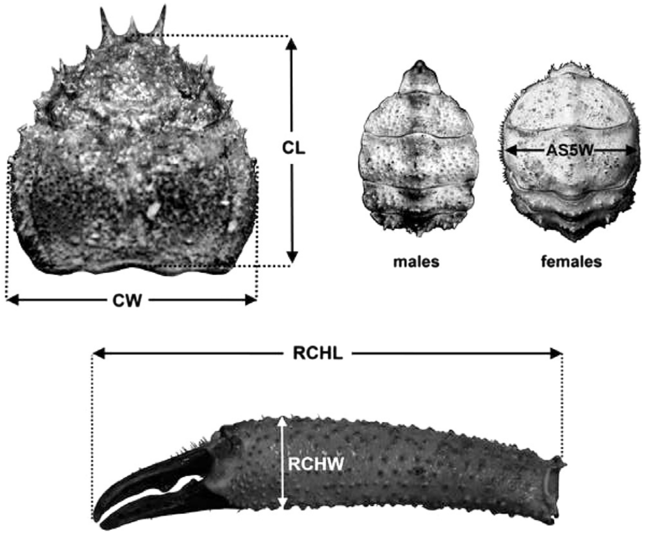

Fig. 1. Measurements taken for each specimen of *Paromola cuvieri*: carapace width (CW), carapace length (CL), width of right chela (RCHW), right hand-length (RCHL), and maximum width of the fifth abdominal somite (AS5W).

Sex (according to the abdomen morphology, Fig. 1), carapace conservation stage, barnacle epibiont species, as well as presence and colour of external eggs or remaining eggs on the pleopods (ovigerous condition) were also recorded. The epizoites collected were identified to the species level. The exoskeleton conservation was macroscopically classified using three categories: I, bright-orange carapace with neither barnacles nor lesions produced by chitinolytic bacteria; II, faded orange carapace with low level of barnacle infestation and lesions; III, dark, faded carapace with high level of barnacles and lesions (Pinho et al., 2001a). Total wet weight (TW), total egg mass (EM) and gonad weight (GW) were recorded, the two last measurements to the nearest 0.1 g.

Crabs were dissected, and the maturity stage was macroscopically assessed using a chromatic criterion adapted from Haefner (1977) and Erdman and Blake (1988). Ovaries were fixed and preserved in 4% buffered formaldehyde and subsequently processed for histological analyses to verify the macroscopic maturity stage. For the histological processing, the fixed tissues were dehydrated in a series of ethanol solutions, cleared in xylene, and then embedded in paraffin in a vacuum chamber. Slices of tissue were sectioned at 5 μm and stained with Harris haematoxylin followed by eosin counterstaining. Evidence of copulation in females was recorded by the vulval condition (open or closed) (Hartnoll, 1969; Haefner, 1977; Mori, 1986).

2.2. Relationships between main variables and sex ratio

The CW–TW relationship was determined for males and females by means of a power function. Differences in the CW–TW and CW–CL relationships between males and females were evaluated by an *F*-test, and differences between values of b and the expected value from isometric growth were evaluated by a *t*-test (Sachs, 1982). Relationships between CW and CL were calculated to facilitate the comparison of data. The sex ratio (males to females) was estimated for the total sample and by size intervals. Sex ratios were statistically tested for significant deviations from the expected 1:1 ratio with a Pearson chi-square goodness-of-fit test (Sokal and Rohlf, 2012). Differences in mean carapace width and total wet weight between sexes were analysed using the Student *t*-test. The Kolmogorov–Smirnov non-parametric *Z*-test was used to analyse the differences in CW and TW ranges in males and females. The mean CW values among depth strata were compared with ANOVA, and then Dunnett's T3 post-hoc test was applied to determine which strata differed (Sokal and Rohlf, 2012).

2.3. *Spawning period and size at first sexual maturity*

The reproductive period was determined by means of the relative proportion of *P. cuvieri* in each sexual maturity stage (both sexes) and the ovigerous condition (females) by season. Further, the gonadosomatic index (GSI) was determined by dividing GW (ovary or testis) by TW and referenced to season and CW. GSI values were compared among seasons with ANOVA, and then Dunnett's T3 post-hoc test was applied to determine which of the seasons differed (Sokal and Rohlf, 2012).

Estimation of size at first sexual maturity was calculated as the proportion of mature females by size class: morphologically with open vulvae and blackened vulvae margins together with medium to large gonads; physiologically in maturity stages II to IV and ovigerous condition (Melville-Smith, 1987). Estimation of size at first sexual maturity for males was determined by the proportion of mature males by size class: specimens in maturity stage II or III. Size at sexual maturity was estimated by fitting data to the logistic equation $P=100/1+\exp(-r(\mathrm{CW}-\mathrm{CW}_{50})$ by non-linear regression, where P is the proportion of morphologically or physiologically mature crabs in each size class, r is a model parameter and CW_{50} the size at 50% maturity. Mean CW values were compared among maturity stages with ANOVA, and then Dunnett's T3 post-hoc test was used to determine which of the samples differed (Sokal and Rohlf, 2012). The absence of differences in mean CW among maturity stages identified with Dunnett's T3 test was verified with paired *t*-test and with ANOVA test.

The relative reproductive potential was estimated for *P. cuvieri* following the method of Goñi et al. (2003). Relative reproductive potential can serve to determine the size class of spawning females that makes the greatest contribution to egg production in a population (Goñi et al., 2003).

The length and width of both chelae were plotted against the CW for males and females and to the AS5W in females to investigate possible changes associated with the pubertal moult (Somerton, 1980; Attrill et al., 1991). For the values for which the data could be separated into two groups, a power equation was fitted to the data by non-linear regression, and the transition points were iteratively searched by increments of 0.1 mm CW (Somerton, 1980). An F statistical test based on the difference between the residual sums of squares was used to determine whether two models fit the data better than a single model fitted to the data (Somerton, 1980). ANCOVA and F test were used to test the difference between the two regressions, corresponding to the pre- and post-pubertal growth phases (Sachs, 1982; Sokal and Rohlf, 2012). The relative growth patterns of both chelae (in length and width) and the AS5W in pre- and post-pubertal phases were analysed via *t*-test (Sachs, 1982).

2.4. *Fecundity and egg morphology*

Ovigerous females from all size classes were used for the morphological study of eggs and to estimate fecundity. Pleopods with attached eggs were removed from females, and egg masses were then placed on 100-μm mesh, washed and isolated from pleopods. After removal of the excess wash water, eggs were weighed (wet weight), and 40 eggs for each female were measured in fresh and used to calculate the maximum diameter (Md in mm), minimum diameter (md in mm), mean diameter (xd in mm), and aspect ratio (Md/md) (Russ, 1990; Tuset et al., 2011). Based on Mori (1986), only females with eggs in the first stage of development were considered for the estimates of *P. cuvieri* fecundity. A subsample of 5% in weight from each selected female was fixed and preserved in buffered 4% formaldehyde and then counted by means of a dissection microscope. The batch fecundity (F), defined as the egg production by batch, was estimated by the gravimetric method (Tuset et al., 2011). A power function was fitted to fecundity versus CW and TW.

Egg morphology was described and classified in four stages correlated with the colour of the egg mass, adapted from Arshad et al. (2006) and Tuset et al. (2011).

3. Results

3.1. *Size-structure*

A total of 674 individuals of *P. cuvieri* were collected. Males ($n=243$) ranged from 38 to 164 mm CW and from 47 to 2574 g TW, and females ($n=431$) ranged from 34 to 109 mm CW and from 46 to 965 g TW. Males were larger and heavier than females. Significant differences in mean CW and TW were found between males (86.3 ± 20.8 mm and 564.2 ± 436.1 g) and females (81.6 ± 10.9 mm and 443.5 ± 143.9 g) (*t*-test, CW $t=3.32$, $p<0.001$; TW $t=4.15$, $p<0.001$). The ranges of CW and TW also differed significantly between males and females (Kolmogorov–Smirnov non-parametric test, CW $Z=2.46$, $p<0.001$; TW $Z=2.53$, $p<0.001$). Significant differences between males and females were found in the CW–TW relationship (*F*-test, $F=5.31$, $p<0.001$), being allometrically negative in all cases (*t*-test, $t>7.69$, $p<0.001$) (Table 1). No significant differences between males and females were found in the CW–CL relationship (*F*-test, $F=1.56$, $p>0.05$), being isometric in all cases (*t*-test, $t<1.88$, $p>0.05$) (Table 1).

3.2. *Sex ratio*

Females were significantly more abundant than males, in the male:female proportion 1:1.77 (χ^2-test, $\chi^2=52.44$ $p<0.001$). Females were more abundant than males in the 80–90 mm CW size class (1: > 2.16 χ^2-test, $\chi^2>25.79$, $p<0.001$). However, males were significantly dominant in size classes larger than 110 mm CW (χ^2-test, $\chi^2>5.56$, $p<0.025$), particularly over 120 mm CW, for which only males were observed (Fig. 2).

The catches of *P. cuvieri* were zero in the 100, 200, 800, 900 and 1000 m depth strata. Mean size decreased at depths >400 m (Fig. 3) from 89.5 to 77.0 mm CW (males) and from 87.0 to 72.6 mm CW (females). Significant differences were found in mean

Table 1
Parameters of CW–TW (TW=a CWb) and CW–CL relationships (CL=a+bCW) for males, females and all crabs of *P. cuvieri*. *a*, intercept; *b*, allometric coefficient; S.E., standard error; r^2, determination coefficient; *n*, number of specimens; *t*, *t*-test value; *, significance at 0.05 level.

Relationship	Sex	*a*	*b*	S.E.(b)	r^2	*n*	*t*
CW-TW	Males	0.0034193	2.668	0.04314	0.932	243	7.698*
CW-TW	Females	0.0012442	2.367	0.06582	0.810	431	9.617*
CW-TW	All crabs	0.0028385	2.703	0.02571	0.913	674	11.55*
CW-CL	Males	4.6671808	1.037	0.01973	0.961	243	1.875
CW-CL	Females	5.6867450	1.023	0.01385	0.932	431	1.660
CW-CL	All crabs	4.7096971	1.034	0.01941	0.949	674	1.751

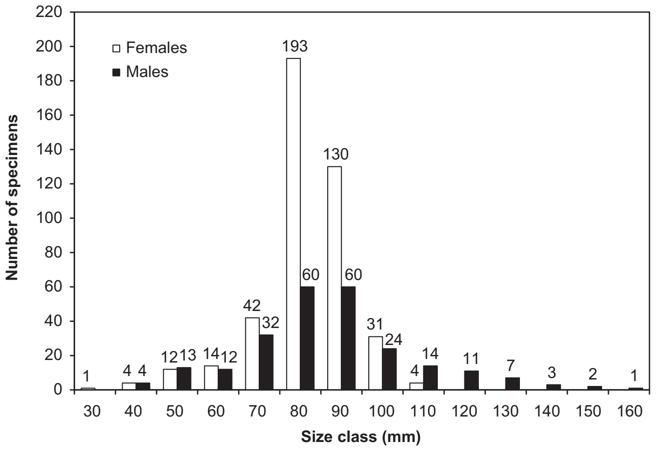

Fig. 2. Number of specimens of males and females of *P. cuvieri*. Numbers correspond to individuals for each size class of 10 mm.

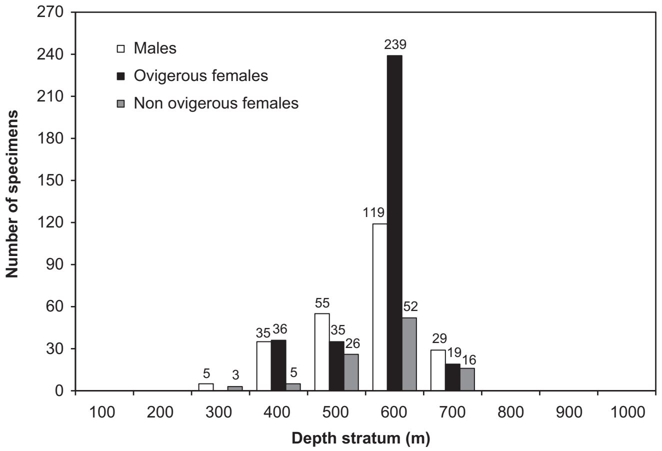

Fig. 4. Number of males and females (by ovigerous or non ovigerous condition) by depth stratum (100 m) of *P. cuvieri*. Numbers correspond to individuals for each size class of 10 mm.

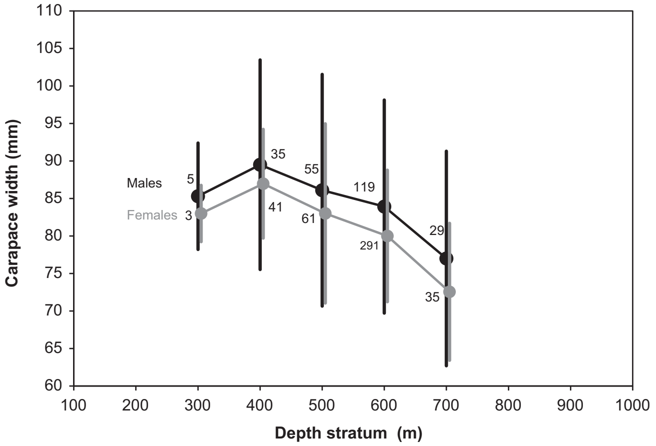

Fig. 3. Variation of the mean size with depth for males and females of *P. cuvieri*. Dotted lines correspond to deviation and numbers to individuals for each depth stratum (100 m).

CW among the different strata (ANOVA, Brown–Forsythe $F > 2.01$, $p < 0.026$). Dunnett's T3 post-hoc test showed significant differences in CW among all strata ($p < 0.05$). Few individuals were caught at the 300 m depth stratum, and the highest abundance was found at the 600 m stratum. Additionally, females were significantly more abundant than males for the depth stratum of 600 m (1:2.45, χ^2-test, $\chi^2 = 72.16$, $p < 0.001$), where the ovigerous females were found in the highest number (Fig. 4). No significant differences were found between males and females in the 300–500 and 700 m depth strata ($\chi^2 < 0.56$, $p > 0.60$).

3.3. *Sexual maturity*

Four categories of ovaries were identified: I, immature/early (translucent/white); II, advanced (orange cream); III, mature (red-wine) and IV, post-spawning (white-ivory) (Fig. 5). Immature/early ovaries (stage I) were small and easy to discern, with six narrow lobules appearing translucent or white, with a thick ovarian wall. Advanced ovaries (stage II) were characterised by an orange-cream aspect and moderately thick lobules. Mature ovaries (stage III) were characterised as large, wine-red masses occupying nearly all the cavity, with oocytes visible to the naked eye. Post-spawning status (stage IV) was defined as a white-ivory ovary with a thin ovarian wall and few remaining eggs. Histologically, early ovary is characterised by oocytes in various stages of early development, all in phase of pre-vitellogenesis. An advanced ovary (stage II) appears with oocytes from early to late phases of vitellogenesis, exhibiting a granular texture arising from the accumulation of yolk globules. A mature ovary (stage III) is dominated by mature oocytes, which are granular in appearance due to the high concentration of yolk globules, and vitellogenesis is complete at this stage. The post-spawned ovary (stage IV) is characterised by unspawned oocytes undergoing reabsorption, which are often surrounded by phagocytes (Fig. 6).

Three categories of testes were identified: I, immature (translucent); II, advanced (white); and III, mature (milk-white) (Fig. 5). Immature testes (stage I) are colourless, with deferent ducts not morphologically differentiated. Advanced testes (stage II) are white, and deferent ducts are morphologically differentiated and partially filled with sperm; deferent ducts range from translucent to white and appear as straight tubes. Mature testes (stage III) were observed as a large, milk-white mass; their deferent ducts, completely filled with sperm, are opaque and appear as a strongly coiled mass.

The total sample of females comprised 108 with immature/early ovaries (mean 71.8 ± 14.3 mm CW, range 34–91 mm CW), 54 with advanced ovaries (mean 84.2 ± 7.2 mm CW, range 62–96 mm CW), 245 with mature ovaries (mean 84.7 ± 6.2 mm CW, range 72–109 mm CW), and 24 with post-spawning ovaries (mean 83.6 ± 7.33 mm CW, range 69–97 mm CW) (Fig. 7). There were significant differences in the mean CW of females among the different stages of ovarian development (ANOVA, Brown–Forsythe $F = 46.79$ $p < 0.0001$). Dunnett's T3 post-hoc test showed one group of ovarian stages with no differences in the mean GSI value among stages (maturity stages II–IV, $p > 0.983$), but there were significant differences between stage I and each stage from II to IV ($p < 0.0001$). Significant differences in mean CW between females with immature/early ovaries (I) and those in advanced (II), mature (III) or post-spawning (IV) stages were verified by paired *t*-tests ($t > 5.7$, $p < 0.001$). The lack of significant differences in mean CW among females with advanced (stage II), mature (stage III) or post-spawning (stage IV) ovaries were verified by paired *t*-tests ($t < 0.708$, $p > 0.480$) and by ANOVA ($F = 0.295$, $p = 0.745$).

Of the sampled females, 329 presented in ovigerous condition (mean 84.41 ± 6.62 mm CW, range 69–109 mm CW), and 102 females were non-ovigerous (mean 71.1 ± 15.1 mm CW, range 34–101 mm CW) (Fig. 7). Females in the non-ovigerous condition were significantly smaller in mean CW than the ovigerous females (*t*-test, $t = 7.44$, $p < 0.001$).

Fig. 5. Scale of sexual maturity stages in *P. cuvieri*. Females: (a) I, immature/early; (b) II, advanced; (c) III, mature; (d) IV, post-spawning. Males: (e) I, immature; (f) II, advanced; (g) III, mature. Scale bar represents 1 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

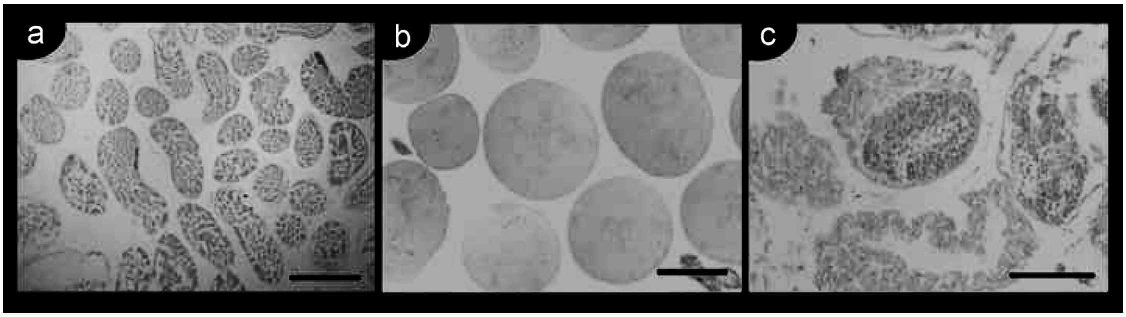

Fig. 6. Histological sections illustrating *P. cuvieri* oocytes at different maturity stages. (a) Advanced ovary with oocytes in secondary vitellogenesis (364 ± 46 μm). (b) Mature ovary with mature oocytes (413 ± 30 μm). (c) Post-spawning ovary with atresia. Scale bar represents (a) 500 μm**,** (b) 250 μm, and (c) 175 μm.

The smallest female with open vulvae measured 62 mm CW, and the largest measured 109 mm CW (Fig. 7). There were significant differences in the mean CW of females with open (84.9 ± 6.5 mm) and closed (72.8 ± 14.1 mm) vulvae (*t*-test, $t = 8.94$, $p < 0.001$).

The length at sexual maturity CW_{50}, based on the maturity, ovigerous, and open vulvae conditions, was estimated as 71.7, 72.0, and 74.0 mm CW, respectively (Fig. 8).

The estimation of the relative reproductive potential showed that specimens in size classes of 80–90 mm CW (75.1% of females)

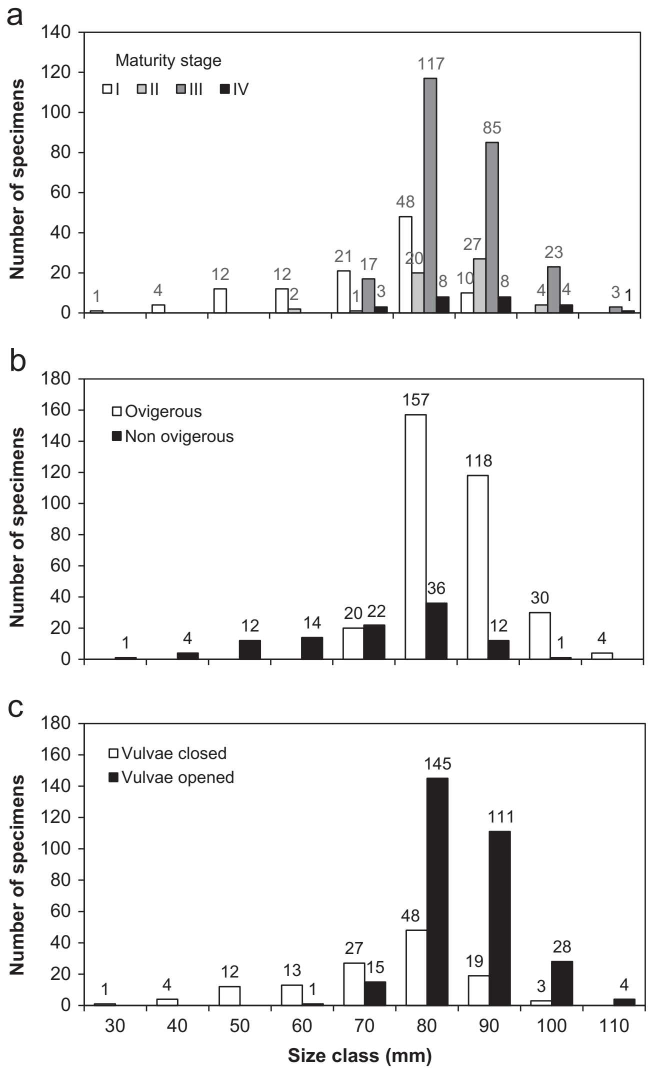

Fig. 7. Number of specimens by (a) maturity stages, (b) ovigerous condition, and (c) vulval condition for females of *P. cuvieri*. Numbers correspond to individuals for each size class of 10 mm.

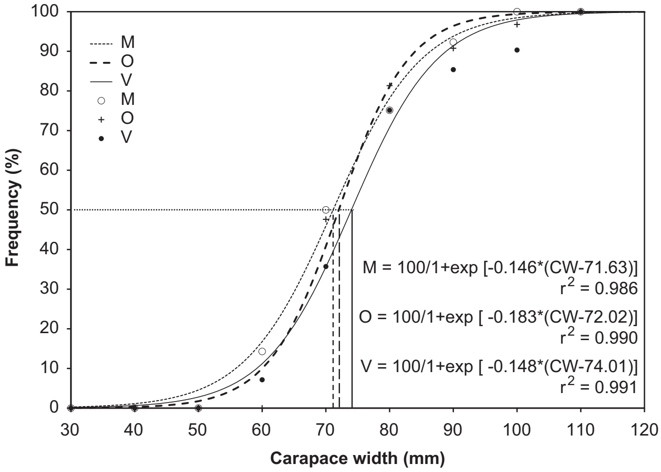

Fig. 8. Ogives for size at first maturity, based on maturity condition (M), ovigerous condition (O) and open vulvae condition (V), for females of *P. cuvieri*. r^2, Determination coefficient.

yielded 83.8% of the total egg production. Specimens smaller than 70 mm CW and larger than 100 CW were 24.9% of females but produced only 16.2% of the eggs. Specimens in the 110-mm CW size class had the highest productivity ratio (1.60), meaning that specimens in this size class were 2.9 times more productive than females in the 70 mm CW.

For the total sample of males, 145 were immature (stage I) (mean 78.1 ± 16.12 mm CW, range 38–115 mm CW), and 98 were

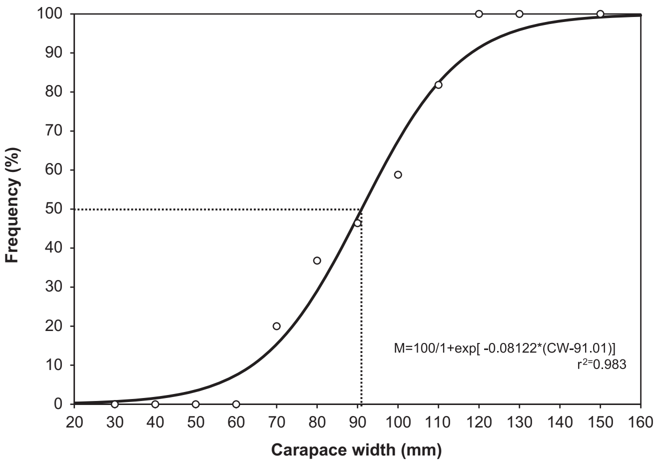

Fig. 9. Ogive for size at first maturity, based on maturity condition (M) for males of *P. cuvieri*. r^2, Determination coefficient.

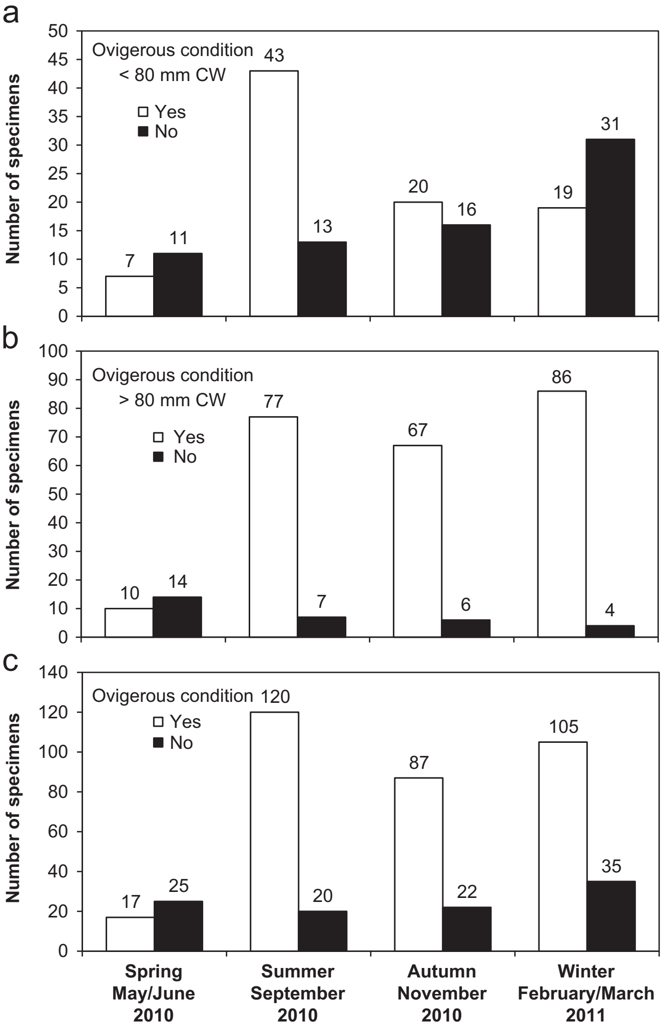

Fig. 10. Number of specimens by ovigerous condition, by size group, and season for females of *P. cuvieri*. (a) < 80 mm CW, (b) > 80 mm CW, and (c) all sizes. Numbers correspond to individuals for each season.

advanced or mature (stages II–III) (mean 98.5 ± 17.6 mm CW, range 67–164 mm CW). Males with gonads in stage I were significantly smaller in mean CW than those in stages II–III (*t*-test, $t > 3.70$, $p < 0.001$). The size at onset of sexual maturity in males (CW_{50}) was estimated at 91.0 mm CW (Fig. 9).

3.4. *Spawning period*

The 329 ovigerous females were observed in all seasons, with the lowest frequency in spring (Fig. 10). Large ovigerous females (> 80 mm CW) were found at high frequency (> 90% of females) in summer, autumn and winter, whereas smaller ovigerous females (< 80 mm CW) were recorded at a high frequency (> 75%) only in summer (Fig. 10).

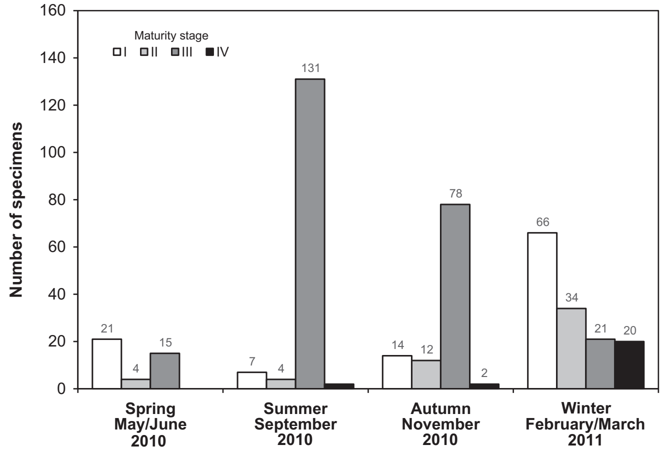

Fig. 11. Number of specimens by maturity stages and season for females of *P. cuvieri*. Numbers correspond to individuals for each season.

Females with mature ovaries were observed in all seasons but were more common in summer and autumn. Females showing ovaries at the post-spawning stage were recorded in summer and autumn but most commonly in winter (Fig. 11). A significant correlation between gonadal maturity stage and egg mass colour pattern was observed ($p = 0.01$).

The gonadosomatic index (GSI) showed high values during all seasons (Fig. 12) but also showed significant differences among seasons (ANOVA, Brown–Forsythe $F > 12.3$, $p < 0.0001$). Dunnett's T3 post-hoc test showed two groups of seasons with no differences in the GSI values (winter–spring, $p > 0.999$; summer–autumn, $p > 0.988$) and showed significant differences in GSI values between seasons of each group ($p < 0.0001$). GSI values are higher for males with a CW greater than 67 mm and for females with a CW greater than 62 mm (Fig. 12).

3.5. *Morphometric maturity*

Width (R/LCHW) and hand-length (R/LCHL) of both chelae for both sexes, as well as maximum fifth abdominal somite width (AS5W) in females, were plotted against CW to investigate possible changes associated with the pubertal moult (Figs. 13 and 14). The relative growth of males showed significant changes along the ontogeny for all selected measurements (*F*-test, $F > 6.77$, $p < 0.005$). Transitions occurred between 91.3 and 92.2 mm CW, and all measurements showed different relative growth patterns before and after their transition points (ANCOVA $p < 0.01$). Allometry in the growth of the chelae was always positive ($t > 5.24$,

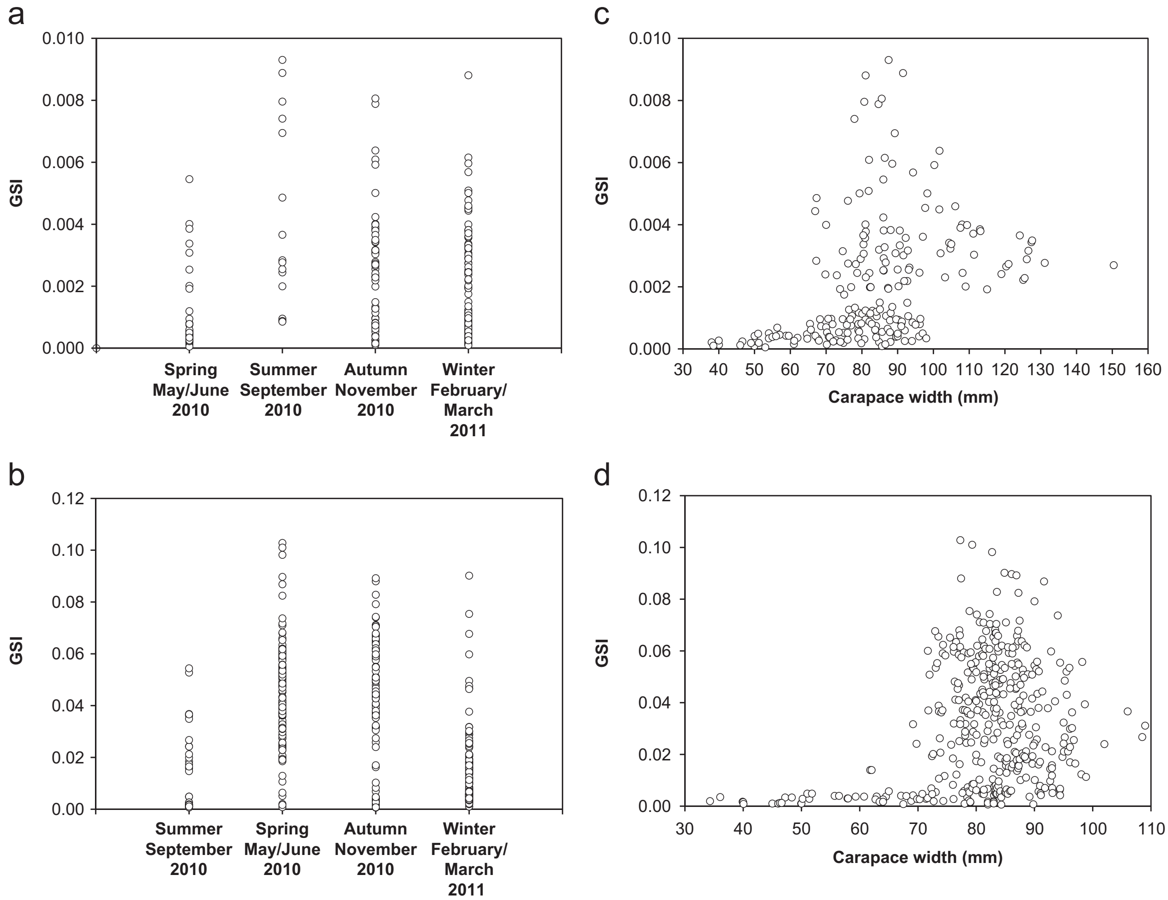

Fig. 12. GSI values by carapace width (mm) and by season for males ((a) and (c)) and females ((b) and (d)) of *P. cuvieri*.

$p < 0.001$) irrespective of their width or length or of the subset considered (pre- or post-pubertal phase); however, the function calculated for males larger than 91.3–92.2 mm CW revealed a significant increase in their slopes ($t > 17.60$, $p < 0.001$) (Fig. 13).

Because no evident discontinuities were observed in the relative growth of both chelae for females along their ontogeny, all points were used for the calculation of regressions. In all chelar measurements, relative growth was allometrically negative (*t*-test, $t > 4.69$, $p < 0.001$). Moreover, no significant differences were found between the regression equations of the right and left chelae in length or width (*F*-test, $F < 1.29$, $p > 0.1$) (Fig. 13). In females, a transition point (*F*-test, $F > 9.85$, $p < 0.005$; ANCOVA $p < 0.01$) was found for AS5W at 73.6 mm CW (Fig. 14). Allometry was positive ($t = 12.50$, $p < 0.001$) before the transition point (pre-pubertal phase), and then the growth pattern became allometrically negative ($t = 18.42$, $p < 0.001$) in the post-pubertal phase (Fig. 14).

3.6. Fecundity and egg development

In stage I, eggs were undivided and fully filled with yolk, and they were observed in orange egg masses ($n = 162$); in stage II, eggs presented a visibly free region of yolk, and they were found in orange or red egg masses ($n = 158$); in stage III, embryos had slightly pigmented eyes growing as crescents ($n = 7$); and in stage IV, embryos had visible pigmented structures, enlarging eyes, segmented appendages and abdomen ($n = 2$). The last two stages were observed in brown egg masses (Fig. 15).

Eggs undivided and fully filled with yolk (stage I) were observed in 49.2% of females carrying eggs. Eggs with the free region of yolk visible (stage II) were recorded in 48.1% of females carrying eggs. Embryos with pigmented eyes (stage III) were recorded in only 2.1% of the females carrying eggs, and eggs in stage IV were observed in only 0.6% of females carrying eggs. Orange egg masses were observed in 260 females (79.1%), red in 60 (18.2%) and brown in 9 females (2.7%).

The eggs present a spherical shape; their development seems not to be completely synchronous, and sometimes two colour patterns can be observed simultaneously, one in the inner part of the egg mass and another in the outer part. Mean egg size increased from 0.585 mm (stage I) to 0.655 mm (stage IV) (Table 2).

The mean number of external eggs carried by female in stage I was calculated as being 315,753 ± 19,267, for a range from 285,050 eggs (carried by a 75-mm CW/284-g TW female) to 361,690 eggs (carried by a 96-mm CW/574-g TW female) (Fig. 16).

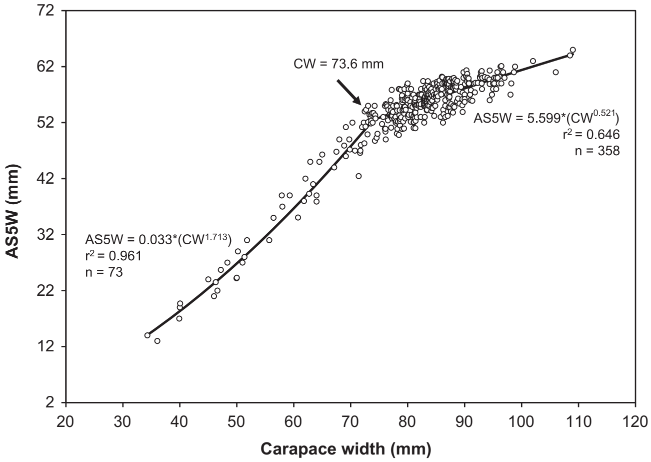

Fig. 14. Maximum width of the fifth abdominal somite (AS5W) plotted against carapace width (CW) in females of *P. cuvieri*. *n*, Number of crabs. r^2, Determination coefficient. Lines fitted correspond to each potential model estimated. Arrows indicate the transition point.

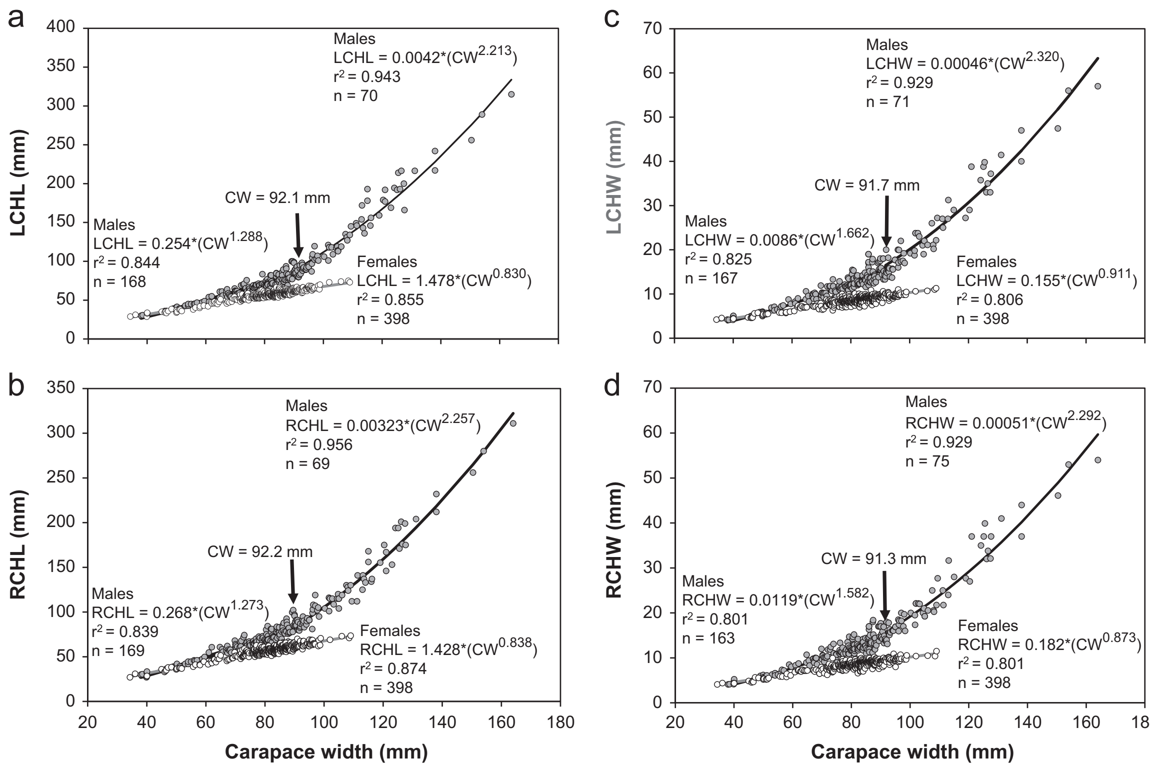

Fig. 13. Right (a) and left (b) chela length (R/LCHL) and chela width (R/LCHW) ((d) and (c)) plotted against carapace width (CW). *n*, Number of crabs. r^2, Determination coefficient. Lines fitted correspond to each potential model estimated. Arrows indicate the transition point.

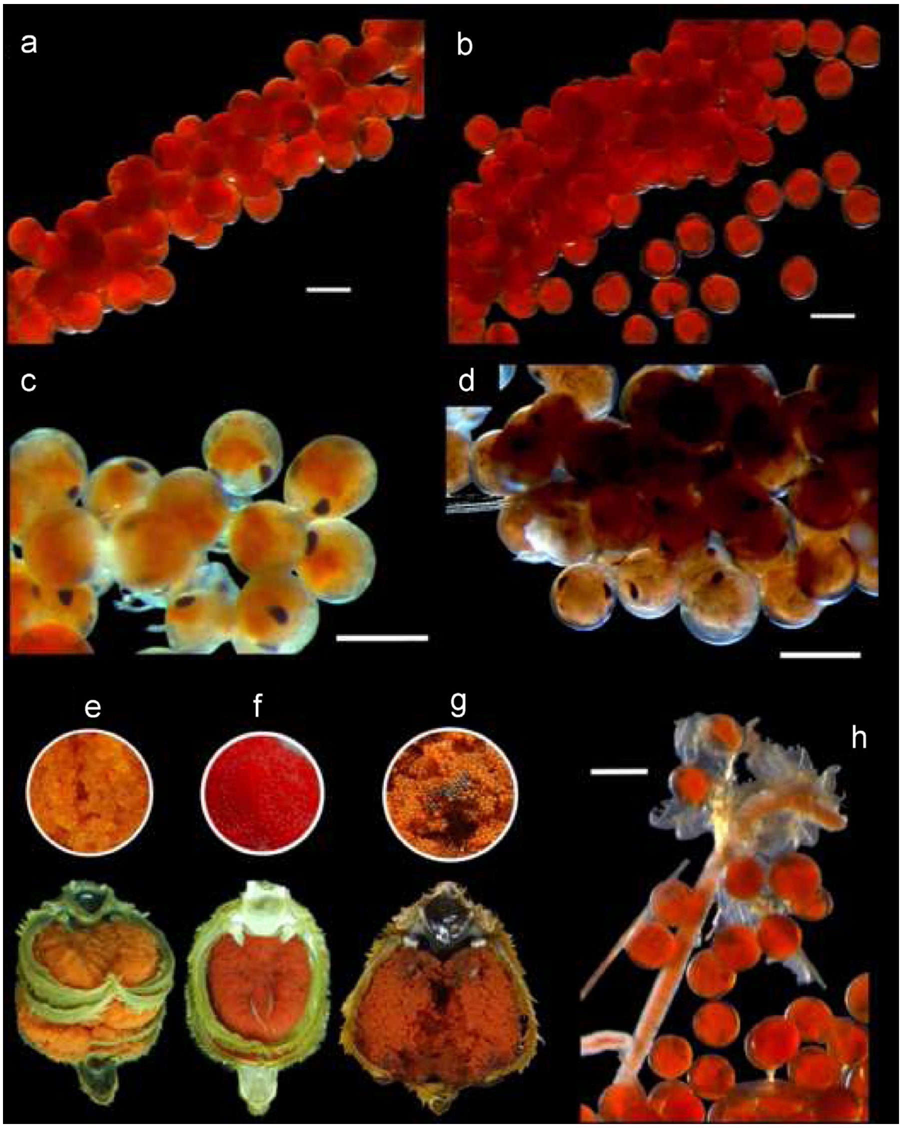

Fig. 15. Egg morphology in *P. cuvieri*: (a) eggs undivided and fully filled with yolk, (b) eggs with a free region of yolk visible, (c) embryos with slightly pigmented eyes, growing as crescents, (d) embryos with visible pigmented structures, enlarging eyes, segmented appendages and abdomen appearing. Colour pattern of egg masses attached to pleopods: (e) orange, (f) red, and (g) brown. (h) Nemertean parasites eating eggs. Scale bar represents 1 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Maximum (*Md* in mm), minimum (*md* in mm), and mean diameters (*xd* in mm), number of specimens (*n*), and aspect ratio (*Ar*) by egg development stage of *Paromola cuvieri.*

Stage	*n*	*Md* (mm)	*md* (mm)	*xd* (mm)	*Ar*
I	20	0.579	0.737	0.585	1.272
II	20	0.587	0.752	0.603	1.281
III	7	0.594	0.821	0.621	1.382
IV	2	0.607	0.841	0.655	1.385

3.7. Epizoites and moult

Three species of thoracic cirripedia were observed on *P. cuvieri*, which were different from those found in the Mediterranean. Many individuals of *Poecilasma aurantia* (Darwin, 1852) (*Cirripedia*, Lepadomorpha, Poecilasmatidae), individually or in clusters, were very commonly found on the carapace and appendages (limbs) of every crab, rarely on the abdominal region and internal surface of carapace. A few individuals of *Poecilasma crassa* (Grey, 1848) were frequently found attached on the anterior ventral region of the crabs, usually on the maxillipeds and rarely on the integument. A unique individual of *Heteralepas microstoma* (Gruvel, 1901) (*Cirripedia*, Heteralepadomorpha, Heteralepadidae) was found attached on the last (fifth) leg of one crab, just on the prehensile subchela formed by the dactylus and propodus. A single record was found of one crab simultaneously hosting the three barnacle species.

Males and females with a clean exoskeleton without lesions (stage I) were observed in all size ranges. Crabs not having recently moulted (stage II or III), showing different level of discoloration with barnacle infestation and lesions, were also observed in all size ranges (Fig. 17).

4. Discussion

4.1. Size frequency distributions and mating pattern

The size frequency distribution of *P. cuvieri* obtained was clearly unimodal for both sexes, and there was a general scarcity of small

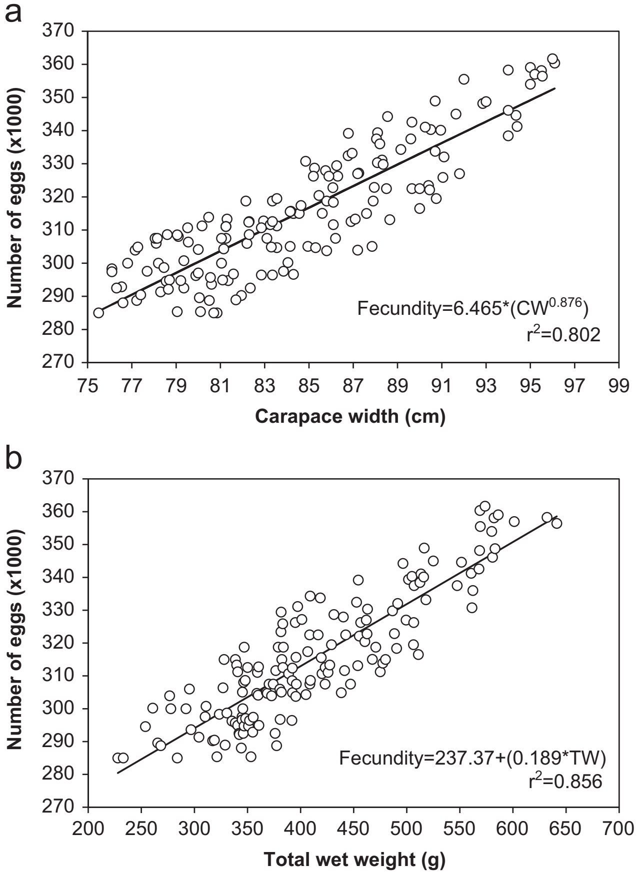

Fig. 16. Fecundity estimates by carapace width (a) and total wet weight (b) for *P. cuvieri*. r^2, Determination coefficient. Lines fitted correspond to each model estimated.

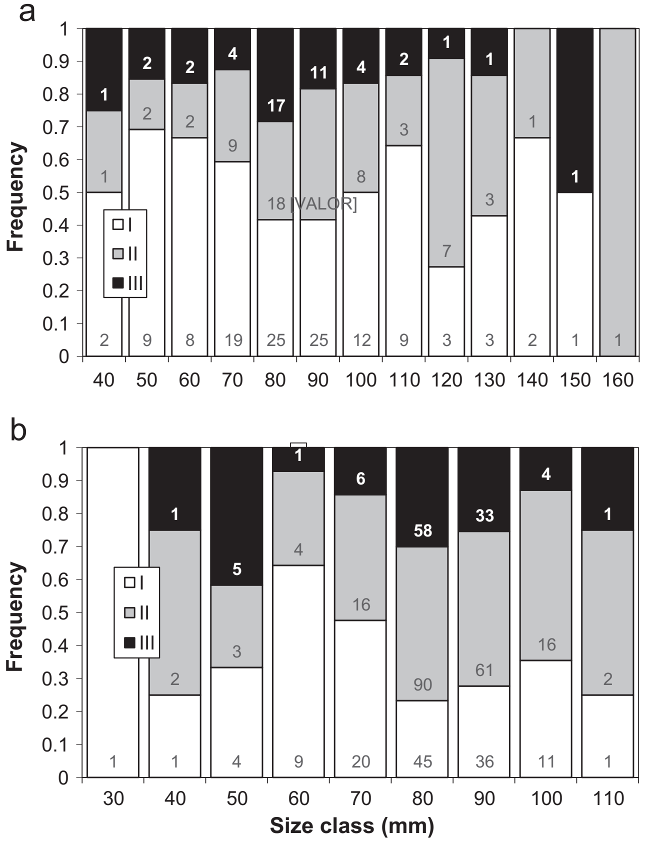

Fig. 17. Frequency of carapace conservation stages by size classes for males (a) and females (b) of *P. cuvieri*. The number of individuals is indicated for each size class and stage. I, bright-orange carapace with neither barnacles nor lesions; II, faded orange carapace with low levels of barnacle infestation and lesions; III, dark, faded carapace with high levels of barnacles and lesions.

individuals. This scarcity could be related to trap selectivity, or possibly to competition for food, for instance, in *C. bellianus*, to a size-dominant behaviour around traps (Pinho et al., 2001b).

P. cuvieri shows a marked sexual dimorphism, which enabled sexing of each crab by the size of the first pair of pereiopods (Braga-Henriques et al., 2012). In males, the first pereiopods are longer than the other three pairs of walking legs and also longer than the carapace. Hartnoll (1982) explained this sexual dimorphism in terms of the greater role played by adult males in courtship, display and combat. The same morphologic pattern has also been reported for *P. cuvieri* from the Mediterranean (Mori 1986) and for many other brachyuran species (e.g., Hartnoll 1974, 1978).

The observed differences in the size frequency distributions between both sexes of *P. cuvieri* reflect a common pattern for deep crabs. Melville-Smith (1989) attributed these differences to the different moulting process for each sex, stating that the unimodal structure could be the result of similar intermoult periods in both immature males and females and of different elapsed periods of time between moults after maturity, with females either moulting less frequently or undergoing smaller size increments per moult than males because of their higher reproductive investment, leading to different growth rates between the sexes.

Males were larger than females, with maximum sizes found of 164 and 109 mm CW, respectively. Both maximum sizes are larger than those recorded by Mori (1986) from the Mediterranean (145 and 100 mm CW), although the same pattern in size between sexes was recorded. In this sense, Mori and Relini (1982) and Elner et al. (1987) noted that the most important factors controlling the pattern of male growth at puberty are the requirements of courtship and mating behaviour. The mating process in many crab species is relatively long, with the male protecting the female while it moults and then using its chela to place the female in the position for mating (Attrill et al., 1991). For this purpose, the male needs a large chela to manipulate the female and a large body size to facilitate enclosing and protecting the female prior to mating. Thus, males must be larger than females to provide the necessary courtship protection and to be able to achieve the mechanics of copulation (Attrill et al., 1991). This requirement correlates well with the different size ranges observed between the sexes and the size at maturity estimated for each sex.

4.2. Length–weight relationship and sex ratio

The allometric pattern found in the Canary Islands population and by Mori (1986) in the relationship between CW and TW seems to be a characteristic of the species. However, males and females do not have equal weight at a given body size, and this may be because the chela weight in males is greater than the weight of the egg mass and of mature ovaries in females (Mori, 1986).

The sex ratio in favour of females found in the present study differed from the observations made by Mori (1986) in the Mediterranean, where the sex ratio was not significantly different from 1:1. However, video footage collected by submersible vehicles around the Azores and in the Mediterranean on coral gardens and deep-sea sponge aggregations recorded higher numbers of females than males (Braga-Henriques et al., 2012; Capezzuto et al., 2012). The ratio found by Mori (1986) may be a result of the limited number of sampled crabs ($n = 137$) and the use of samples from fish markets during a long time period. The samples for this study were collected with traps covering different habitats, and they may thus reflect the true sex ratio of a poorly exploited *P. cuvieri* population. In this work, males dominated the large size classes and, according to Morgan (1980), this may result from sex-specific growth rates or from the reproductive cost of females. Additionally, the higher abundance of females than males may be due to the high percentage of ovigerous females recorded throughout the year, thereby allowing the constant presence of females available for mating.

The limits of the depth distribution of *P. cuvieri*, with the highest population found at 600–700 m, may be explained by the high presence of *C. affinis* inhabiting deeper bottoms, mainly at 600–1000 m. The reduction of the mean size with the increase of depth, with smaller individuals in the deeper areas and larger in shallow ones, may be related to the presence of *C. bellianus* in shallower waters allowing an effective coexistence with this aggressive species. This pattern of reduction of mean size with depth has also been observed in other deep-sea decapod species (Sardà and Cartes, 1993).

4.3. *Spawning season and reproductive pattern*

P. cuvieri from the Canary Islands showed spawning activity all year round, with the highest activity during summer. This high breeding activity in summer may result from higher temperatures. This reproductive cycle is similar to that recorded by Mori (1986) in the Mediterranean, where mature females were also collected throughout the year. The highest presence of ovigerous females detected in summer is consistent with the findings of Lo Bianco (1909) in the Gulf of Naples (March–August), Monod (1956) in the West Africa (March–October), and Zariquiey (1968) in the Iberian Peninsula (March–July, October–November). Mori (1986) found the highest number of females carrying eggs during April and May, a seasonal lag with respect to the Canaries. This may be due to differences in latitude and temperature between the two areas.

The distribution of ovigerous females by size and season in *P. cuvieri* suggests that the spawning season may be size-specific. Large females (>80 mm CW) tend to spawn mainly from summer to winter, whereas smaller females (<80 mm CW) spawn ($>80\%$) in summer. Additionally, the correlation observed between the gonadal maturity stage and the egg mass colour pattern suggests that the growth of the carried eggs and gonadal maturation are asynchronous among individuals. In addition, the presence of females with advanced gonad stage and orange egg mass, as well as with mature gonad stage and brown egg mass, suggests continuous reproduction based on the concurrence of the ovulation and the release of eggs. Further, the very low percentage of large females in the non-ovigerous condition with mature gonads suggests that the time between the release of eggs and a new egg mass is short. Based on this broad reproductive period, Mori (1986) also suggested that *P. cuvieri* is capable of producing more than one brood per season. Two or more broods per season have been suggested for other deep crab species and have been interpreted as a consequence of the food-limited characteristic of the deep-water environment (Erdman and Blake, 1988; Erdman et al., 1991; Pinho et al., 2001a).

Like all *Dromioidea*, females of *P. cuvieri* present characteristics of primitivism in reproduction, having a genital opening in the coxa of the third pereiopod, whereas the spermathecae are paired invaginations of the sternal tegument along the 7–8 sutures (Hartnoll, 1975; Mori, 1986).

In males of *P. cuvieri*, the sperm is not encapsulated in spermatophores but is free in the deferent ducts. However, their maturity may be only physiological, not functional, because their appendages may be too short to manage a precopulatory embrace (Mori, 1986). This is possible only when their chelae have undergone further allometric growth in respect to the body. This phenomenon is known for a great number of the brachyuran species (e.g., Hartnoll, 1974; Chaix, 1979; Abelló and Sardà, 1982).

The frequency distribution of the vulval condition indicates that the size at which 50% of females with open vulvae is very similar (<2 mm CW) to the size at physiological sexual maturity. In almost all cases examined, females of *P. cuvieri* presented evidence of mating on their vulval margins. Abrasion marks around the vulval margins have been considered as signs of copulation in many species of crabs as a result of abrasive activity of male pleopods during mating (Haefner, 1977). A similar pattern was documented by Mori (1986) for *P. cuvieri* in the Mediterranean waters, indicating that both physiological and morphological maturation occur at approximately the same time. The significant differences between the sizes of immature and mature females of *P. cuvieri* allowed the validation of the vulvae condition as a good external indicator of sexual maturity, as it has been considered in many brachyuran crabs (Hartnoll, 1969; Mori, 1986).

4.4. *Estimates of size at first maturity*

Many previous studies have identified discontinuities in the relative growth rate of deep crab body parts, such as abdomen width in females and chela size in males, which have been considered to indicate the morphological size of maturity (Hartnoll, 1974, 1982; Hall et al., 2006). In this work, positive allometry in chela length was observed in males over the entire size range of animals sampled, with a marked increase in relative growth rate after 92 mm CW, whilst females appeared to have a negative relative growth rate of chelae over the entire size-range. The change in the slope in the allometric growth of the chela observed in males of *P. cuvieri* represents the transition from immature to mature crabs. These two stages of development are probably separated by a moult to maturity, which can be reached over a wide range of sizes for distinct individuals. Similarly, Hartnoll (1974, 1982), Clayton (1990) and Claverie and Smith (2009) indicated that the increased relative growth of chelae in males after puberty is common in crabs. The allometric change observed can be controlled by behavioural (Conan and Comeau, 1986; Comeau and Conan, 1992) and/or hormonal changes (Comeau and Conan, 1992; Cormier et al., 1992). In *P. cuvieri*, it coincides with differentiation of primary sexual characteristics (gonads). In many species, the growth of the chela is required by the males to efficiently mate with females as an adaptation to hold the female during the precopulatory embrace (Conan and Comeau, 1986; Comeau and Conan, 1992; Sainte-Marie and Hazel, 1992). Additionally, the greater development of chela in males may be due to the exhibition of aggressive behaviour among males for territory or for mating. In this sense, Braga-Henriques et al. (2012) indicated that this species exhibited an agonistic behaviour, indicated by the elevation of the chelipeds to a medium ventral plane.

Increased relative growth of chelae in males after puberty is common in crabs (Hartnoll, 1974, 1982; Clayton, 1990; Claverie and Smith, 2009), and it can be an evolutionary response to male–male competition for access to mates (Sneddon et al., 1997). Because chelae are used for agonistic interactions in *P. cuvieri* (Braga-Henriques et al., 2012), long chelae confer an advantage during male–male interactions (Sneddon et al., 1997). Negative allometry recorded in female chelae suggests that no intraspecific competition for food or shelter exists in this species (Hartnoll, 1974; Claverie and Smith, 2009).

Positive allometry in abdomen width was found before the 73 mm CW, but with a decrease in relative growth rate after this length. The high change in female abdomen allometry with the carapace width suggests that the morphological size of maturity is well defined in the sampled females. The allometric patterns observed may be interpreted as a redistribution of energy demanded after maturation, leading to variation in growth rate due to different demands between developing organs (Nijhout and Emlen, 1998; Claverie and Smith, 2009). The size range in which relative growth of the fifth abdominal segment changes is clearly associated with the maturation of the vulvae, copulation and insemination, gonad development, and extrusion of eggs. In this sense, females become sexually mature within the size range of 65–75 mm CW. Most females >70 mm CW showed signs of copulation, and their ovaries were in advanced to mature stages of development. Additionally, few females <70 mm CW were ovigerous.

Mature females with broader abdomens are presumably able to carry more eggs (Hartnoll, 1974; Claverie and Smith, 2009). After maturation, energy is needed to produce eggs, and the abdomen may already be wide enough to effectively carry all the eggs produced by the female; consequently, the allometric abdominal growth rate can be slowed for older females.

The size at maturity obtained for *P. cuvieri* suggests that the minimum landing size (MLS) should not be set lower than 92 mm CW. This conservative minimum landing size, equal to or higher than length at functional maturity, would safeguard immature individuals until they reach the size at which they can contribute to the reproductive capacity of the population. In a precautionary approach, Tallack (2007) and Robinson (2008) suggested that the morphometric size at maturity, as an estimation of a functional size at maturity, is recommended as a biological support to establish a legal size.

Considering the newness of this fishery, the absence of landing statistics, and a lack of knowledge pertaining to population biomass, an initial precautionary MLS of 95 mm CW would seem worthy of consideration by regulatory bodies. A fishery regulated on the basis of a MLS of 95 mm CW and a low rate of females in the catches could be sufficient to preserve the reproductive potential of the species. A MLS of 95 mm CW is larger than the size at which females yield the greatest contribution to egg production, and the average size of females caught is below this MLS. However, given that the species is not regulated by means of a catch limit, if a MLS close to the size at morphometric maturity for males is adopted, the exploitation of males might result in a reduction of the number of dominant males able to fertilise females (Sainte-Marie et al., 1997; Orensanz et al., 1998). These circumstances suggest the need to implement additional management measures. Consequently, an examination of the validity of the MLS proposed for the fishery must be reviewed to ensure a management strategy that would avoid the possible future overfishing of the species. Alternative management measures could be implemented, such as the establishment of closed areas to protect the spawning females and/or a catch prohibition on females carrying eggs, which could contribute to preserving the breeding stock prior to extrusion of eggs.

4.5. *Egg development and fecundity*

The pattern of egg development analysed here is very similar to the general embryonic pattern observed in many brachyuran crabs, including an increase in egg size from newly spawned eggs to those just prior to hatching (Arshad et al., 2006; Tuset et al., 2011). Based on Mori (1986), only females of *P. cuvieri* with eggs in the first developmental stage have been considered for the fecundity estimates because it is not possible to consider the egg losses due to parasites during embryonic development. Nemertean predators were observed in all bearing females from the Canaries, with an average presence of 657 specimens per female. The final number of eggs released may be smaller in the Canary Islands when compared with the Mediterranean population; Mori (1986) found only 77% of females infected by parasites, with a lower average presence.

The large eggs recorded for this species may provide the nutritional capacity to migrate from depths of 600 m to surface waters to complete the larval development (Erdman et al., 1991). Clarke (1982) suggested that the large eggs and slow development times that are characteristic of cold-water invertebrates are adaptations to patterns of seasonal food availability. Larvae migrating to surface waters would encounter the onset of warmer temperatures, which would increase the rates of development and metamorphosis (Erdman et al., 1991).

P. cuvieri appears to have continuous reproduction throughout the year (Mori, 1986). Off the Canary Islands, females carrying eggs probably move to deeper waters to avoid the presence of other crab species such as *C. bellianus*, which exhibits an aggressive behaviour pattern.

This work found that *P. cuvieri* fecundity increases with the increase of size or wet weight of individuals, as reported for other brachyurans (Melville-Smith, 1987; Erdman and Blake, 1988; Hines, 1988; Arshad et al., 2006; Tuset et al., 2011). However, in deep-sea crabs, it has been noted that carapace width and wet weight are not good predictors of fecundity, due to the variability in the number of eggs lost during incubation, diseases, predation, or other types of natural failure of egg development (Perkins, 1971). This high variability suggests that females carry eggs for a long time during the incubation period (Haefner, 1977; Erdman et al., 1991; Tuset et al., 2011). The examination of females with eggs in different stages of development could influence the fecundity estimates, and a further study on the relationship between level of parasite infestation and eggs lost would provide a better estimation of fecundity.

The fecundity estimate from the present work (285,050–361,690 eggs; 75–96 mm CW) is similar to that estimated by Mori (1986) for the same species (163,000–376,000 eggs; 80–101 mm CW). Additionally, the estimate obtained is similar to those found for other deep-sea crabs, including *Chaceon maritae* (107,000–350,000 eggs; 70–114 mm CW) (Melville-Smith, 1987), *Chaceon quinquedens* (36,000–226,000 eggs; 90–118 mm CW) (Hines, 1988), *C. bellianus* (299,100–670,500 eggs; 140–181 mm CW) (Quiles et al., 2001) or *C. affinis* (199,690–566,956 eggs; 105–160 mm CW) (Tuset et al., 2011), all of which show a positive correlation between female size and number of eggs. According to these data, *P. cuvieri* may be less susceptible to overfishing than *C. affinis* and *C. bellianus*, which are captured together with *P. cuvieri*, because *P. cuvieri* has a higher fecundity than these other crabs. Further, considering that *P. cuvieri* is captured only with baited traps, control of gear selectivity, using escape vents to avoid capture of individuals under 95 mm CW, could be a more suitable option to protect reproductive potential for the species (Tallack, 2007). Although crabs under 95 mm CW can be discarded alive and intact, trap escape vents are a better option considering the depths involved and the fact that crabs may be preyed upon on their way back to the seabed. Tallack (2007) noted that if a discarded deep-sea crab returns uninjured to the seabed, it is likely to be displaced horizontally and may land on an unfavourable substratum.

4.6. *Epizoites and moult*

Exoskeletons of *P. cuvieri* that have not recently moulted are blackened or discoloured in abraded or damaged areas, and they are usually infested with lepadid barnacles. The association of lepadids and discolouration serves as an indicator of the time lapse since the last moult, although the exact length of time cannot presently be determined (Haefner, 1977).

Mori and Manconi (1990) carried out a study on the macroepizoites associated with *P. cuvieri* from the Mediterranean Sea. These authors included a list of the macroepizoites separated per stage of maturity in both pre- and post-puberty *P. cuvieri*. This list includes mainly polychaetes and actinians but also the thoracic cirripedia *Scalpellum scalpellum* (Linnaeus, 1767) and *Verruca stroemia* (O.F. Müller, 1776). The authors concluded that different settlements according to the stage of maturity of the crabs are probably due to both the stability of the exoskeleton over time, affecting the settlement, and to the body surface; in the case of crustaceans, this stability is related to the moult frequency. Before reaching sexual maturity, pre-puberty individuals must in fact undergo several moults, making their exoskeletons unstable substrata that can be colonised only by rapidly growing species, such as several polychaete species (*Nicolea* and *Hydroides*). The presence of a richer and more diversified epizoitic assemblage on post-puberty males and females implies that their exoskeletons provide a more stable substratum (80% of the total epizoites were found on post-puberty males), indicating greater stability and a lower moulting frequency. Only 60% of the epizoites were found on the females. This difference with respect to the males at the same stage, could, however, be connected with the larger size of the males. It is therefore possible that, even for the females, post-puberty moults are very infrequent.

The recent occurrence of a moult can be detected by a still-soft exoskeleton lacking external marks, abrasions or epifauna. The number of *P. cuvieri* showing evidence of a recent moult was low ($n=7$), and these only occurred in October and November. Males (75, 93, 93, 127 and 148 mm CW) and females (96 and 109 mm CW) in ecdysis spanned a wide size range, including large individuals. Mori (1986) suggested that in males, as in females, the puberty moult may coincide with the final moult because none of the post-puberty males or females collected were observed in ecdysis. Mori (1986) only observed two males (63 and 73 mm CW) in a post-moulting stage and two other pre-puberty (93 and 101 mm CW) males in pro-ecdysis. Similarly, three basic formats for brachyuran growth were listed by Hartnoll (1982): indeterminate growth with no terminal ecdysis, determinate growth with maturity occurring before the final instar, and determinate growth with maturity delayed until the final instar. Obviously, the best confirmation of the growth pattern in a species is by observation of moulting (Attrill et al., 1991), or lack of it, in living specimens, which was not possible in *P. cuvieri*. However, several features of the samples of *P. cuvieri* offer clues to the nature of its growth pattern. The presence of a normal size distribution of males and females with a tail of surviving and still moulting larger individuals could indicate a population with indeterminate growth (Attrill et al., 1991). However, this supposition must be confirmed by further studies.

Related with the integument condition, Wenner et al. (1987) indicated that the presence of blackened abraded areas on the exoskeletons can be attributed to damage caused by chitinolytic bacteria. Similar marks were noted on all size-ranges of *P. cuvieri*, and in several cases the damage was quite severe. However, large specimens have also been recorded with partial soft carapaces and without marks or epibionts, not supporting the existence of terminal moult.

Several studies in the literature have reported the presence of poecilasmatids on deep-sea crabs in the Macaronesian archipelagos (the Azores, Madeira and the Canaries): *P. aurantia* on *C. affinis* (Wirtz et al., 2006) and on *P. cuvieri* (Darwin, 1851); and *P. crassa* on *C. affinis* (Southward, 1998) and on *P. cuvieri* (Darwin, 1851). As far as we know, this is the first record of *H. microstoma* as an epizoite on crustaceans.

Given that *P. aurantia* was often found to be the only epizoite on *P. cuvieri*, while *P. crassa* was always observed in combination with the former barnacle species, it can be concluded that *P. aurantia* is the first epizoite to colonise the exoskeleton of *P. cuvieri*. Furthermore, there is a remarkable relationship between the number of individuals of *P. aurantia* (i.e., the colonisation degree) and the age of the carapace of the *P. cuvieri*. Therefore, the sequential presence of *P. crassa*, once the carapace and limbs are covered with *P. aurantia*, may indicate a stage approaching carapace moulting. We observed a similar process in the deep-sea crab *C. affinis*. However, two *P. cuvieri* have been recorded recently (one male and one ovigerous female) from off the Cape Verde Islands bearing some individuals of *P. crassa* on the maxillipeds, the fleshy base of the legs, and the copulatory pleopods.

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New and rare records of teleost fishes from the Cape Verde Islands (eastern-central Atlantic Ocean)

by

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Abstract. – As a result of six exploratory surveys and several opportunistic catches in the Cape Verde Islands from a few metres to about 1000 m of depth, a list of 66 species of teleost fishes is given, six of which are first records from the archipelago: *Gnathophis mystax* (Congridae), *Nezumia africana*, *Nezumia duodecim* (Macrouridae), *Ectreposebastes imus* (Scorpaenidae), *Paraliparis* sp. (Liparidae) and *Lappanella fasciata* (Labridae). Additionally, data on six poorly-known species is also given: *Myroconger compressus* (Myrocongridae), *Myrichthys pardalis*, *Phaenomonas longissima* (Ophichthidae), *Sphagemacrurus hirundo* (Macrouridae), *Gadella imberbis* and *Physiculus cyanostrophus* (Moridae). Data includes distribution, habitat, morphometry and reproduction.

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Résumé. – Nouveaux ou rares signalements de poissons téléostéens des îles du Cap-Vert (océan Atlantique centre-oriental).

Six campagnes exploratoires ainsi que quelques captures opportunistes réalisées de quelques mètres jusqu'à environ 1000 m de profondeur aux îles du Cap-Vert ont permis d'établir une liste comprenant 66 espèces de poissons téléostéens. Six espèces sont signalées pour la première fois aux îles du Cap-Vert : *Gnathophis mystax* (Congridae), *Nezumia africana*, *Nezumia duodecim* (Macrouridae), *Ectreposebastes imus* (Scorpaenidae), *Paraliparis* sp. (Liparidae) et *Lappanella fasciata* (Labridae). La présence de six autres espèces mal connues est confirmée pour cet archipel : *Myroconger compressus* (Myrocongridae), *Myrichthys pardalis*, *Phaenomonas longissima* (Ophichthidae), *Sphagemacrurus hirundo* (Macrouridae), *Gadella imberbis* et *Physiculus cyanostrophus* (Moridae). Les données présentées concernent la distribution, l'habitat, la morphométrie et la reproduction.

Key words
Teleostei
Eastern Atlantic
Cape Verde Islands
Fish traps
New records

The first specific account on the Cape Verde Islands' ichthyology was done by Osório (1911), who summarized previous records and gave a list of 48 species deposited in the collections of Museu Bocage (Lisbon). Subsequent accounts and notes based either on field work or bibliographic research were published by Cadenat (1951), Franca and Vasconcelos (1962), Cadenat and Roux (1964), Hartog (1984), Edwards (1986), Hensley (1986), Wirtz and Bath (1989), Bath (1990a, b), Reiner (1996, 2005), Brito *et al*. (1999, 2007), Matallanas and Brito (1999), Munroe *et al*. (2000), Brito and Miller (2001), González *et al*. (2004, 2010), Menezes *et al*. (2004), Monteiro (2008), González and Tariche (2009), Wirtz (2009), Almeida *et al*. (2010), Pereira *et al*. (2012) and Wirtz *et al*. (2013).

In a broader geographic scale, studies by Fowler (1936), Quéro *et al*. (1990) and Lloris *et al*. (1991) also include species from the Cape Verde Islands.

According to the above mentioned contributions and considering that the knowledge on the marine biodiversity of Cape Verde is still incomplete, in particular in the deep-sea, and some records need confirmation (see Brito *et al*., 2007; González and Tariche, 2009; González *et al*., 2010), the list of fish species from the archipelago can attain ca. 520 species (ca. 320 of which are deep-sea living species).

Following six exploratory surveys off the Cape Verde Islands, a list of new records and data on little known teleost fishes is given herein. Data on distribution, morphometry and reproduction of the species studied are presented. Sev-

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eral contributions to the knowledge of the ichthyology of the Cape Verde Islands were already published based on these collections: González *et al*. (2004) (the first record of *Myroconger compressus*, *Platyberyx opalescens* and *Pagrus africanus*), González *et al*. (2010) (the family Moridae from the Cape Verdes with first record of *Physiculus cyanostrophus*) and Almeida *et al*. (2010) (first record of *Synaphobranchus affinis*).

MATERIAL AND METHODS

Six exploratory fish-trapping surveys of the bottom fauna of the Cape Verde Islands were carried out off the islands of Boa Vista, Santiago, including the Bancona Bank, São Vicente, Santa Luzia, Sal, and São Nicolau, between 2003 and 2012, at depths down to 1000 m (Fig. 1). Fishing operations during the first two cruises (2003 and 2005) covered a depth range between 435 m and 1060 m, in order to search for new living resources off the islands of Boa Vista, which is characterised by a sediment-covered broad shelf and slope, and Santiago, with a narrow shelf and slope dominated by hard substrata. The remaining cruises (2010-2012) were mainly directed to the exploration and stock assessment of the striped soldier shrimp (*Plesionika edwardsii*) between 66 m and 458 m depth and covered four additional islands (Tab. I).

In all cruises bottom traps (BT) and semifloating shrimp traps (SFST, operated around 2.4 m above the seafloor) (González *et al*., 1992, 2004) were used as fishing gear. On average, all traps were deployed for 16-18 h. Atlantic chub mackerel (*Scomber colias*) (Scombridae) was used as bait during the first two cruises and mackerel scad (*Decapterus macarellus*) (Carangidae) in the remaining ones (Tab. I).

Several opportunistic catches using bottom traps, pole-and-line or hand net, while ships were anchored, provided additional interesting specimens.

The present work follows the best practice approach to overcome unverified and unverifiable "first records" as proposed by Bello *et al*. (2014).

Voucher specimens were deposited in the collections of the Museu de História Natural do Funchal (MMF), the Museo de Ciencias Naturales de Tenerife (TFMC), The Natural History Museum (BMNH) and the Muséum national

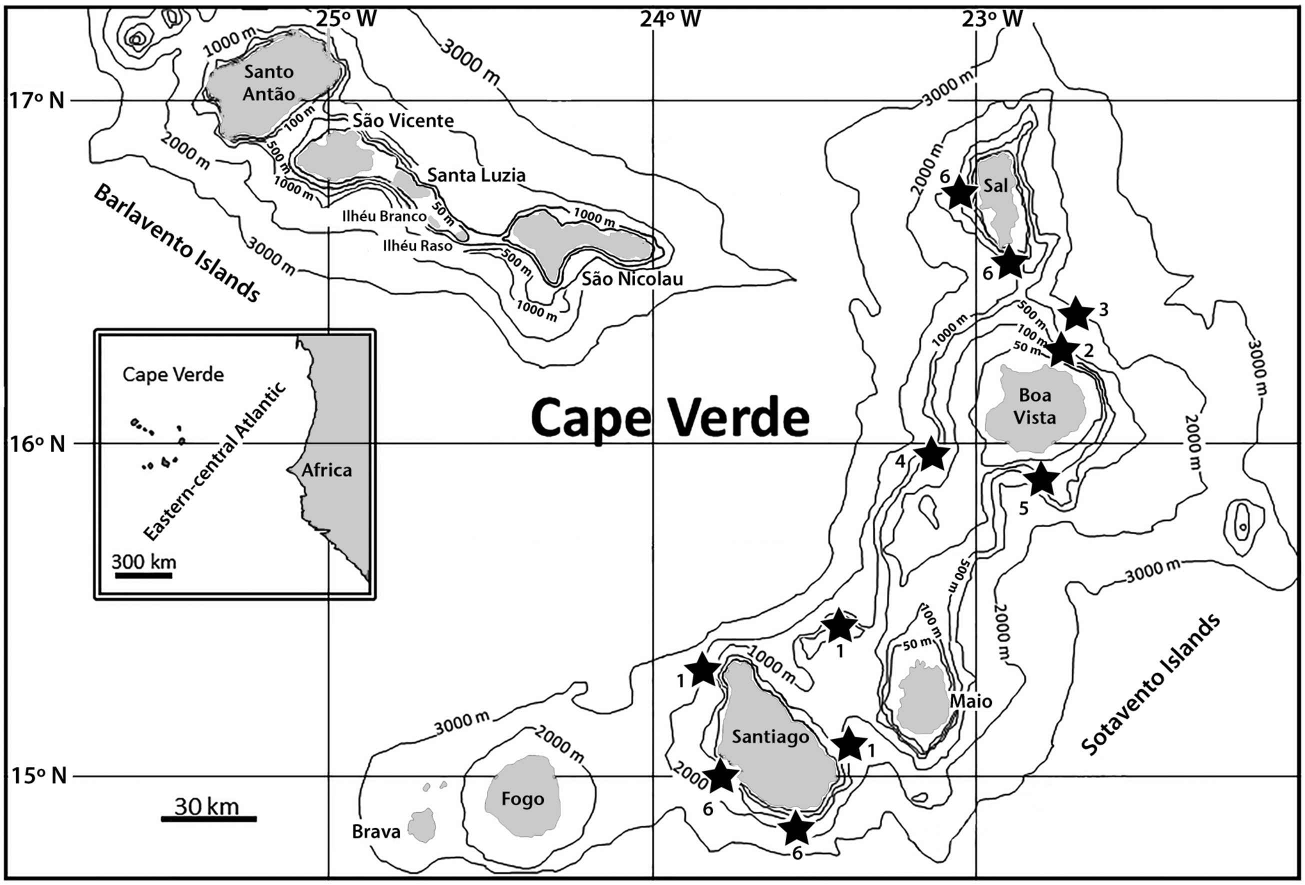

Figure 1. - Collection locations for the first records of teleost fishes from the Cape Verde Islands: (★) 1: *Gnathophis mystax*; 2: *Nezumia africana*; 3: *Nezumia duodecim*; 4: *Ectreposebastes imus*; 5: *Paraliparis* sp.; 6: *Lappanella fasciata*.

Table I. - List of cruises, locations, gear used and depth of sampling, from which specimens were obtained (BT: bottom traps; SFST: semi-floating shrimp traps).

Project	Cruise	Research vessel	Islands	Dates	Collecting gear	Depth interval (m)
HYDROCARPO	Taliarte 2003-08	Taliarte	Boa Vista, Santiago	Aug. 10-23, 2003	BT	435-975
HYDROCARPO	Cabo Verde 2005-06	Pixape II	Boa Vista, Santiago	Jun. 4-16, 2005	BT, SFST	447-1060
PROACTIVA	Cabo Verde 2010-04	Prof. I. Lozano	S.Vicente, Sta. Luzia	Apr. 12-30, 2010	BT, SFST	81-425
MARPROF-CV	Camarão-1	Prof. I. Lozano	Santiago	Nov. 17-30, 2011	BT, SFST	66-364
MARPROF-CV	Camarão-2	Prof. I. Lozano	Boa Vista	Mar. 3-15, 2012	BT, SFST	94-289
MARPROF-CV	Camarão-3	Prof. I. Lozano	Sal, S.Nicolau	Jul. 10-25, 2012	BT, SFST	74-458

d'Histoire naturelle (MNHN). Muscle tissue samples taken from each specimen were stored at ICCM (Iniciativa de Colecciones de Ciencias Marinas) from the University of Las Palmas de Gran Canaria. Additional unpreserved material was included in the present account whenever relevant for species' depth range or biological information.

Meristic and morphometric measurements (in mm) were made following Hubbs and Lagler (1958). SL: standard length; TL: total length; PAL: pre-anal length; PDL: pre-dorsal length; HL: head length. Institutional abbreviations follow Sabaj Pérez (2014). Taxonomical arrangement follows Nelson (2006) and taxonomy used according to Froese and Pauly (2014) and Eschmeyer (2014).

RESULTS AND DISCUSSION

The list of the species collected is given in table II, with indication of depth interval, collection gear and island where specimens were caught. Of the 66 species of teleost fishes collected, six are recorded for the first time from the Cape Verde Islands, data on six poorly-known species is also given, and the presence of three species is now confirmed in waters of this archipelago. These 17 species are detailed as follows:

Myroconger compressus **Günther, 1870**

Material examined. - MMF41909, 606 mm TL, MMF41910, 526 mm TL, MMF41911, 390 mm TL, 16º15'N 23º05'W, Baía de Sal Rei, Boa Vista Island, 215 m, cruise Cabo Verde 2005-06, sta. 22, 5 Jun. 2005, SFST.

Additional material. - 171 specimens, 303-620 mm TL, caught between 104 and 905 m depth, from off São Vicente, Santa Luzia, Boa Vista, Santiago and Sal islands.

Remarks. - A tropical demersal species occurring in a few scattered localities of the eastern Atlantic: from St. Helena, and Dakar, Senegal (Smith, 1990), São Tomé and Príncipe (Smith, 1990; Afonso *et al*., 1999), the Cape Verde Islands (Brito *et al*., 1999; González *et al*., 2004; Menezes *et al*., 2004; González and Tariche, 2009), and the Vavilov Underwater Ridge (the eastern part of the Atlantic Ocean) (Parin *et al*., 2010). The present material was caught in both traps used (Tab. II). Their major presence in bottom traps (81%) confirms its demersal nature. Gonad examination revealed that the red eel is a gonochoristic species. The 620 mm TL specimen is apparently the largest ever recorded (538 mm TL: Smith, 1990).

Echelus pachyrhynchus **(Vaillant, 1888)**

Material examined. - TFMCVP/01581, 410 mm TL, 16º09'N 23º06'W, Ponta do Sol, Boa Vista Island, 295-299 m, cruise Cabo Verde 2005-06, sta. 1/3, soft bottom, 5 Jun. 2005, BT; MMF36366, 465 mm TL, 15º56'N 22º42'W, Ponta Medronha, Boa Vista Island, 210 m, cruise Cabo Verde 2005-06, sta. 73, soft bottom, 9 Jun. 2005, SFST; TFMCVP/01582, 465 mm TL, 15º52'N 22º46'W, S of Ponta do Roque, Boa Vista Island, 240 m, cruise Cabo Verde 2005-06, sta. 90, soft bottom, 10 Jun. 2005, SFST.

Additional material. - 10 specimens, 407-513 mm TL, caught on soft bottoms, with certainty between 175 m and 460 m depth, from off São Vicente, Boa Vista and Santiago islands, cruises Cabo Verde 2005-06 and Cabo Verde 2010-04.

Remarks. - A deep-water bathydemersal species burrowing in sand or mud on the upper-slope at a 200-500 m depth range (Leiby, 1990; Froese and Pauly, 2014). Known from the eastern Atlantic, from Morocco to Angola and central Namibia (Bianchi *et al*., 1993; Froese and Pauly, 2014), including the Cape Verde Islands (Leiby, 1990; Reiner, 1996, 2005; Froese and Pauly, 2014). Although the present material was caught in both traps, 76% occurred in bottom traps, therefore confirming its demersal nature. The 513 mm TL specimen is apparently the largest of this species ever recorded (485 mm TL: Leiby, 1990).

Myrichthys pardalis **(Valenciennes, 1839)**

Material examined. - MMF43114, 390 mm TL, 16º35'N 22º54'W, Baía de Santa Maria, Sal Island, cruise Cabo Verde 2005-06, caught at surface over a substrate of sand and pebbles with green (*Avrainvillea* sp.) and red algae and rhodoliths at 13 m depth, 21 Jul. 2012, hand net.

Additional material. - Another specimen was caught at 15º26'N 23º27'W, Bancona Bank, NE of Santiago Island,

Table II. - Systematic list of the species collected, with depth of capture, number of individuals caught, collecting gear and location. First records in bold. SV: São Vicente, SZ: Santa Luzia, BV: Boa Vista, ST: Santiago, SL: Sal, and SN: São Nicolau; * incidental collection; 0: no catches, –: collecting gear not operated at this depth in this island.

			Total	Collecting gear			Islands					
Order / Family	Species	Depth of capture (m)		BT	SFST	Other	SV	SZ	BV	ST	SL	SN
Anguilliformes												
Myrocongridae	*Myroconger compressus*	104-925	174	142	32		8	2	23	130	11	
Muraenidae	*Gymnothorax maderensis*	149-250	10	0	10		7					3
	Gymnothorax polygonius	88-220	103	29	74		11	7	7		16	62
	Gymnothorax vicinus	41-96	6	6	0				3	2	1	
	Muraena helena	83-300	256	72	184		39	8	9	41	154	5
	Muraena robusta	47	1	1	0				1			
Synaphobranchidae	*Synaphobranchus affinis*	191-1060	427	279	148		1		117	307		2
Ophichthidae	*Echelus myrus*	118-339	27	8	19				18	9		
	Echelus pachyrhynchus	175-460	13	10	3		1		8	4		
	Myrichthys pardalis	0	2			2				1	1	
	Phaenomonas longissima	0	1			1			1			
Colocongridae	*Coloconger cadenati*	260-900	273	226	47				179	92		2
Congridae	*Conger conger*	66-344	63	38	25		3	5	7	36	9	3
	Gnathophis mystax	110-289	7	7	0					7		
Stomiiformes												
Gnostomatidae	*Cyclothone microdon*	300-500	1	1*	-				1			
Stomiidae	*Stomias affinis*	500-700	2	2*	-				2			
Aulopiformes												
Synodontidae	*Synodus synodus*	140-150	1	1	0					1		
Polymixiiformes												
Polymixiidae	*Polymixia nobilis*	66-289	8	8	0					7	1	
Gadiformes												
Macrouridae	*Hymenocephalus italicus*	300-500	1	1	-				1			
	Nezumia aequalis	500-700	1	1	-				1			
	Nezumia africana	191-198	1	1	-				1			
	Nezumia duodecim	831-1023	2	2	-				2			
	Sphagemacrurus hirundo	268-292	1	1	0					1		
Moridae	*Gadella imberbis*	192-400	3	1	2				1	2		
	Laemonema laureysi	305-745	58	57	1				38	18		2
	Physiculus cyanostrophus	90-339	459	12	447		31	62	14	315	22	15
	Physiculus spp.	104-506	80	5	75			5	25	44	6	
Phycidae	*Phycis phycis*	50-700	20	19	1				16	1	2	1
Beryciformes												
Trachichthyidae	*Gephyroberyx darwinii*	126-450	3	3	0				1	1	1	
Holocentridae	*Sargocentrum hastatum*	74-96	1	1	0						1	
Gasterosteiformes												
Syngnathidae	*Hippocampus algiricus*	175-274	1	1	-				1			
Aulostomidae	*Aulostomus strigosus*	104-131	4	1	3			4				
Scorpaeniformes												
Scorpaenidae	***Ectreposebastes imus***	651-670	1	1	-				1			
	Helicolenus dactylopterus	175-659	37	34	3				8	27	2	
	Neomerinthe folgori	110-378	13	7	6		3		1	9		
	Pontinus kuhlii	89-360	352	117	235		41	3	17	178	98	15
	Scorpaena elongata	106-270	15	15	0					1	13	1
	Scorpaena laevis	25	1			1						1

Table I. - Continued.

			Total	Collecting gear			Islands					
Order / Family	Species	Depth of capture (m)		BT	SFST	Other	SV	SZ	BV	ST	SL	SN
Liparidae	***Paraliparis* sp.**	502-592	1	1	-				1			
Perciformes												
Serranidae	*Anthias anthias*	104-225	7	3	4		1			5	1	
	Cephalopholis taeniops	104-121	1	1	0					1		
	Epinephelus goreensis	113-180	2	1	1			1			1	
	Rypticus saponaceus	66-74	1	1	0					1		
	Serranus atricauda	66-180	41	3	38		4	11		9	17	
Carangidae	*Seriola fasciata*	132-148	1	0	1		1					
Caristiidae	*Platyberyx opalescens*	776-800	1	1	-				1			
Lutjanidae	*Lutjanus goreensis*	51-60	5			5			5			
Haemulidae	*Parapristipoma humile*	70-135	20	5	15		2	3			6	9
	Pomadasys perotaei	11-55	5	1	-	4			4	1		
Sparidae	*Boops boops*	100-230	2	2	0				2			
	Dentex macrophthalmus	89-592	1081	146	935		25	4	1027		25	
	Pagellus acarne	67-335	2210	1252	958		591	117	1477	20	5	
	Pagrus africanus	100	2	2	-				2			
	Spondyliosoma cantharus	90-187	1	1	0						1	
Mullidae	*Pseudupeneus prayensis*	74-96	1	1	0						1	
Labridae	*Acantholabrus palloni*	74-302	13	0	13		4	1		6	2	
	Bodianus scrofa	104-131	6	1	5		2	1		1	2	
	Lappanella fasciata	102-125	7	0	7					4	3	
Trachinidae	*Trachinus* sp.	122-137	1	1	0				1			
Blenniidae	*Ophioblennius atlanticus*	112-220	2	2*	0					2		
Gempylidae	*Promethichthys prometheus*	125-197	6	0	6		2	1	2		1	
Caproidae	*Antigonia capros*	96-234	12	0	12		8		4			
	Capros aper	113-182	3	1	2				3			
Tetraodontiformes												
Tetraodontidae	*Sphoeroides marmoratus*	74-96	2	2	0						2	
	Sphoeroides pachygaster	66-255	309	51	258		76	91	113	13	15	1

cruise Taliarte 2003-08, caught at surface over a hard substrate at 35-40 m depth, 17 Aug. 2003, hand net.

Remarks. - A tropical demersal eastern Atlantic species found burrowing in coarse sand along rocky coasts. Known from the Canary Islands and Western Sahara (Leiby, 1990), the Cape Verdes (Franca and Vasconcelos, 1962; Blache and Cadenat, 1971; Brito *et al*., 1999) and São Tomé Island (Afonso *et al*., 1999) to Annobon Island, Equatorial Guinea (Leiby, 1990). Information on its bathymetric distribution is scarce. In the Canaries it has been found between 3 and 15 m (Brito *et al*., 2002), and recently between 1 and 25 m (in sea grass meadows) (Espino *et al*., 2007; Arturo Boyra, pers. com. 2014). Our specimens were caught while actively swimming at surface at night, over 13 to 35 m depth, probably due to the large number of small organisms concentrated around the vessel, attracted by its bright lights.

***Phaenomonas longissima* (Cadenat & Marchal, 1963)**

Material examined. - MMF42806, 430 mm TL, 10 mm PDL, 16º09'N 22º55'W, Baía do Sal Rei, Boa Vista Island, at surface over a substrate of sands and stones at 20 m depth, cruise Camarão-2, 14 Mar. 2012, hand net.

Remarks. - This tropical benthic species was first recorded from the Cape Verdes by Cadenat and Roux (1964) as *Sphagebranchus foresti*. The specimen was X-rayed and vertebral count was 205. In the Atlantic Ocean it is known from Senegal and Ghana and from the islands of Cape Verde, Ascension and St. Helena; also from Brazil (Froese and Pauly, 2014). Found from tide pools down to 60 m depth, sometimes burrowing in sand or mud (McCosker *et al*., 1989; Leiby, 1990). Our finding seems to be the first collection of this species swimming freely at surface.

***Gnathophis mystax* (Delaroche, 1809)** (Fig. 2A)

Material examined. - MMF39446, 365 mm TL, MMF43111, 380 mm TL, MMF43112, 315+ mm TL, 15º26'N 23º26'W, Bancona Bank, NE of Santiago Island, 110-172 m, cruise Cabo Verde 2005-06, sta. 152/154, rocky bottom, 13 Jun. 2005, BT; MMF43113, 395 mm TL, 15º16'N 23º46'W, Tarrafal, Santiago Island, 155-175 m, cruise Camarão-1, sta. 2, rocky bottom, 18 Nov. 2011, BT.

Additional material. - Three specimens, cruise Cabo Verde 2005-06: 315+ and 380 mm TL, 15º26'N 23º26'W, Bancona Bank, NE of Santiago Island, 110-172 m, sta. 152/154, rocky bottom, 13 Jun. 2005, BT; 390 mm TL, a ripe female, 15º04'N 23º27'W, Ponta da Achada da Baleia, Santiago Island, 275-289 m, sta. 232/234, soft bottom, 16 Jun. 2005, BT.

Remarks. - A subtropical demersal species found on muddy or sandy bottoms of the shelf and continental slope between 80 m and 800 m depth. Known in the eastern Atlantic from southern Portugal to Morocco and the Canary Islands (Brito *et al*., 2002), including the Mediterranean (Bauchot and Saldanha, 1986; Bauchot, 1987; Froese and Pauly, 2014). The voucher specimen MMF39446 has 33 lateral line pores anterior to anus. Our material was caught on both rocky and soft bottoms between 110 and 289 m depth. This is the first record for this species from the Cape Verde Islands and the southernmost in the Atlantic Ocean. The finding of a ripe female proves the presence of a viable population.

***Nezumia africana* (Iwamoto, 1970)** (Fig. 2B)

Material examined. - MMF43121, 65.2 mm PAL, 41.2 mm HL, 16º17'N 22º46'W, E of Ponta Antónia, Boa Vista Island, 191-198 m, cruise Cabo Verde 2005-06, sta. 35/37, 7 Jun. 2005, BT.

Remarks. - A tropical benthopelagic species occurring along the slope down to 732 m depth. Previously known only from the Gulf of Guinea in the eastern-central Atlantic (Cohen *et al*., 1990; Geistdoerfer, 1990; Froese and Pauly, 2014), it is recorded for the first time from the Cape Verde Islands, which fixes the northernmost limit of its distribution.

***Nezumia duodecim* (Iwamoto, 1970)** (Fig. 2C)

Material examined. - MMF39286, 72.8 mm PAL, MMF39287, 62.9 mm PAL, 16º18'N 22º44'W, E of Ponta Antónia, Boa Vista Island, 831-1023 m, cruise Cabo Verde 2005-06, sta. 48, 7 Jun. 2005, BT.

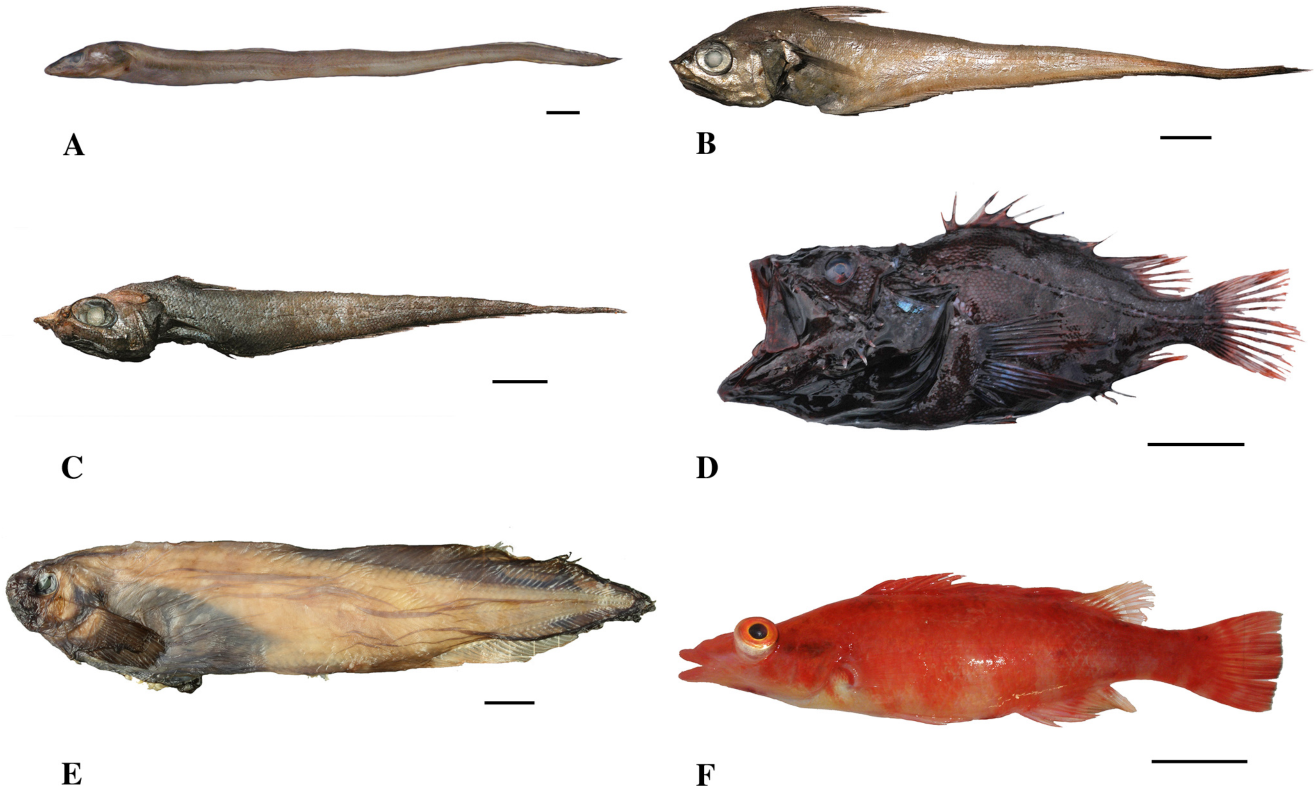

Figure 2. - First records of teleost fishes from the Cape Verde Islands. **A**: *Gnathophis mystax*, SL 365 mm, MMF39446; **B**: *Nezumia africana*, PAL 65.2 mm, MMF43121; **C**: *Nezumia duodecim*, PAL 72.8 mm, MMF39286; **D**: *Ectreposebastes imus*, SL 91 mm, MMF48816; **E**: *Paraliparis* sp., SL 251 mm, TFMC-VP/01377; **F**: *Lappanella fasciata*, SL 140 mm, MMF42284. Scale bars = 20 mm.

Remarks. - A benthopelagic deep-water species found between 329 and 1261 m depth. Known only from the eastern Atlantic, from Mauritania (24ºN) to Angola (Cohen *et al*., 1990). Apparently found deeper in the northern part of its range (Merrett and Marshall, 1981). This is the first record of this species from the Cape Verde Islands.

***Sphagemacrurus hirundo* (Collett, 1896)**

Material examined. - MMF42815, partially damaged, 180 mm PDL, 160 mm HL, 15º08'N 23º47'W, Ribeira da Barca, Santiago Island, 268-292, cruise Camarão-1, sta. 8-D2, rocky bottom, 27 Nov 2011, BT.

Remarks. - A benthopelagic deep-water species found between 873 m and 2330 m depth (Merrett and Domanski, 1985; Geistdoerfer, 1990). An eastern Atlantic species mostly known from insular areas and adjacent seamounts: the Azores (Collett, 1896, holotype), Madeira (Geistdoerfer, 1986), the Canaries (Merrett and Domanski, 1985) and the Cape Verde Islands (Maio Island) (Roule, 1919). Also present in the Bay of Cadiz (Nybelin, 1948). This is the southernmost record for the species.

***Gadella imberbis* (Vaillant, 1888)**

Material examined. - MMF42808, 229 mm TL, 209 mm SL, 15º01'N 23º44'W, Ponta Covinha, Santiago Island, 260-270 m, cruise Camarão-1, sta. 10, rocky bottom, 21 Nov. 2011, SFST; MMF42809, 230 mm TL, 207 mm SL, 15º55'N 22º53'W, E of Ponta Taráfe, Boa Vista island, 192-236 m, cruise Camarão-2, sta. 18, rocky bottom,14 Mar. 2012, SFST.

Remarks. - This species was recorded for the first time from Cape Verde by Vaillant (1888) (as *Brosmiculus imberbis*) and collected again by González *et al*. (2010). The present material is the third record of this species from the Cape Verde Islands and the northernmost limit (Boa Vista island) for *G. imberbis* in the eastern Atlantic.

***Physiculus cyanostrophus* Anderson & Tweddle, 2002**

Material examined. - MMF42538, 326 mm TL, 295 mm SL, 195-220 m, st. 170, MMF42539, 246 mm TL, 221 mm SL, 174-175 m, sta. 186, rocky bottom, both from Baía do Tarrafal, Santiago Island, approx. at 15°14'N 23°45'W, cruise Cabo Verde 2005-06, 14 Jun. 2005, NB.

Additional material. - A total of 459 specimens of this species were caught and are being used for a biology study by one of the authors (RTP).

Remarks. - Specimens were collected seasonally between 2010 and 2012, off all the islands surveyed, between 90 m and 339 m depth. Since 97.4% of the catches (447 specimens) were made with SFST, this species is confirmed as benthopelagic. Furthermore it is a more abundant species than suspected before by González *et al*. (2010), due to the fact that those authors have used mostly BT. Up to the present, this species seems to be geographically restricted to Angola (Anderson and Tweddle, 2002) and the Cape Verde Islands (González *et al*., 2010). Due to its relative abundance, size, and flesh quality, it will eventually be a species of some commercial interest and caught, as a by-catch, in the trap fishery for striped soldier shrimp *Plesionika edwardsii* (Brandt, 1851) around the Cape Verde Islands.

***Physiculus* spp.**

Material examined. - MMF39704, 254 mm TL, 232 mm SL, Boa Vista Island, off Ponta do Sol, 16°19'N-23°03'W, 420-506 m, cruise Cabo Verde 2005-06, sta. 5/7, bottom trap, 5 Jun. 2005, BMNH 2013.5.10.1, 226 mm TL, 207 mm SL, same locality and capture data as holotype; MNHN 2013-0648, 230 mm TL, 212 mm SL, same locality and capture data as MMF39704 and MMF42536, 159 mm TL, 144 mm SL, MMF42537, 187 mm TL, 172 mm SL, 15°14'N-23°34'W, Cidade Velha, Santiago Island, 108-111 m, cruise Camarão-1, sta. 14-D4, rocky bottom, 25 Nov. 2011, SFST.

Remarks. - The material examined has revealed at least two different species, eventually new to science, and are therefore being under study.

***Hippocampus algiricus* Kaup, 1856**

Material examined. - TFMC-VP/01858, 73.6 mm SL, 15.7 mm HL, 15º02'N-23º45'W, Ponta Covinha, Santiago Island, 175-274 m, cruise Cabo Verde 2005-06, sta. 200/202, 15 Jun. 2005, BT.

Remarks. - A tropical benthic eastern-central Atlantic species found from Senegal to Angola, including São Tomé and Príncipe Islands (Lourie *et al*., 1999; Froese and Pauly, 2014). According to Wirtz *et al*. (2013), this species was previously recorded from the Cape Verdes by Reiner (1996, 2005) and Brito *et al*. (1999) as *H. punctulatus*, and by González and Tariche (2009) as *H. hippocampus*. It inhabits shallow inshore waters (Reiner, 1996, 2005). The present material was caught at between 175 m and 274 m depth, which enlarges considerably its vertical distribution in more than 150 m. The specimen examined has 19 dorsal rays, 13 pectoral rays, and 12+35 rings. The presence of this species is confirmed in waters of this archipelago.

***Ectreposebastes imus* Garman, 1899** (Fig. 2D)

Material examined. - MMF48816, 110 mm TL, 91 mm SL, 15º58'N 23º06'W, Ponta Varandinha, Boa Vista Island, 651-670 m, cruise Cabo Verde 2005-06, sta. 128, 12 Jun. 2005, BT.

Remarks. - A circumtropical mid- to deepwater species found above the upper slope and deep continental shelf and in the vicinity of oceanic islands, at a 150 m to 2000 m depth, usually at 500-850 m (Bianchi *et al*., 1999; Poss and Eschmeyer, 2002; Froese and Pauly, 2014). It occurs in tropical, subtropical and temperate seas of the Indian, Pacific, western and eastern Atlantic oceans. In tropical West Africa it can be found from Sierra Leone to Cameroon, including the Gulf of Guinea (Eschmeyer and Collette, 1966; Eschmeyer, 1969; Froese and Pauly, 2014). It has recently been recorded for the first time off the Canary Islands, at a 800 m to over 1500 m depth, which extends the northern limit of its distribution in the Atlantic Ocean (Escánez and Brito, 2011). The present material being caught on BT, may indicate that this species is benthic in the area. This is the first record of this species from the Cape Verde Islands.

***Paraliparis* sp.** (Fig. 2E)

Material examined. - TFMC-VP/01377, 260 mm TL, 258 mm SL, 15º49'N 22º46'W, S of Ponta do Roque, Boa Vista Island, 502-592 m, cruise Cabo Verde 2005-06, sta. 91, 10 Jun. 2005, BT.

Remarks. - Ten species of *Paraliparis* are known from the North Atlantic Ocean, and one from the Mediterranean. One Atlantic species (*P. copei*) has four recognized subspecies (Chernova *et al*., 2004; Chernova and Møller, 2008). Our specimen needs to be compared at least with all the Atlantic species and for the time being we have opted not to assign our specimen to any known species or subspecies. This is the first record of this genus from the Cape Verde Islands.

***Acantholabrus palloni* (Risso, 1810)**

Material examined. - MMF41912, 310 mm TL, 261 mm SL, MMF41913, 307 mm TL, 256 mm SL, 16º45'N-25º03'W, Vale Flamengos, São Vicente Island, 180-240 m, cruise Cabo Verde 2010-04, sta. 8-D3, rocky bottom, 30 Apr. 2010, SFST.

Additional material. - Seven specimens: 320 mm TL, 275 mm SL, São Pedro, São Vicente Island, 206-247 m, cruise Cabo Verde 2010-04, sta. 2, rocky bottom, 14 Apr. 2010, SFST; a post-spawn male, 200 mm TL, 160 mm SL, Vale Flamengos, São Vicente Island, 180-240 m, cruise Cabo Verde 2010-04, sta. 8, rocky bottom, 16 Apr. 2010, SFST; a post-spawn male, 290 mm TL, 240 mm SL, Ponta dos Piquinhos, Santa Luzia Island, 112-136 m, cruise Cabo Verde 2010-04, sta. 16, rocky bottom, 19 Apr. 2010, SFST; a post-spawn male, 330 mm TL, 275 mm SL, Ponta Lobo, Santiago Island, 109-109 m, cruise Camarão-1, sta. 19, rocky bottom, 24 Nov. 2011, SFST; a post-spawn male, 326 mm TL, 274 mm SL, two immature males, 235 mm TL, 192 mm SL, 231 mm TL, 191 mm SL, S of Ponta Leste, Santiago Island, 104-121 m, cruise Camarão-1, sta. 18-D2, rocky bottom, 25 Nov. 2011, SFST.

Remarks. - A temperate eastern Atlantic species inhabiting (adults) coastal waters near rocky or sandy bottoms, also found reef-associated, between 30 and 500 m depth (Schneider, 1990; Froese and Pauly, 2014). It has been recorded from Norway south to Cape Lopez, Gabon and including the Azores, Madeira and the Canary Islands. Also present in the Mediterranean and Adriatic seas (Gomon and Forsyth, 1990; Schneider, 1990; Froese and Pauly, 2014). The presence of this species in Cape Verde is given for the first time by Reiner (1996), but with no collection details. Wirtz *et al*. (2013) mention a photograph of this species. The material examined in the present paper represents in fact the first confirmed record of this species from the Cape Verde, present in at least four islands of this archipelago, between 104 m and 247 m depth. All specimens were collected in SFST, therefore indicating the benthopelagic nature of this species in these waters.

***Lappanella fasciata* (Cocco, 1833)** (Fig. 2F)

Material examined. - MMF42284, 158 mm TL, 140 mm SL, MMF42812, 150 mm TL, 127 mm SL, 14º54'N-23º34'W, East of Cidade Velha, Santiago Island, 108-111 m, cruise Camarão-1, sta. 14-D2/14-D4, rocky bottom, 25/27 Nov. 2011, SFST; MMF48813, 172 mm TL, 146 mm SL, MMF48814, 156 mm TL, 136 mm SL, 15º01'N-23º44'W, Ponta Covinha, Santiago Island, 104-112 m, cruise Camarão-1, sta. 12-D3, rocky bottom, 28 Nov. 2011, SFST; MMF42811, 167 mm TL, 140 mm SL, MMF42810, 151 mm TL, 129 mm SL, 16º35'N 22º55'W, Baía de Santa Maria, Sal Island, 102-105 m, cruise Camarão-3, sta. 12-D3, rocky bottom, 21 Jul. 2012, SFST; MMF42807, 141 mm TL, 120 mm SL, 16º44'N 23º01'W, Palmeira, Sal Island, 105-125 m, cruise Camarão-3, sta. 2-D3, rocky bottom, 22 Jul. 2012, SFST.

Remarks. - A subtropical reef-associated species, ranging from 35 m to 200 m depth (Gomon and Forsyth, 1990), found in deep rocky areas (Quignard and Pras, 1986; Froese and Pauly, 2014). It is known from the south-western and central Mediterranean Sea and in the eastern Atlantic it was known only from the Josephine Bank, Madeira and the Canary Islands (Maul, 1949, 1976; Quignard and Pras, 1986; Brito *et al*., 2002; Dulčić *et al*., 2006*)*. This is the first time this species is recorded from the Cape Verde Islands, which enlarges its area of distribution by 1400 km to the South. All specimens were collected in SFST, therefore indicating the benthopelagic nature of this species in these waters.

It is interesting to note that in the eastern Atlantic Ocean this species has a patchy distribution on islands and associated seamounts. Its continental counterpart, *Lappanella guineensis* Bauchot, 1969, is so far restricted to Sierra Leone (Bauchot, 1969; Gomon and Forsyth, 1990; Froese and Pauly, 2014). Assuming that these species are not cryptic to the point that have been overlooked along the West African coast, this rather eccentric distributions should foster a detailed genetic study of these two species, along all their areas of occurrence to shed some light on its colonization pattern.

***Trachinus* sp.**

Material examined. - MMF42285, 119 mm TL, 101 mm SL, 15º55'N-22º56'W, Ponta Lacacão, Boa Vista Island, 122-137 m, cruise Camarão-2, sta. 15, rocky bottom with sand, 7 Mar. 2012, BT.

Remarks. - Body proportions, meristics and colour pattern do not match with descriptions of any of the known *Trachinus* species occurring in waters of the Cape Verde Islands and adjacent seas. Although this specimen seems to be close to *Trachinus pellegrini* Cadenat, 1937, it may belong to a still undescribed species and an in-depth taxonomical and genetic study is being done, the results of which will be published elsewhere.

CONCLUSION

The present account results from a series of surveys using unconventional collecting gear – fish traps at bottom and near bottom (2.4 m above seafloor). Attractiveness to bait, feeding habits of the species and habitat preferences account to the selectivity of the fishing gear and reflects on the specific composition of the catches.

Among the 66 species collected, six are first records from the Cape Verde Islands. The findings of *Gnathophis mystax* (Congridae) represent the southernmost record (Santiago Island, at 15º04'N) for this species. Also the catches of *Lappanella fasciata* (Labridae) represent the southernmost record (Santiago Island, at 14º54'N) for this species, while *Nezumia africana* (Macrouridae) the northernmost (Boa Vista Island, at 16º17'N). *Nezumia duodecim* and *Ectreposebastes imus* (Scorpaenidae) are not so unexpected, as they occur north and south of the Cape Verde Islands. *Paraliparis* sp. is a rather interesting record, as the family Liparidae has never been recorded from the archipelago. The nearest record is *P. copei wilsoni* Richards, 1966 from Gabon, only known from the holotype. A preliminary examination of our specimen do not allow us to assign it to this species.

The presence of *Echelus pachyrhynchus* (Ophichthidae), *Hippocampus algiricus* (Syngnathidae) and *Acantholabrus palloni* (Labridae) is now confirmed in waters of this archipelago.

Regarding the poorly-known Cape Verdean species, *Myroconger compressus* (Myrocongridae) is a gonochoristic species based on gonad examination, and the 620 mm TL specimen is apparently the largest ever recorded. The collections of specimens of *Myrichthys pardalis* (Ophichthidae) while actively swimming at surface at night, over 13 to 35 m of depth, were probably due to the large number of small organisms concentrated around the vessel, attracted by its bright lights. Also the finding of one specimen of *Phaenomonas longissima* (Ophichthidae) seems to be the first collection of this species swimming freely at surface. The capture of one specimen of *Sphagemacrurus hirundo* (Macrouridae) represents the southernmost record (Santiago Island, at 15º08'N) for this species. The present material is the third record (just three records since 1888) of *Gadella imberbis* (Moridae) from the Cape Verde Islands and the northernmost limit (Boa Vista Island, at 15º55'N) for this species in the eastern Atlantic. *Physiculus cyanostrophus* (Moridae) is a more abundant species in Cape Verdean waters at 90-340 m depth than suspected before.

Since only one specimen of *Trachinus* has been collected, we have opted to wait for further collections in order to identify this specimen to species level.

Physiculus sp. (Moridae) specimens are being studied in detail and will eventually reveal to be new species to science.

Based on the position of the traps in relation to the seafloor, we can confirm the benthic nature of 24 species and the benthopelagic nature of 19. The collection of two Stomiiformes (*Cyclothone microdon* and *Stomias affinis*), typical mesopelagic species (Haedrich, 1997), and two juveniles of *Ophioblennius atlanticus* (Blenniidae), which occur pelagically over deep water (Bath, 1990c), inside bottom traps, can only be explained as an incidental collection while traps were being hauled. For the remaining 20 species data is not conclusive.

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