ANTONIO MANUEL GARCÍA MEDEROS

Fishery and Ecology of Pomacentrids off Gran Canary Island - Pesca y Ecología de Pomacéntridos en la Isla de Gran Canaria

Departamento de Biología

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ULPGC

D. JOSÉ MANUEL VERGARA MARTÍN , SECRETARIO DEL DEPARTAMENTO DE BIOLOGÍA DE LA UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA,

CERTIFICA,

Que el Consejo de Doctores del Departamento en su sesión de fecha............................tomó el acuerdo de dar el consentimiento para su tramitación, a la tesis doctoral titulada "Fishery and ecology of pomacentrids off Gran Canary island – Pesca y ecología de pomacéntridos en la isla de Gran Canaria" presentada por el doctorando D. Antonio Manuel García Mederos y dirigida por el Doctor Fernando Tuya Cortés y por el Doctor Víctor Manuel Tuset Andújar.

Y para que así conste, y a efectos de lo previsto en el Artº 6 del Reglamento para la elaboración, defensa, tribunal y evaluación de tesis doctorales de la Universidad de Las Palmas de Gran Canaria, firmo la presente en Las Palmas de Gran Canaria, a........de noviembre de dos mil quince.

FISHERY AND ECOLOGY OF POMACENTRIDS OFF GRAN CANARY ISLAND – PESCA Y ECOLOGÍA DE POMACÉNTRIDOS EN LA ISLA DE GRAN CANARIA.

Programa de Doctorado

“ECOLOGÍA Y GESTIÓN DE LOS RECURSOS VIVOS MARINOS.”

Memoria presentada por el Licenciado D. Antonio Manuel García Mederos para la obtención del Doctorado en Ciencias del Mar en la Universidad de Las Palmas de Gran Canaria.

El doctorando,
Fdo.: Antonio Manuel García Mederos

El director,
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ÍNDICE

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Por el año 2002, cuando terminé los estudios de Ciencias del Mar, jamás pensé que estaría trabajando en algo relacionado con el mar y mucho menos que haría una tesis. Con lo poco que me gusta a mí hablar en público!!!.

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CAPÍTULO 1

INTRODUCCIÓN GENERAL

ÍNDICE

1 Introducción

Las Islas Canarias son un archipiélago situado entre 100-450 km de la costa noroeste de África. Su origen volcánico se manifiesta en una plataforma continental muy estrecha, sobre todo en las islas más occidentales, lo que afecta a las características topográficas e hidrográficas de la costa, y por lo tanto la distribución de las especies marinas (Brito 1984, 1991; Falcón et al. 1996; Landaeta et al. 2012). Los ecosistemas cercanos a la costa se caracterizan por una alta biodiversidad y fragilidad, como resultado de la representación reducida, en términos de abundancia, de la mayor parte especies (Pascual 2004; Tuya et al. 2014). Más de 100 especies de peces son explotadas por la pesca artesanal en Canarias (García-Cabrera 1970; Pascual 1991; Bas et al. 1995; Pajuelo and Lorenzo 1995; Mancera-Rodríguez and Castro 2004, 2015; Martín-Sosa 2012). Sin embargo, sólo un reducido número de familias (Scaridae, Sparidae, Mullidae, Pomacentridae y Monacanthidae) y algunas especies proporcionaron rendimientos de pesca relativamente altos, en términos de biomasa, concretamente: *Sparisoma cretense (Linnaeus, 1758)*, *Dentex gibbosus (Rafinesque, 1810)*, *Diplodus* spp., *Mullus surmuletus Linnaeus, 1758* , *Pagrus* spp., *Pagellus* spp. y *Sarpa salpa (Linnaeus, 1758)*.

Por otro lado, a pesar del bajo peso, tres especies de pequeño tamaño son importantes en términos de abundancia: *Stephanolepis hispidus (Linnaeus, 1766)*, *Chromis limbata* (Valenciennes, 1833) y

Similiparma lurida (Cuvier, 1830) – *anteriormente conocida como Abudefduf luridus* (Cooper et al. 2014). En este sentido, las especies de pequeño tamaño no suele tener interés comercial (Golani et al. 2002), pero en las Islas Canarias estas especies son apreciadas y se encuentran en algunos mercados locales.

Los pomacéntridos (damiselas) son una familia de peces diversos, que incluye 29 géneros y 387 especies distribuidas a lo largo de los océanos tropicales del mundo (Allen 1991; Nelson 2006; Robertson 1998; Eschmeyer 2013). Se encuentran entre los primeros peces descritos por Linneo, allá por el siglo XVIII, y, posteriormente, han recibido la atención de otros taxónomos y naturalistas (Bleeker 1877; Cuvier y Valenciennes 1830). En cuanto al número de especies, esta familia es el tercer mayor grupo de peces en los ecosistemas de arrecifes de coral, después Gobiidae (> 1.500 especies) y Labridae (> 600 especies) (Wainwright y Bellwood 2002), a pesar de que a menudo llegan a abundancias mayores en los arrecifes (Frederich et al. 2009). Su papel ecológico y el comportamiento agonístico han dado lugar a una gran cantidad de estudios que los ha llevado a ser utilizados como organismos modelo para probar cuestiones ecológicas (Frederich et al. 2009).

Los pomacéntridos juegan un papel importante en la organización de comunidades de arrecifes bentónicos (Ceccarelli et al. 2001), ya que pueden afectar a la composición de algas del arrecife de 3 formas diferentes: (1) alimentándose directamente de algas; (2) con su actividad herbívora (pastaje) y (3) excluyendo indirectamente a otros peces herbívoros competitivos.

La etimología de Pomacentridae proviene del griego poma, -atos = cubierta, opérculo + griega, kentron = picadura (Froese y Pauly 2015).

Son principalmente marinos y raramente de aguas salobres. Se encuentran en todos los mares tropicales, principalmente del Indo-Pacífico. Tiene una fosa nasal a cada lado de la cabeza, nariz doble en algunas especies de *Chromis* y *Dascyllus*. El cuerpo generalmente es alto y comprimido, con una boca pequeña. La línea lateral está incompleta e interrumpida. La aleta anal tiene 2 espinas generalmente y muy rara vez tiene 3. Sin dientes palatinos. La talla que llegan a alcanzar es de 35 cm de longitud máxima. En la misma especie, su coloración es variable entre individuos y las zonas. La mayoría de las especies son herbívoras, aunque también pueden ser omnívoros y planctívoros (Froese y Pauly 2015). Su dieta generalmente va desde zooplancton y larvas (Leis et al. 2002), a una combinación de zooplancton y / o macrófitos, dependiendo de la especie (Allen 1991).

Son territorialitas y muy agresivos defendiendo su territorio. La puesta está formada por huevos elípticos demersales que son custodiados por los machos. En esta familia, además de los peces damiselas, se incluyen los peces anemona o payaso (Amphiprioninae), que viven en estrecha asociación con las grandes anémonas de mar. Muchas especies se encuentran entre las más resistentes a vivir en acuarios, aunque algunas especies son extremadamente agresivas (Allen 1991; Froese y Pauly 2015).

En Canarias, coexisten dos especies, *Similiparma lurida* y *Chromis limbata* (Brito et al. 2002; Espino et al, 2007; Froese y Pauly 2014). También aparecen ocasionalmente *Abudefduf saxatilis* (Linnaeus, 1758), *Chromis chromis* (Linnaeus, 1758) y muy raramente *Stegastes imbricatus* Jenyns, 1840 (Brito et al. 2002; Froese y Pauly 2015).

2 Descripción de las especies

Similiparma lurida (Cuvier, 1830)

GÉNERO *Similiparma*

Etimología de *Similiparma*: Del latín "similis" (como, parecido) en referencia a la semejanza con las especies del género *Parma* (Hensley, 1986). *Parma* del latin, parma, -ae, pequeño escudo (Allen y Hoese 1975).

El género *Similiparma* representa parte de la fauna endémica de la Macaronesia (Humphries 1979). Este género se parece en gran medida al género Parma, difiriendo en los radios de la aleta caudal y en tener la membrana de la aleta pectoral mayor entre sus radios. Los adultos habitan zonas costeras rocosas. Los huevos son demersales y se adhieren al sustrato. Los machos guardan y airean los huevos (Froese y Pauly 2015).

LA ESPECIE

NOMENCLATURA

Nombre científico

El nombre científico es *Similiparma lurida*

Sinonimias

Otros nombre científicos usados para esta especie son: *Abudefduf luridus* Cuvier, 1830, *Chaetodon luridus* Cuvier, 1830, *Chaetodoton luridi* Gemlin, 1789, *Glyphisodon luridus* Cuvier, 1830 y *Stegastes imbricatus* (Jenyns, 1842).

Nombres comunes

El nombre común aceptado por la FAO: Canary damsel.

Nombres vernáculos: fula negra en español, castanheta-preta en portugués y demoiselle à ailes bleues en francés.

POSICIÓN TAXONÓMICA

SUBPHYLUM: VERTEBRATA

SUPERCLASE: GNATHOSTOMATA

Grado Teleostomi

Clase Actinopterygii

Subclase Neopterygii

División Teleostei

Subdivisión Euteleostei

Superorden Acanthopterygii

Ordén Perciformes

Familia Pomacentridae

Género Similiparma (Hensley, 1986)

DESCRIPCIÓN

Tiene una la aleta dorsal con 13 espinas seguidas de 16-17 radios blandos, en la aleta anal tiene 2 espinas seguidas de 13-14 radios blandos. Aleta caudal bifurcada. Puede alcanzar tallas de hasta 150 mm de LT. El sexo es indiferenciado externamente, aunque en época de puesta se puede distinguir al macho ya que es el encargado de limpiar, custodiar y guardar los huevos (Froese y Pauly 2015). En algunos individuos se puede observar, en la región caudal, tonalidades anaranjadas o rosáceas, sin que se sepa a qué obedece este fenómeno (Espino et al. 2007).

HÁBITAT Y DISTRIBUCIÓN GEOGRÁFICA

Es una especie subtropical (40°N - 13°N, 29°W - 11°W). Su distribución está localizada en la región macaronésica (Atlántico Nororiental), apareciendo en las islas de Azores, Madeira, Salvajes, Canarias, Cabo Verde, Portugal y Senegal (Brito et al. 2002; Froese y Pauly 2015).

Comúnmente está asociada con arrecifes en las regiones subtropicales, donde los individuos crecen hasta unos 15 cm de longitud, y se alimentan principalmente de algas y pequeños invertebrados (Froese y Pauly 2015; Reiner 1996).

En Canarias, es una especie muy abundante en todas las islas, encontrándose en fondos rocosos y rocoso-arenosos hasta profundidades de 50 metros (Brito et al. 2002; Espino et al. 2007). Se caracteriza por ser un pez muy territorial nadando cerca de sus refugios. Cuando otros individuos, u otros peces de especies diferente se le acercan, pueden verse intensas persecuciones con las que tratan de ahuyentarlos, llegando incluso a enfrentarse a buceadores (Espino et al. 2007).

INTERÉS ECOLÓGICO

Desde un punto de vista científico, todos los pomacéntridos tienen gran valor por su importancia ecológica dentro de los ecosistemas, debido a su dieta y la interacción que tienen con los invertebrados, manteniendo a raya el crecimiento excesivo de algas (Ceccarelli et al. 2001, Schmiing et al. 2013).

VALOR COMERCIAL

Su importancia no es tan alta en términos comerciales ya que es poco consumida. Principalmente es capturada para ser utilizada como cebo vivo, aunque en algunos lugares se preparan fritas para comer. Su valor de mercado es poco importante y tiene un bajo interés pesquero (Golani et al. 2002).

***Chromis limbata* (Valenciennes, 1833)**

GÉNERO *Chromis*

Etimología de *Chromis*: El nombre proviene del griego chromis = un pez, quizá una perca (Romero, 2002).

Los peces de este género se encuentran entre las pocas especies conocidas de pomacéntridos que habitan en los arrecifes de coral de profundidad, tal vez es un reflejo de su principal alimento (zooplancton), en contraste con las especies de otros géneros que dependen principalmente de las algas bentónicas. La mayoría de los peces damisela pertenecen al género *Chromis*. Estos peces son populares en los acuarios domésticos por su pequeño tamaño, brillantes colores y tolerancia a una baja calidad del agua (Pyle et al. 2008).

LA ESPECIE

NOMENCLATURA

Nombre científico

El nombre científico es *Chromis limbata* (Valenciennes, 1833)

Sinonimias

Otros nombre científicos que se han utilizado para esta especie son: *Heliases limbatus* Valenciennes, 1833 y *Heliazes marginatus* Valenciennes, 1843.

Nombres comunes

El nombre común aceptado por la FAO es: Azores chromis.

Los nombres vernáculos son: fula blanca en español, castanheta-branca o castanheta amarela en portugués y castagnole à queue rayée en francés.

POSICIÓN TAXONÓMICA

SUBPHYLUM: VERTEBRATA

- SUPERCLASE: GNATHOSTOMATA
  - Grado Teleostomi
    - Clase Actinopterygii
      - Subclase Neopterygii
        - División Teleostei
          - Subdivisión Euteleostei
            - Superorden Acanthopterygii
              - Ordén Perciformes
                - Familia Pomacentridae
                  - Género Chromis Cuvier, 1814

DESCRIPCIÓN

Tiene una la aleta dorsal con 14 espinas seguidas de 11-12 radios blandos, en la aleta anal tiene 2 espinas seguidas de 10-12 radios blandos. Aleta caudal bifurcada. Puede alcanzar tallas de hasta 120 mm de LT (Froese y Pauly 2015). Se alimenta de organismos plánctonicos y de pequeños invertebrados. Se reproduce en los meses de verano, adquiriendo los machos tonalidades violáceas intensas y colaborando con las hembras en la defensa de la puesta (Espino et al. 2007).

HÁBITAT Y DISTRIBUCIÓN GEOGRÁFICA

Chromis limbata es una especie subtropical (40°N - 5°S, 32°W - 12°E). Su distribución está localizada en Atlántico Oriental, apareciendo en las islas de Azores, Madeira, Canarias, y desde Senegal hasta el Congo (Brito et al. 2002; Froese y Pauly 2015).

Es frecuente en zonas de rocas y mixta (rocas y arenal). Se alimenta de pequeños invertebrados y organismos planctónicos, su comportamiento es menos territorial que la fula negra (*Similiparma lurida*). En época de reproducción, el macho adopta unas tonalidades más violáceas y a los ejemplares juveniles se les puede encontrar entre las púas del erizo *Diadema africana*. Está asociada a arrecifes, a profundidades entre 5 y 45 metros (Froese y Pauly 2015).

En Canarias, es una especie bentopélagica muy abundante en todas las islas, encontrándose en fondos rocosos y rocoso-arenosos. En zonas costeras, sobre todo en blanquizales, suele formar cardúmenes a media agua (Brito et al. 2002; Espino et al. 2007).

INTERÉS ECOLÓGICO

Es una de las pocas especies de peces cuya abundancia se correlaciona positivamente con la presencia de erizos *Diadema africana* en fondos rocosos (Espino et al. 2007).

VALOR COMERCIAL

En algunas zonas del Archipiélago Canario es capturada para el consumo humano. Su carne es de buena calidad, aunque por su pequeño tamaño tiene escaso interés comercial (Espino et al. 2007).

***Abudefduf saxatilis* (Linnaeus, 1758)**

GÉNERO *Abudefduf*

Etimología de *Abudefduf:* proviene de los términos árabes *abu* y *def*, que significan «padre» y «lateral» respectivamente, junto al sufijo enfático en plural *-duf*. El significado literal sería «padre con prominentes lados (Romero 2002).

Las especies de *Abudefduf* se alimentan de plancton, huevos de otras especies y en general predando en los arrecifes de las áreas tropicales y subtropicales del océano Atlántico e Indo-Pacífico (Allen

1991). Son los representantes de mayor tamaño de los peces damisela, con longitudes de 13 a 30 cm. Habitualmente, tienen una coloración plateada, azulada, blanca o gris clara, con franjas verticales oscuras de anchura y número variables (Allen 1991). En general, se agrupan en pequeños grupos o individualmente y tienen un comportamiento muy territorial (Allen 1991; Lieske y Myers 1994). Su dieta son principalmente algas, gasterópodos y cangrejos pequeños (Lieske y Myers 1994).

LA ESPECIE

NOMENCLATURA

Nombre científico

El nombre científico es *Abudefduf saxatilis* (Linnaeus, 1758)

Sinonimias

Otros nombre científicos que se han utilizado para esta especie son: *Chaetodon saxatilis* Linnaeus, 1758, *Glyphidodon saxatilis* (Linnaeus, 1758), *Abudefduf saxiatilis* (Linnaeus, 1758), *Abudefduf sexatilis* (Linnaeus, 1758).

Nombres comunes

El nombre común aceptado por la FAO es: Sergeant-major.

Los nombres vernáculos son: fula sargento y petaca rayada en español, castanheta en portugués y sergent major en francés.

POSICIÓN TAXONÓMICA

SUBPHYLUM: VERTEBRATA

SUPERCLASE: GNATHOSTOMATA

Grado Teleostomi

Clase Actinopterygii

Subclase Neopterygii

División Teleostei

Subdivisión Euteleostei

Superorden Acanthopterygii

Ordén Perciformes

Familia Pomacentridae

Género Abudeduf (Forsskål, 1775)

DESCRIPCIÓN

Tiene una la aleta dorsal con 13 espinas seguidas de 12-13 radios blandos, en la aleta anal tiene 2 espinas seguidas de 10-12 radios blandos. Comúnmente es de color gris plata ventralmente, amarillo brillante dorsalmente, con cinco bandas de color marrón oscuro a negro en casi todo el cuerpo y alcanza un tamaño máximo de hasta aproximadamente 150 mm de longitud estándar (LS) (Allen 1991).

HÁBITAT Y DISTRIBUCIÓN GEOGRÁFICA

Abudefduf saxatilis es una especie subtropical (41°N - 37°S, 89°W - 14°E) en profundidades de 0 a 20 metros (Allen 1991). Su distribución en el Océano Atlántico Occidental es desde Canadá a Uruguay, y abundante en los arrecifes del Caribe. En el Océano Atlántico Occidental, se encuentran alrededor de las islas del Atlántico medio, Cabo Verde, y a lo largo de la costa tropical de África occidental hasta el sur de Angola. Se encuentra estrictamente en el Atlántico (Freitas y Araújo 2006; Froese y Pauly 2015).

Es una especie litoral, que viven en aguas poco profundas en una amplia variedad de hábitats (arena y fondos rocosos, arrecifes de coral, marismas, etc.) (Lloris y Rucabado 1990). Normalmente, habita en el borde superior de las pendientes de los arrecifes de 1 a aproximadamente 12 metros de profundidad (Allen 1975). Generalmente es de color gris plata continuo, amarillo brillante anteriormente, con cinco barras de color marrón oscuro a negro transversalmente al cuerpo y alcanza un tamaño máximo de hasta aproximadamente 150 mm LS (Allen 1991). Los machos adultos adoptan un color de fondo azulado cuando guarda los huevos (Froese y Pauly 2015).

En las Islas Canarias, se trata de una especie rara de encontrar (Brito et al. 2002), se registró por primera vez dos ejemplares en 1991 (Brito 1991).

Chromis chromis **(Linnaeus, 1758)**

GÉNERO *Chromis*

Etimología de *Chromis*: El nombre proviene del griego chromis = un pez, quizá una perca (Romero, 2002).

Los peces de este género se encuentran entre las pocas especies conocidas de pomacéntridos que habitan en los arrecifes de coral de profundidad, tal vez es un reflejo de su principal alimento (zooplancton), en contraste con las especies de otros géneros que dependen principalmente de las algas bentónicas. La mayoría de los peces damisela pertenecen al género *Chromis*. Estos peces son populares en los acuarios domésticos por su pequeño tamaño, brillantes colores y tolerancia a una baja calidad del agua (Pyle et al. 2008).

LA ESPECIE

NOMENCLATURA

Nombre científico

El nombre científico es *Chromis chromis* (Linnaeus, 1758)

Sinonimias

Otros nombre científicos que se han utilizado para esta especie son: *Sparus chromis Linnaeus, 1758, Heliastes chromis (Linnaeus, 1758)*.

Nombres comunes

El nombre común aceptado por la FAO es: Damselfish.

Los nombres vernáculos son: castañuela en español, castanheta en portugués y castagnole en francés.

POSICIÓN TAXONÓMICA

SUBPHYLUM: VERTEBRATA
- SUPERCLASE: GNATHOSTOMATA
  - Grado Teleostomi
    - Clase Actinopterygii
      - Subclase Neopterygii
        - División Teleostei
          - Subdivisión Euteleostei
            - Superorden Acanthopterygii
              - Ordén Perciformes
                - Familia Pomacentridae
                  - Género Chromis Cuvier, 1814

DESCRIPCIÓN

Tiene una la aleta dorsal con 14 espinas seguidas de 9-11 radios blandos, en la aleta anal tiene 2 espinas seguidas de 9-11 radios blandos. De tonalidad de pardo oscura, llegando a alcanzar una longitud total de 250 mm y el cuerpo aplanado lateralmente. La aleta caudal es ahorquillada. Los juveniles, de hasta un centímetro de longitud, son de un vistoso azul eléctrico (Allen 1991).

HABITAT Y DISTRIBUTION

Chromis chromis es una especie subtropical (46°N - 12°S, 32°W - 36°E) que se encuentra entre 2 a 40 m de profundidad (Allen 1991). Es una especie muy común en el mar Mediterráneo además de encontrarse en el Atlántico oriental desde la costa de Portugal al Golfo de Guinea y Angola (Quignard y Pras 1986). También, se distribuye a lo largo del mar Adriático, viviendo sobre o cerca de arrecifes rocosos, o por encima de las praderas de pastos marinos, principalmente, a una profundidad de 3-35 m (Jardas 1996). De conducta gregaria, se agrupa en cardúmenes poco densos a poca profundidad, especialmente en costas rocosas. Los adultos defienden de forma muy agresiva sus territorios, especialmente las puestas (Jardas 1996).

En las Islas Canarias es muy raro de encontrar (Froese y Pauly 2015).

3 Justificación y objetivos

En el primer capítulo de la Tesis Doctoral se analizaron las capturas de las trampas para peces (nasas), modalidad de pesca artesanal más importante en las aguas costeras de las Islas Canarias (Atlántico oriental). A partir de las capturas de nasas desplegadas entre mayo y octubre de 2009 en isla de Gran Canaria, a una profundidad entre 20 y 50 m, se llevó a cabo una descripción cuantitativa de las capturas en términos de abundancias y biomasas de peces. Además, se ha analizado la estructura de tamaños de peces de especies objetivo, como una forma de evaluar el estado de las poblaciones. Los resultados de este capítulo indicaron que los pomacéntridos *C. limbata* y *S. lurida* son dos de las especies de peces más capturadas, en términos de abundancia.

En una segunda parte, el objetivo fue proporcionar información biológica y ecológica sobre la estructura de la población de *Similiparma lurida* en arrecifes rocosos de Gran Canaria (Islas Canarias, Atlántico noreste). En primer lugar, se evaluó la ecología reproductiva y los patrones de crecimiento. Este enfoque proporciona información relevante desde la perspectiva de la pesca, es decir, proporcionando datos como la temporada de desove y primera talla de madurez. En segundo lugar, analizamos los patrones espaciales y temporales de la abundancia, la descripción de los patrones de reclutamiento anuales y, por tanto, la posible sincronización entre la reproducción y el reclutamiento posterior de esta especie. Además, se ha tratado de determinar si la variación en los patrones de abundancia de adultos, subadultos y juveniles varió a pequeña escala espacial en relación con la composición del hábitat y su complejidad. En general, la integración de esta información proporciona una visión holística sobre el ciclo de vida de esta especie.

En el último capítulo, se analizó la variabilidad morfo-funcional de pomacéntridos de Canarias, tanto intra como inter-específica, para detectar cambios ontogénicos, dilucidar la presencia de stocks en la isla de Gran Canaria y determinar el grado de disparidad morfológica entre las especies de pomacéntridos . Además, se determinó el nivel de variabilidad interespecífica y comprobamos la equivalencia morfológica y funcional de dos peces damiselas recientemente descritos (*A. saxatilis* y *C. chromis*) para evaluar su posible establecimiento exitoso en aguas de las Islas Canarias.

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CAPÍTULO / CHAPTER 2

THE STRUCTURE OF A NEARSHORE FISH ASSEMBLAGE AT AN OCEANIC ISLAND: INSIGHT FROM SMALL SCALE FISHERIES THROUGH BOTTOM TRAPS AT GRAN CANARY ISLAND (CANARY ISLANDS, EASTERN ATLANTIC).

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The structure of a nearshore fish assemblage at an oceanic island: insight from small scale fisheries through bottom traps at Gran Canary Island (Canary Islands, eastern Atlantic)

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Abstract – Unsuitable management of fisheries may lead to overexploitation of marine resources. Oceanic islands with narrow continental shelves, in particular, are sensitive to unsustainable levels of fishing intensity. Fish traps are the modality of artisanal professional fishing more important in the coastal waters of the Canary Islands (eastern Atlantic) to capture demersal resources, which are deployed all year-round and allow a release of undersized captures. We aimed at studying the structure of nearshore fish assemblages through deployment of benthic bottom traps carried out at Gran Canary Island. A quantitative description of catches, in terms of abundance, biomass and sizes, of traps deployed from May to October 2009, between *ca.* 20 to 50 m depth, was carried out. We used this information to test whether the structure of nearshore fish assemblages at the island scale varied between three zones located at the NW, NE and E of the island with varying habitat structure. A total of 58 species (22 families) were collected for the overall study from a total of 2568 deployed traps. The species *Sparisoma cretense* (25% of the total biomass), the family Sparidae (16 species, 44%) and *Mullus surmuletus* (4%) accounted for more than 73% of the total catch in terms of biomass. The parrotfish, *S. cretense*, was the fish with the largest catches in terms of number of individuals, followed by *Dentex gibbosus*, *Diplodus vulgaris*, *Stephanolepis hispidus*, *Chromis limbata* and *Mullus surmuletus*. Differences in the structure of the fish assemblage at the island scale were not predicted by differences in the type of bottom. Fishing yields were similar between the NW (0.16 ± 0.02 kg trap^{-1} day^{-1}) and NE side of the island (0.19 ± 0.01 kg trap^{-1} day^{-1}), being lower at the E zone (0.15 ± 0.01 kg trap^{-1} day^{-1}). The most abundant species, the parrotfish *S. cretense*, had a mean size close to its first maturity sizes (SFM$_{50}$), while both *D. gibbosus* and *D. vulgaris* were below SFM$_{50}$. In general, the mean size of Sparids was well below SFM$_{50}$, an indication of overexploitation, while *M. surmuletus* and *S. hispidus* reached a mean size beyond their first maturity sizes.

Keywords: Ichthyofauna / habitat / diversity / coastal fishery / Atlantic Ocean

The structure of a nearshore fish assemblage at an oceanic island: insight from small scale fisheries through bottom traps at Gran Canary Island (Canary Islands, eastern Atlantic).

INDEX

1 INTRODUCTION

In the last century, unsuitable management of fisheries, including artisanal, industrial and recreational, has led to overexploitation of marine resources in most of the world's coastal areas (Sadovy de Mitcheson et al. 2013; Chiappone et al. 2004; Pauly 2008; FAO 2012), while fishing methods such as trawling are contributing to a continuous degradation of marine habitats worldwide (Messieh et al. 1991; Collie et al. 1997; Watling and Norse 1998; Eno et al. 2013). In many areas of the globe, however, promotion of sustainable fisheries is complex, e.g. not all landings of fisheries are controlled and the use of multiple gear types create an unfavourable regulation, particularly for coastal fisheries (Hernández-García et al., 1998; McClanahan and Mangi 2001). In addition, recreational fishing may be an uncontrolled source of fishing and contribute to depauperate certain fishery resources. This situation is especially worrying at oceanic islands with reduced continental shelves, where reduced coastal habitats provide finite resources that are easily threatened by unsustainable levels of fishing intensity (Rhodes et al. 2011; SPC 2013; Menezes et al. 2013).

The Canary Islands is an archipelago located between *ca*. 100-450 km off the northwest African coast. Its volcanic origin is manifested in the absence, or very narrow, coastal shelf, particularly in the westernmost islands, what affects topographic and hydrographical features of the coast, and hence the distribution of marine species (Brito 1984, 1991; Falcón et al. 1996; Landaeta et al. 2012).

Nearshore ecosystems are characterised by a high biodiversity and fragility, resulting from the reduced representation, in terms of abundance, of most species (Pascual 2004; Tuya et al. 2014). In this archipelago, over 100 fish species are exploited by small-scale fisheries using multiple gears, such as seine nets, traps and hand-lines (García-Cabrera 1970; Pascual, 1991; Bas et al. 1995; Pajuelo and Lorenzo 1995; Mancera-Rodríguez and Castro 2004, 2015; Martín-Sosa 2012). The structure of the Canarian fishing fleet shows a high social and economic dependency on small-scale fishing (FAO, 2011; EU Fisheries in Canary Islands, 2013). The assessment and further management of these resources is complicated, because the knowledge of biological parameters is restricted to the main commercial species (González and Lozano 1992; Pajuelo and Lorenzo 1995, 1996, 1999; García-Díaz et al. 1997, 2006; Méndez-Villamil et al. 1997; Pajuelo et al. 2006, González et al. 2012). Importantly, there are no available historical, temporal, series of catches and fishing effort for all gears and ports (Hernández-García et al. 1998), what avoid proper evaluation of fishing trends through decades.

Deployment of fish traps is the modality of artisanal professional fishing more important in the coastal waters of this archipelago, which is practised all year-round (Bas et al. 1995; Melnychuk et al. 2001; Martín-Sosa 2012). This is a passive capture technique, whose advantages in relation to others gears are the simplicity in their design, construction and use in the case experienced fishermen

(Hubert et al. 2012). Moreover, this is one of the few gears that can be used when strong winds and swells occur in the coast and there is the possibility of fish selection on board to release part of captures (i.e. undersized individuals). Although there is a high variability between islands and fishing ports, Couce-Montero (2009) estimated through surveys an average number of fish traps per vessel of 180 units. Still, few studies using fish traps as a way to describe fishery resources have been published in the world (Smolowitz 1978; Matsuoka et al. 2005; Erzini et al. 2008, Newman et al. 2011, Langlois et al. 2015). In this study, we initially aimed at improving the knowledge of small scale fisheries through bottom traps at Gran Canary Island (Canary Islands) by providing a quantitative description of catches in terms of fish abundances and biomasses. We analysed the structure of fish sizes of targeted species, as a way to evaluate the status of populations. We finally sought to determine whether the structure of nearshore fish assemblages at the island scale varied spatially between zones with varying habitat structure.

2 MATERIALS AND METHODS

2.1 Study area

This study focused on Gran Canary Island, which is located at the centre of the Canarian Archipelago, being the third largest island (1,532 km^2) with 45 km of diameter and a maximum elevation of 1,950 m above the sea level (Carracedo et al. 2002). Each island within the Canarian Archipelago consists of an independent large volcanic structure. The shallow subtidal platforms around each island are not continuous except between the islands of Lanzarote and Fuerteventura, and as a result each island has its own independent shallow benthic populations (Sangil et al. 2013). Sediments and rocky reefs mainly compose nearshore bottoms, with a high variability in the distribution and complexity of these habitats, which can be colonized by a range of canopy-forming species (Tuya and Haroun 2006, Tuya et al. 2014). By taken advantage of a published marine cartography for the entire island (GRAFCAN 2008), we grouped the bottom types in three categories: hard (i.e. rocky reefs), medium (i.e. cobbles-dominated bottoms) and soft (i.e. sandy bottoms).

Data were collected at three zones which are located in the vicinity of 3 ports within each area (Fig. 1). In the north-western coast (NW, Agaete), artisanal fishing is performed in an area mainly dominated by soft bottoms (86 %) with a wide offshore platform relative to the other two zones. Commercial fishing is performed when sea conditions are adequate, since this stretch of the coast is very exposed to strong trade winds and oceanic swells from the N and NW. In the north-eastern coast (NE, Las Palmas), fishing is also majorly carried out in an area dominated by soft bottoms (70 %), but on a much reduced offshore platform. In the eastern coast (E, Taliarte), bottoms are also dominated by soft substrates (77 %). This zone has a narrow offshore platform.

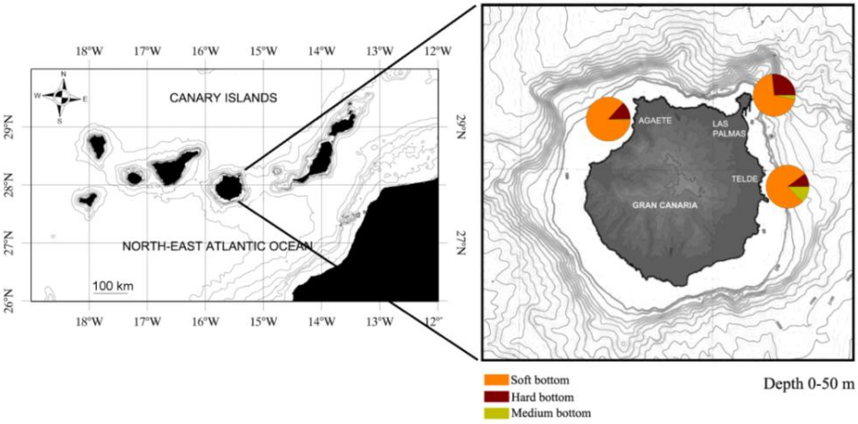

Fig. 1. Map of the three zones at Gran Canaria island: NW - Agaete, NE - Las Palmas, and E - Taliarte; the percentages of each bottom type is included for each zone, hard (i.e. rocky reefs), medium (i.e. cobbles-dominated bottoms) and soft (i.e. sandy bottoms).

2.2 Fishery data collection

Data on catch and effort (number of days and boats) of fish trapping were provided by the local authority of Gran Canary Island (*Cabildo de Gran Canaria*) and was collected by fisheries officials on board. Still, governance and erection of laws is regulated through the fisheries authority of the Canary Islands (*Viceconsejería de Pesca y Aguas*). This database is composed by the captures of 609 (NW), 1138 (NE) and 821 (E) fish traps deployed by the artisanal commercial fishing fleet between May and October 2009. All captured individuals were brought inland; a special permit was provided by the *Viceconsejería de Pesca y Aguas* in this regard. In all cases, traps were circular, ranging between 130-300 cm in diameter, and 34-100 cm in height, which were built with wire mesh (32-51 mm of mesh size) and a single funnel entrance; a door is used to include bait and extract catches (Fig. 2a). Traps were located between *ca*. 20 to 50 m depth (mean depth = 31 m) at the 3 zones, either individually or using a long-line method that joins 2-3 traps together in a gang (Fig. 2b). The number of days that traps were placed on the seafloor varied between 3 and 30 days, depending on oceanographic (wind and swell) conditions and target species. The entire fish catch for each trap (commercial plus the discarded fraction, which is usually returned alive to the sea) was retained for further analyses. The species were then identified, classified (Fischer et al. 1981), weighted and placed within a taxonomic hierarchy according to Nelson’s *Fishes of the World* (Nelson 2006).

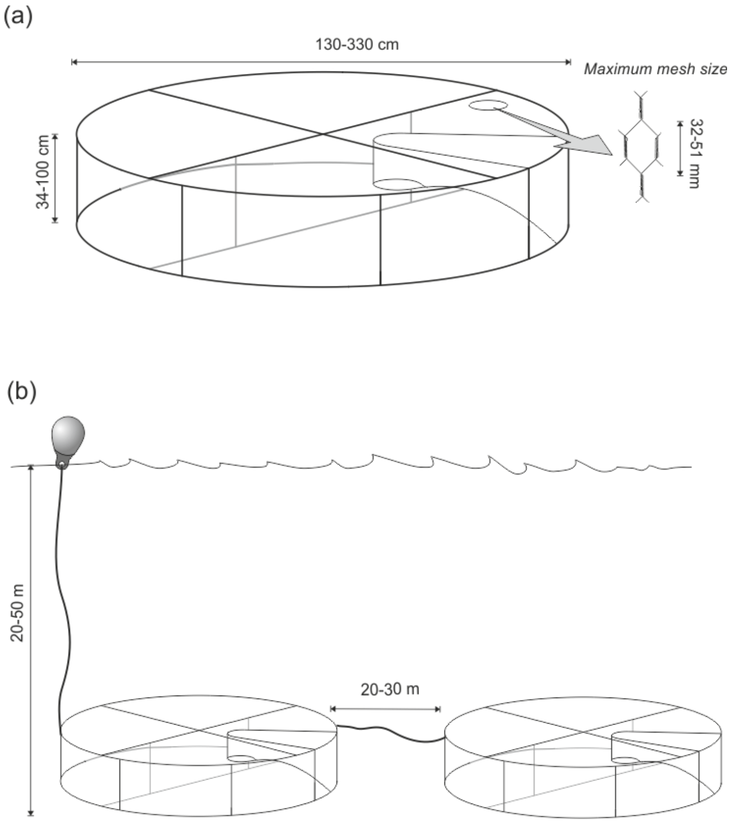

Fig. 2. Fish trap used by the artisanal fishing fleet (a) and long-line method, joining 2 traps together in a gang (b).

2.3 Statistical analysis

Data of abundance and biomass were firstly standardized using the catch per unit effort (i.e. per trap and day, CPUE). To test for differences in the multivariate structure of fish assemblages (CPUEs) between the 3 geographical zones, the non-parametric ANOSIM test was performed (Clarke and Warwick 1994; Tuya et al. 2006a). This analysis compares the average rank similarities within the predefined groups of samples with the average similarity between groups. Values of R close to 1 indicate strong separation in terms of assemblage structure, while values close to 0 indicate a lack of differences (Pusch et al. 2004). When a significant difference ($p < 0.05$) was detected, a similarity percentage breakdown (SIMPER) (Clarke and Warwick 1994) was conducted to determine which species were representatives of specific assemblages (i.e. within each zone) and their contribution to dissimilarities between each pair of zones (Clarke and Warwick 1994).

A permutational analysis of variance via the PERMANOVA package (Anderson *et al.*, 2008) was run on a Euclidean distance matrix to test for differences in catch per unit effort (CPUE) in terms of the total biomass. Although PERMANOVA was originally designed for analysis of multivariate data, it can also be used to analyse univariate data and, unlike ANOVAs, do not assume that data are normally distributed (Anderson et al. 2008; Garside et al. 2014). We performed 9,999 random permutations of the raw data under a reduced model.

To evaluate whether variation in the amount of bottom types (rocky, medium and soft) between the 3 zones contributed to explain variation in the structure of fish captures between zones, a multivariate multiple regression model, using the DISTLM routine (Anderson 2001), was implemented. This analysis tested the significance of these relationships by fitting a linear model based on Bray-Curtis dissimilarities from square-root transformed data and using a ‘forward’ selection procedure.

Finally, for the main commercial fish species in terms of abundance, the mean size per zone was compared via a *t*-student test with the size at first maturity (SFM_{50}), as provided by the local literature. This is an indicator of the level of species’ specific exploitation (Sharpe and Hendry, 2009).

All multivariate procedures were carried out via the PRIMER v6 (Clarke and Gorley, 2006) and PERMANOVA+ (Anderson et al. 2008) statistical package.

3 RESULTS

3.1 Composition and abundance of the fishery

A total of 45 species belonging to 20 families were collected in the NW coast (Table 1). The species *Sparisoma cretense* (33 % of the total biomass), the family Sparidae (12 species, 30 %) and *Mullus* *surmuletus* (13 %) accounted for more than 75% of the total catch in terms of biomass. Nevertheless, species of low weight, such as *Similiparma lurida* and *Chromis limbata*, were important in terms of abundance (17 %). In the NE coast, 37 species (16 families) were captured, where Sparidae (13 species, 43 % of the total biomass) and *Sparisoma cretense* (35 %) accounted for >75% of catches in terms of biomass (Table 1). *Stephanolepis hispidus* was only relevant in terms of abundance (14 % of the total abundance). Finally, a total of 43 species (17 families) were collected from the E coast (Table 1). The family most representative, in terms of biomass, was Sparidae (16 species, 60 % of the total biomass), followed by *Sparisoma cretense* (15 %); *Similiparma lurida* and *Chromis limbata* were, again, important in terms of abundance (11 %). Other species (i.e., *Mycteroperca fusca* or *Epinephelus marginatus*) or families (Serranidae or Haemulidae) with a high commercial value were exclusively captured occasionally.

The fish assemblage from the E zone was not different, in terms of assemblage structure, relative to those fish assemblages from the NW and NE zones (ANOSIM, R= 0.042 and R= 0.085; $p>0.05$, respectively). The fish assemblage from the NW differed relative to that from the NE (R= 0.185; $p<0.05$). The parrotfish, *Sparisoma cretense*, was the fish species with the highest number of individuals at the three zones, followed by *Mullus surmuletus* in the NW, *Stephanolepis hispidus* in the NE and *Diplodus vulgaris* in the E zones (Table 1). *S. cretense* contributed to more than 10% of dissimilarities within each zone. In terms of biomass, *S. cretense* and *Dentex* *gibbosus* attained the highest values at the three zones, contributing to more than 30% of dissimilarities between zones. These species were followed by *M. surmuletus* in the NW and E zones, and *S. hispidus* in the NE (Table 2). Differences in the structure (composition and abundance) of the fish assemblages between zones were not predicted by differences in the type of the bottom (rocky, soft, medium) (all terms, $P > 0.05$).

Table 1. Fish species collected between May and October 2009. Total abundance (number of individuals); total biomass (g); size range (TL in cm); N, number of fish traps. The SFM_{50} is included according to González et al. (2012). * Non-commercial species, ^ endemic species of the Macaronesian region.

Species	First maturity SFM_{50} (cm)	NW - Agaete (N=609)			NE - Las Palmas (N=1138)			E - Telde (N=821)		
		n	Biomass (kg)	Size range (cm)	*n*	Biomass (kg)	Size range (cm)	*n*	Biomass (kg)	Size range (cm)
Aulostomidae										
Aulostomus strigosus *		4	1.200	51-66	-	-	-	-	-	-
Balistidae										
Balistes capriscus	20.00 FL	27	18.983	27-43	111	25.179	20-43	34	11.068	18-39
Bothiidae										
Bothus podas *		62	2.669	10-20	18	1.102	15-21	9	0.330	13-22
Carangidae										
Pseudocaranx dentex	37	-	-	-	6	10.833	44-52	10	10.181	40-62

Table 1. Continued.

Seriola dumerili		-	-	-	-	-	-	1	1.752	55
Seriola fasciata		3	18	71-93	-	-	-	2	3.776	52-55
Seriola rivoliana		1	7.988	80	-	-	-	1	0.594	36
Trachurus trachurus	25	35	7.32	17-23	-	-	-	-	-	-
Congridae										
Conger conger	200	2	6.29	86-115	3	10.138	73-104	3	7.898	13-93
Haemulidae										
Parapristipoma octolineatum		13	2.138	21-29	5	0.832	20-24	13	1.426	19-24
Pomadasys incisus		97	7.746	15-22	104	7.827	15-24	65	5.007	14-23
Labridae										
Bodianus scrofa ^		4	3.078	31-41	3	3.334	38-42	-	-	-
Coris julis *		2	0.288	23-23	-	-	-	-	-	-
Thalassoma pavo *		1	0.072	18	-	-	-	3	0.135	21

Table 1. Continued.

Xyrichtys novacula *		-	-	-	1	1	19	-	-	-
Monacanthidae										
Aluterus scriptus *		-	-	-	-	-	-	1	0.014	57
Stephanolepis hispidus	14.90	3	0.190	13-16	737	69.193	9-27	201	16.457	10-26
Mugilidae										
Liza aurata *		-	-	-	-	-	-	8	3.058	31-37
Mullidae										
Mullus surmuletus	16.60	231	43.163	15-28	152	17.979	11-28	113	14.393	18-32
Muraenidae										
Enchelycore anatina		4	1.494	71-86	-	-	-	-	-	-
Gymnothorax unicolor	56.54	11	8.710	69-88	-	-	-	-	-	-
Muraena augusti	55.76	7	4.921	64-88	-	-	-	-	-	-
Muraena helena	75.13	-	-	-	-	-	-	2	3.608	85-98

Table 1. Continued.

Phyciidae										
Phycis phycis	37	1	3.948	41	-	-	-	-	-	-
Pomacentridae										
Similiparma lurida *^		56	1.278	11-14	137	6.028	10-16	105	4.604	11-15
Chromis limbata *^		511	23.417	11-17	54	4.692	11-14	344	12.361	11-15
Scaridae										
Sparisoma cretense	23.30	634	100.849	15-42	1716	253.446	16-36	564	67.791	15-37
Argyrosomus regius		-	-	-	-	-	-	5	4.774	44-50
Umbrina canariensis		1	0.180	23	2	0.360	20-21	1	0.130	22
Scorpaenidae										
Scorpaena porcus		-	-	-	12	1.262	14-25	12	1.452	15-26
Scorpaena scrofa		3	0.230	14-15	3	0.254	13-15	-	-	-

Table 1. Continued.

Serranidae										
Epinephelus marginatus		2	1.524	42-44	4	3.118	36-52	6	8.667	36-51
Mycteroperca fusca ^	33.50	3	3.750	39-42	9	16.451	25-42	6	13.360	15-42
Serranus atricauda	19.30	24	4.194	13-30	21	3.221	20-34	21	1.847	19-24
Serranus cabrilla	16.60	1	0.06	17	-	-	-	-	-	-
Serranus scriba	17.30	10	1.054	20-24	99	8.414	17-23	64	6.163	16-24
Sparidae										
Boops boops	13.40	75	6.840	10-33	24	2.590	20-25	41	3.639	18-27
Dentex dentex	50	-	-	-	-	-	-	4	7.368	72
Dentex gibbosus	38.60	186	41.795	16-61	284	84.737	12-71	735	95.364	15-44
Diplodus annularis	12.80	-	-	-	78	3.679	13-18	5	0.290	14-18
Diplodus cervinus cervinus	32.70	6	2.046	22-29	31	14.816	15-36	3	0.428	18-28
Diplodus puntazzo	29.20	4	2.404	26-38	4	0.780	18-32	58	5.010	24-36

Table 1. Continued.

Diplodus sargus cadenati	21.60	97	10.183	16-26	138	19.609	15-31	416	27.762	13-33
Diplodus vulgaris	20.90	243	25.297	13-28	343	36.213	12-24	521	46.493	11-29
Lithognathus mormyrus	24.60	-	-	-	1	0.41	31	-	-	-
Oblada melanura		-	-	-	-	-	-	6	1.386	24-28
Pagellus acarne	19.40	19	2.760	14-24	37	4.530	18-27	16	1.738	19-23
Pagellus erythrinus	23.20	10	2.156	15-32	80	9.814	17-31	220	24.560	16-32
Pagrus auriga	53.30	27	11.601	17-33	61	6.581	8-34	65	8.294	12-27
Pagrus pagrus	26.70	9	22.138	21-50	60	23.992	8-52	63	14.286	13-44
Sarpa salpa	29.40	51	20.615	18-27	525	64.550	19-34	84	21.009	18-38
Sparus aurata	40	1	0.124	31	-	-	-	2	0.802	26-34
Spondyliosoma cantharus	22.70	160	22.354	10-29	282	35.409	15-28	212	19.758	14-37
Synodontidae										
Synodus saurus *		1	0.032	34	-	-	-	-	-	-

Table 1. Continued.

Tetraodontidae										
Canthigaster capistrata *		2	0.089	10-13	2	0.034	11-13	3	0.056	10-12
Sphoeroides marmoratus *		3	0.19	13-17	2	0.052	13-14	1	0.082	15
Triglidae										
Trigloporus lastoviza	29.60	-	-	-	1	0.154	23	-	-	-
Zeidae										
Zeus faber		1	0.357	39	-	-	-	-	-	-

Table 2. Results of the SIMPER routine testing for dissimilarities between each pair of zones, based on abundance data. The species are in decreasing order of contribution. *δi*, mean dissimilarity; *δi*%, contribution of each species to mean dissimilarity; SD: standard deviation.

Agaete *vs.* Las Palmas δ_i=82.11			Agaete *vs.* Telde δ_i=84.41			Las Palmas *vs.* Telde δ_i=81.65		
Species	δ_i%	δ_i/SD	Species	δ_i%	δ_i/SD	Species	δ_i%	δ_i/SD
S. cretense	1.06	14.17	*S. cretense*	0.99	12.02	*S. cretense*	1	14.49
M. surmuletus	0.86	9.55	*M. surmuletus*	0.82	9.61	*S. hispidus*	0.94	9.48
S. hispidus	0.81	7.67	*D. vulgaris*	0.88	9.1	*D. gibbosus*	0.74	9.43
D. vulgaris	0.87	7.67	*D. gibbosus*	0.64	8.04	*D. vulgaris*	0.83	8.69

Table 2. Continued.

S. cantharus	0.93	6.29	*C. limbata*	0.61	6.44	*S. cantharus*	0.92	6.34
D. gibbosus	0.61	5.66	*S. cantharus*	0.86	6.2	*D. sargus cadenati*	0.63	5.42
C. limbata	0.55	5.3	*D. sargus cadenati*	0.67	5.71	*P. erythrinus*	0.62	5.17
S. salpa	0.55	4.63	*P. erythrinus*	0.54	4.5	*M. surmuletus*	0.73	4.9
D. sargus cadenati	0.69	4.28	*P. incisus*	0.52	4.06	*S. salpa*	0.51	4.84
P. incisus	0.54	4.04	*S. hispidus*	0.5	3.84	*C. limbata*	0.47	3.39
P. erythrinus	0.48	3.42	*B. boops*	0.54	3.33	*S. lurida*	0.58	3.36
S. lurida	0.6	3.11	*S. salpa*	0.51	3.16	*B. capriscus*	0.42	2.92
B. boops	0.51	3	*S. lurida*	0.61	2.99	*P. pagrus*	0.52	2.84
B. podas	0.48	2.32	*P. auriga*	0.54	2.57	*S. scriba*	0.58	2.84
P. auriga	0.56	2.32	*B. podas*	0.46	2.25	*P. auriga*	0.58	2.65
B. capriscus	0.39	2.3	*B. capriscus*	0.41	2.14	*P. incisus*	0.42	2.34

Table 2. Continued.

S. scriba	0.48	1.96	*P. pagrus*	0.48	1.8	*S. atricauda*	0.41	1.24
P. acarne	0.4	1.85	*P. acarne*	0.4	1.69			
P. pagrus	0.38	1.72	*S. scriba*	0.44	1.47			

3.2 Fishing yields

The catches of commercial species (González et al. 2012) represented a 91 % in the NW, 99 % in the NE and 96 % in the E, respectively, i.e. only nine species were considered as 'discard' (Table 1). Significant differences in the average catch per unit effort (CPUE**)** were detected between zones (permutation-based ANOVA; pseudo-F= 109.9, P< 0.001). *A posteriori* pairwise tests indicated that fishing yields were similar between the NW (0.16 ± 0.02 kg trap^{-1} day^{-1}) and NE (0.19 ± 0.01 kg trap^{-1} day^{-1}), being lower at the E zone (0.15 ± 0.01 kg trap^{-1} day^{-1}).

3.3 Mean size of capture

We evaluated the level of fish overexploitation, in terms of fish sizes relative to their corresponding first maturity sizes (SFM_{50}), for nine Sparids (*Dentex gibbosus*, *Diplodus sargus*, *Diplodus vulgaris*, *Pagellus acarne*, *Pagellus erythrinus*, *Pagrus auriga*, *Pagrus pagrus*, *Sarpa salpa* and *Spondyliosoma cantharus*), the parrotfish (*S. cretense*), the goat fish (*M. surmuletus*) and the filefish (*S. hispidus*). Independently of the zone, the mean size of Sparids was below the first maturity sizes (SFM_{50}), except for *P. acarne* from the NE and E zones (Fig. 3). The most abundant species, the parrotfish *S. cretense*, had a mean size close to its first maturity sizes (SFM_{50}), while *M. surmuletus* and *S. hispidus* reached a mean size at the three zones larger than their SFM_{50}. All *t*-tests indicated significant differences in mean sizes of all fishes with regard to the SFM_{50}, except both *P. erythrinus*(NW) *and S. cretense* (NW).

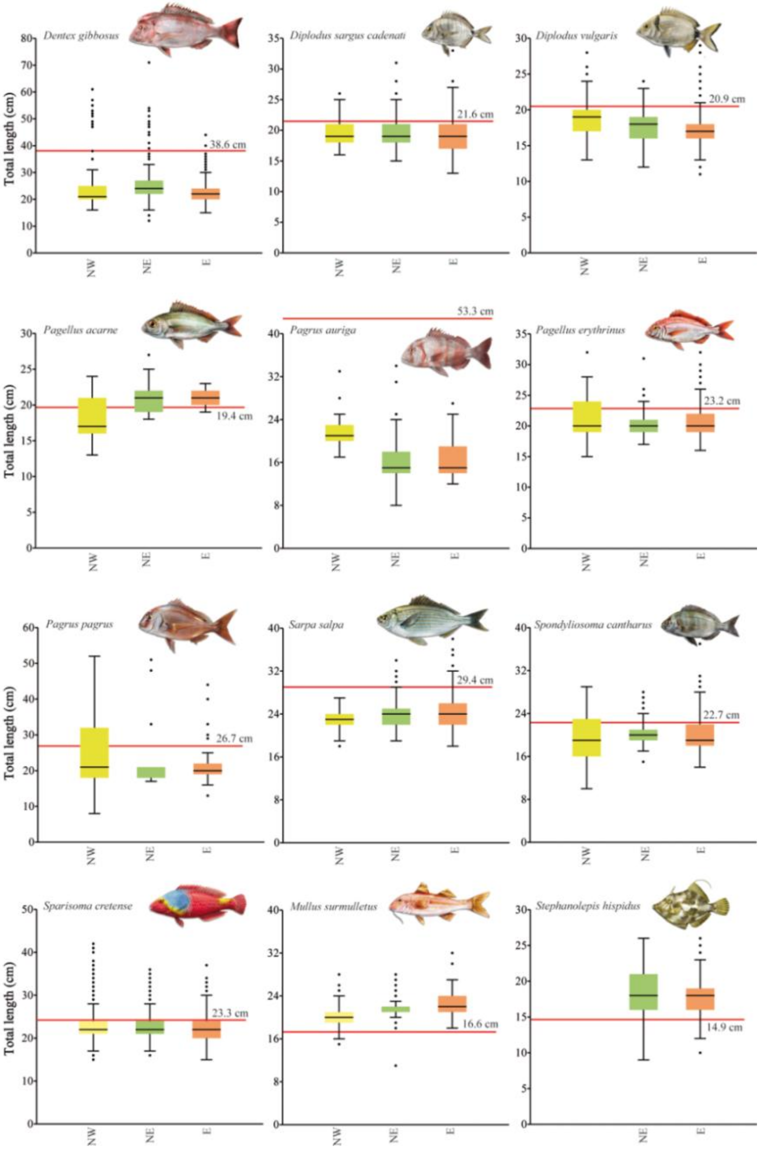

Fig. 3. Mean size of captured fish species at each zone; the SFM$_{50}$

(red line) is included, according to González et al. (2012). All *t*-tests indicated significant differences in mean sizes of all fishes with regard to the SFM_{50}, except both *P. erythrinus* (NW) *and S. cretense* (NW).

4 DISCUSSION

Our study has demonstrated that the artisanal trap fishery at Gran Canaria Island is highly unselective, catching a wide variety of fishes (37-45 species) from many families (16-20). In addition, only a reduced number of families (Scaridae, Sparidae, Mullidae, Pomacentridae and Monacanthidae) and species provided relatively high fishing yields, in terms of biomass, in particular: *S. cretense*, *D. gibbosus*, *Diplodus* spp., *M. surmuletus*, *Pagrus* spp., *Pagellus* spp. and *S. salpa.* Despite low weights, three small-sized species were relevant in terms of abundance: *S. hispidus*, *C. limbata* and *S. lurida*. In this sense, small-sized species are not usually considered as of commercial relevance (Golani et al. 2002), but in the Canary Islands these species are appreciated and found in some local markets.

Local variation in the structure and abundance of fish assemblages were detected between the NW and NE sectors of Gran Canaria Island. The fish assemblage of the NW zone was differentiated by the abundance of micro-carnivores and meso-carnivores species (e.g. *C. limbata*, *M. surmulletus*, *P. acarne* and *Pomadasys incisus*), which typically feed on benthic organisms, i.e., shrimps, amphipods, polychaetes, molluscs (Tuya et al. 2004; Domanevskaya and Patokina 1984; Fehri-Bedoui and Gharbi 2008). In contrast, three herbivorous/omnivorous fishes, *S. cretense*, *S. hispidus* and *S. salpa* (Clements and Livingston 1983; Petrakis and Papaconstantinou 1990; Jadot et al. 2000, 2002), dominated the fish assemblage from the NE zone. *S. salpa* is a species that may opportunistically feed upon the POM produced by anthropogenic activities (Boyra et al. 2004; Dempster et al. 2004; Tuya et al. 2005, 2006b), while *S. hispidus* is associated with bottoms of fine sediments (Mancera-Rodríguez and Castro-Hernández 2004, 2015). In addition, this variation could be also related to the presence and abundance of dominant algal functional groups. For example, frondose fucoid species are more dominant on swell-exposed shores (NW) than on swell-protected shores, whereas turf-algae show a reversal pattern (Tuya and Haroun 2006).

Several studies have concluded that the coastal resources off the Canary Islands have long been over-exploited (Bas et al. 1995; Pajuelo and Lorenzo 1995; Falcon et al. 1996; Tuya et al. 2004). Most likely, this is the result of several interplaying factors, such as the improvement in materials for building traps, a large capability and autonomy of artisanal boats, better port infrastructures, increased local market demands and, importantly, the advent of recreational fishing in the last decades, which may capture up to 60% of the total capture at some islands, for example in Gran Canaria Island (RESPESCAN 2008; Castro and Hernández-García 2012). This has been reflected in a progressive decline in the mean fishing yields at Gran Canary island in the last 4 decades, from 2.2 Kg $trap^{-1}day^{-1}$ in the 1970s at the south of the island (Castro and Hernández-García 2012) to 0.14-0.18 kg $trap^{-1}day^{-1}$ (this study) at the north-east of the island, although this value is similar to that provided by Hernández-García et al. (1998) for the eastern side of Gran Canary island (0.15 and 0.21 kg $trap^{-1}day^{-1}$) from 1989 to 1996. In any case, the average number of fish traps per artisanal fishing vessel has decreased (approximately from 275 in the 1990s to 180), following a 65% reduction in the size of the operating fleet from 1996 to nowadays (Bas et al. 1995; Hernández-Garcia et al. 1998; Couce-Montero 2009). Despite a lack of specific studies, the regional government (through the local fisheries authority) and fishermen are aware that fishing yields have severely decreased in the last 4 decades (REPESCAN 2008), but relevant management implications have not been accomplished, as a result of a lack of political willingness.

Fisheries regulations are often difficult to enforce in areas facing overexploitation; the size of fishery species become smaller through time, and fishermen claim for a decrease in the minimum size of commercialization, despite local fishermen has also willingness to increase other minimum size of captures (e.g. *Mullus surmuletus* and *Epinephelus marginatus*). However, a well-managed fishery is expected to use fishing gears that catch most of the available species at sizes that do not undermine sustainability (McClanahan and Mangi 2001). In our case study, the majority of commercially captured species were juveniles and sub-adults; in the case of hermaphrodite species, most individuals have not reversed sex. In any case, it is important to point out that, under normal conditions, fishermen should have released these captures back to the sea. Only those fish species maturing at small sizes, e.g. *M. surmuletus* and *S. hispidus* (Pajuelo et al. 1997; Mancera-Rodríguez and Castro-Hernández 2004, 2015), which have short life-cycles and high turnover rates might be able to withstand overexploitation. These species are trappable because their life history characteristics enable them to persist despite high rates of fishing mortality. However, remaining species, particularly in the case of Sparids, could be overexploited, as previously indicated by other works (Pajuelo and Lorenzo, 1995, 1996, 1999; REPESCAN, 2008). It is worth noting, moreover, that the first maturity size (SFM_{50}) of most fish species were obtained many years ago, and might have changed.

A limitation of this study is that data only corresponds to a reduced temporal window (May to September 2009), what could limit our conclusions and so our inference capacity to other circumstances. Nevertheless, at the light of our results and previous studies in the study region, it is recommended an effective management of resources, implying a reducing fishing pressure (professional and, importantly, recreational), to study the proper use of fish traps (e.g. mesh structure and redesign systems to reduce ghost fishing, systems to locate lost traps), study and update first maturity sizes (SFM_{50}) of the main commercial species, socio-educative programmes to raise awareness in the necessity of conservation and a larger number of marine reserves providing essential refuges for species that are particularly vulnerable to overexploitation (Francour et al. 2001; Roberts, 2005; Kellner et al, 2007; Kerwath et al, 2013; Buxton et al, 2014).

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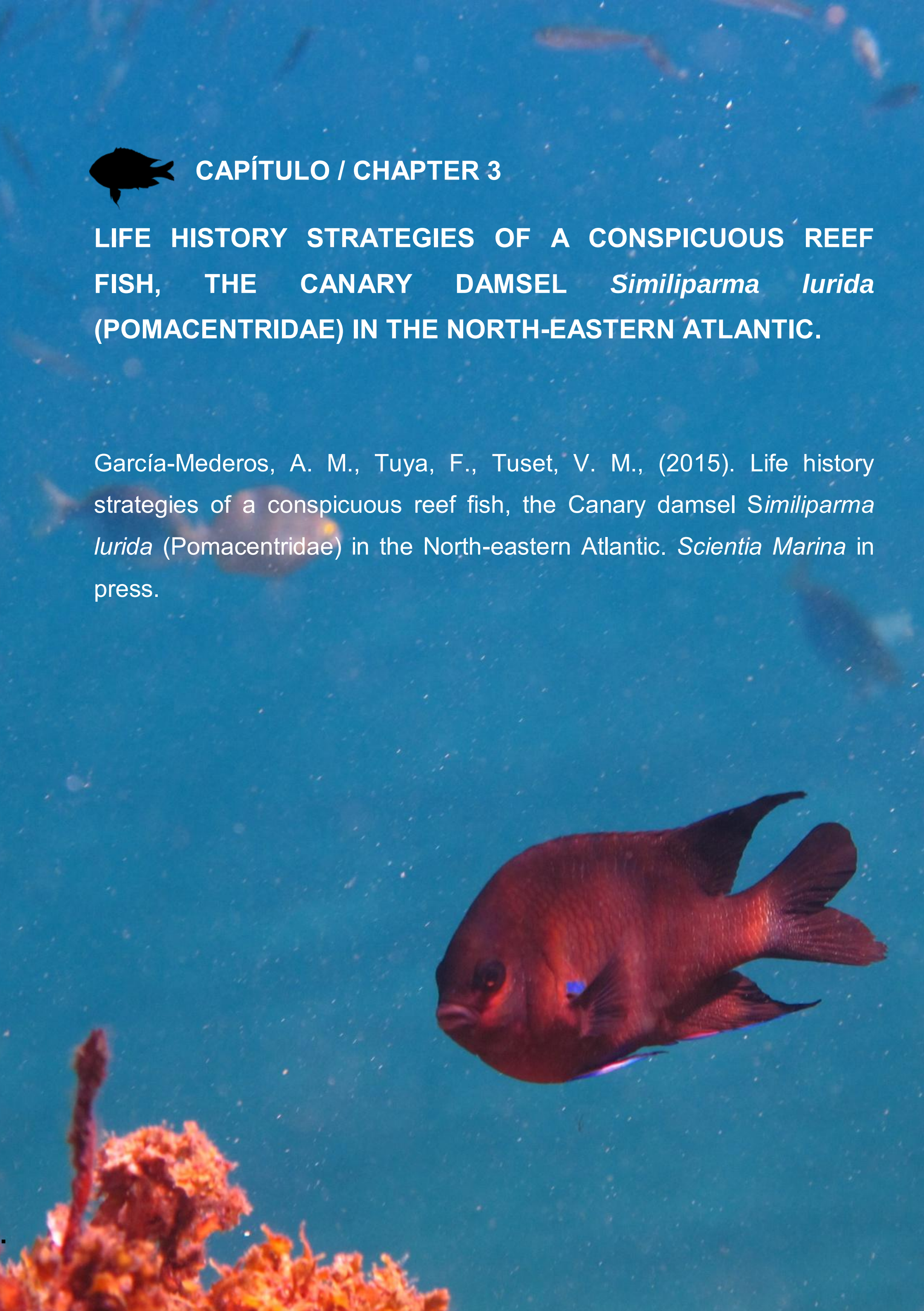

CAPÍTULO / CHAPTER 3

LIFE HISTORY STRATEGIES OF A CONSPICUOUS REEF FISH, THE CANARY DAMSEL *Similiparma lurida* (POMACENTRIDAE) IN THE NORTH-EASTERN ATLANTIC.

García-Mederos, A. M., Tuya, F., Tuset, V. M., (2015). Life history strategies of a conspicuous reef fish, the Canary damsel S*imiliparma lurida* (Pomacentridae) in the North-eastern Atlantic. *Scientia Marina* in press.

Life history strategies of a conspicuous reef fish, the Canary damsel *Similiparma lurida* (Pomacentridae) in the North-eastern Atlantic.

INDEX

1 INTRODUCTION

A crucial goal in fish population ecology is to describe the temporality of key life-story traits, such as growth, reproduction (spawning) and subsequent recruitment in the benthic system. Such information is essential for proper management of fish species when subjected to human exploitation (Caldow and Wellington 2003, Morgan 2008, Smallwood et al. 2013).

The pomacentrids (damselfishes) are a diverse fish family, including *ca*. 29 genera and 396 species distributed throughout tropical to temperate oceans of the world (Robertson 1998, Nelson 2006, Eschmeyer 2015). They are among the first fishes described by Linnaeus, back in the XVIII century, and they have subsequently received the attention of other well-known fish taxonomists and naturalists (Bleeker 1877, Cuvier and Valenciennes 1830). In terms of the number of species, this family is the third-largest fish group in coral-reef ecosystems, after Gobiidae (>1500 species) and Labridae (>600 species) (Wainwright and Bellwood 2002), although they often reach larger abundances on reefs (Frédérich et al. 2009).

Most damselfishes are territorial and show aggressive behaviour when defending their territories (Randall et al. 1997, Randall 2005, Gordon et al. 2015); this behaviour have led to a plethora of studies that have used them as model organisms to test a range of ecological and behavioural questions (Frédérich et al. 2009). Pomacentrids deposit elliptical eggs, which have a tuft of adhesive filaments, on the substratum (Hutchinson 2006). During the incubation time, males, but in some cases females, guard eggs until they hatch, frequently attacking intruders (Allen et al. 2006). This parental care may range from hiding eggs, to guarding their offspring in elaborately prepared structures for up to several months (Balshine and Sloman 2011). Moreover, damselfishes change their colour patterns according to their reproductive patterns (Souza et al. 2011). The bridal colour (Bakker and Mundwiler 1994), size (Schmale 1981, Côté and Hunte 1989) and courtship behaviour are phenotypic characteristics of males to improve their reproductive success (Knapp and Kovach 1991). Because patterns of sexual development differ among pomacentrids, attempts to assess gonadal development require data of the different phases of the fish life cycle and at different times of the year (Sadovy de Mitcheson and Liu 2008). Recruitment of pomacentrids is widespread on onshore reefs, but juveniles may prefer alternative microhabitats relative to adults; ontogenetic shifts in habitat preferences can influence the spatial distribution of adult and juvenile damselfishes (Lirman 1994).

The diversity of damselfishes drops rapidly with increasing latitude (Kingsford 1999). This pattern can be observed in the oceanic archipelagos of the North-eastern Atlantic, including Azores, Madeira, Canaries and Cabo Verde. In Azores, two species cohabit, *Similiparma lurida* (Cuvier, 1830) and *Chromis limbata* (Valenciennes, 1833) (Santos et al. 1997, Leite et al. 2009, Afonso et al. 2013, Froese and Pauly 2015). Both species also occur in Madeira, in addition to *Abudefduf saxatilis* (Linnaeus, 1758) and *Chromis chromis* (Linnaeus, 1758) (Freitas and Araújo 2006, Wirtz et al. 2008, Froese and Pauly 2015). In the Canary Islands, it also occasionally appears *Stegastes imbricatus* Jenyns, 1840 in addition to the species mentioned before (Brito et al. 2002; Froese and Pauly 2015). Finally, in Cabo Verde Islands, five species are abundant, including: *A. saxatilis*, *Abudefduf taurus* (Müller & Troschel, 1848), *Chromis lubbocki* Edwards, 1986, *Similiparma hermani* (Steindachner, 1887), and *S. imbricatus*; seven species are occasional, including: *Abudefduf hoefleri* (Steindachner, 1881), *C. chromis*, *Chromis cyanea* (Poey, 1860), *Chromis multilineata* (Guichenot, 1853), *Microspathodon chrysurus* (Cuvier, 1830), *S. lurida*, and *Stegastes leucostictus* (Müller and Troschel, 1848) (Wirtz et al. 2013, Freitas 2014, Hanel and John 2014).

Damselfishes are excellent species as biological indicators, since they are small-sized, abundant, non-migratory, and easily recognizable in the field and, moreover, are not usually a fishing target (Linton and Warner 2003). In the Canary Islands, *S. lurida*, before known as *Abudefduf luridus* (Cooper et al. 2014), is a common fish inhabiting shallow-water rocky bottoms, especially vegetated reefs (Brito et al. 2002, Tuya et al. 2004), being abundantly captured by the artisanal fisheries fleet through traps deployed at <50 metres of depth (García-Mederos et al. 2015). Knowledge on this species in the Macaronesian area is limited to its ethology and spawning seasonality in the Azores Islands (Mapstone and Wood 1975, Afonso and Santos

2005). In this study, the main goal was to provide biological and ecological information on the population structure of *S. lurida* on rocky reefs at Gran Canary Island (Canary Islands, north-eastern Atlantic). First, we assessed the reproductive ecology and inferred growth patterns. This approach provides relevant information from a fisheries perspective, i.e. spawning seasons and first maturity sizes. Secondly, we analysed the spatial and temporal patterns of abundance, describing annual recruitment patterns and, therefore, connecting the timing between reproduction and subsequent recruitment. Additionally, we sought to determine whether variation in abundance patterns of adults, sub-adults and juveniles varied at small spatial scales in relation to habitat composition and complexity. Overall, integration of this information provided insight on the life history of this species.

2 MATERIAL AND METHODS

2.1 Study area

This study was performed in Gran Canaria Island (Fig. 1), which is located at the centre of the Canarian Archipelago, with ca. 45 km of diameter and a maximum elevation of 1950 m above the sea level (Carracedo et al. 2002). Sediments and rocky reefs mainly compose nearshore bottoms, with a high variability in the distribution and complexity of these habitats, which can be colonized by a range of canopy-forming species (Tuya and Haroun 2006, Tuya et al. 2014).

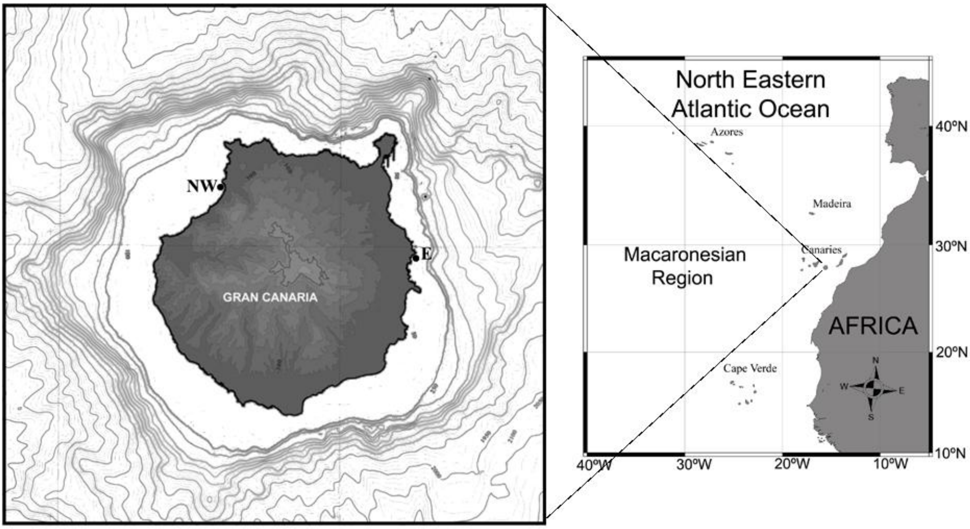

Fig. 1. Location of study localities at Gran Canary Island (eastern Atlantic Ocean).

2.2 Biological sampling

A total of 629 specimens were collected, from January to December 2012, at Telde (eastern of the island, Fig. 1), through bottom trapping carried out by the local artisanal fleet. Traps were deployed between 18 and 30 m of depth, either individually or in strings of 2-3 traps along a fishing rope. The number of days that traps were placed on the seafloor varied between 3 and 10 days. For each individual, the total length (*TL*, mm), total weight (*TW*, g), and gutted weight (*GW*, g) were recorded. The sex and stage of sexual maturation (EMS) was recorded by a macroscopic examination of the gonads. Gonads were firstly removed and weighed to the nearest 0.01 g (GNW). Maturity stages (MS) were classified as: immature (I), developing (II), spawning (III), regressing (IV) and regenerating (V) (Brown-Peterson et al. 2011). The sagittae otoliths were used to determine fish age. They were extracted from all individuals, cleaned and stored dry in plastic vials.

2.3 Age and growth

The right otolith was selected to determine fish age. As otolith weight is considered as an indicator of fish growth rate (e.g. Pawson 1990, Fletcher 1991, Cardinale et al. 2000), the criterion was based on the absence of significant differences in mean weight between left and right otoliths (Student *t*-test, $t = 0.0098$, $p = 0.992$, n= 200).

First, whole otoliths were immersed in a 1:1 glycerin–alcohol solution and observed under a stereomicroscope (NIKON SMZ 1000) using reflected light and a dark background. This method, however, did not provide reliable age estimates and thus, a random subsample of 200 otoliths was selected to perform the study through sectioning. For that, whole otoliths were embedded in epoxy resin and two or three transverse sections (1 mm thick) were cut through the central region with a slow-speed circular saw (Buehler, ISOMET-TM) to obtain a section that included the otolith core. Otolith sections were then mounted on a glass slide using Crystalbond as a mounting media and polished using decreasing grit abrasive paper (3M Lapping Film). Sections that included the core were examined under a compound microscope with transmitted light (Axioplan, Zeiss; Carl Zeiss Inc., Oberkochen, Germany) connected to a digital camera (ProgRresTM C10 plus; Jenoptik, Jena, Germany). Under transmitted light, the core and opaque bands appear as dark rings, and the wider translucent bands as clear or hyaline rings. The count path of the annuli was from the nucleus toward the tip of the inner face next to the sulcus, where the deposition of seasonal rings appeared clearly defined (Fig. 2a).

To assess the precision of readings, one experienced reader counted opaque bands without knowledge of fish size at least twice. To minimize reading bias, the two readings were separated 2-3 months after randomization in the process of readings. When readings differed, a third reading was taken. An otolith was only considered unreadable, and so excluded from the analysis, when the differences between readings did not improve after this procedure. The coefficient of variation (CV= SD/mean) was used to measure precision of annuli counts together with a paired t-test to statistically compare differences between readings (Chang 1982, Campana 2001). To assess the yearly pattern of deposition of otolith annuli, the appearance of each otolith margin was recorded as opaque or translucent.

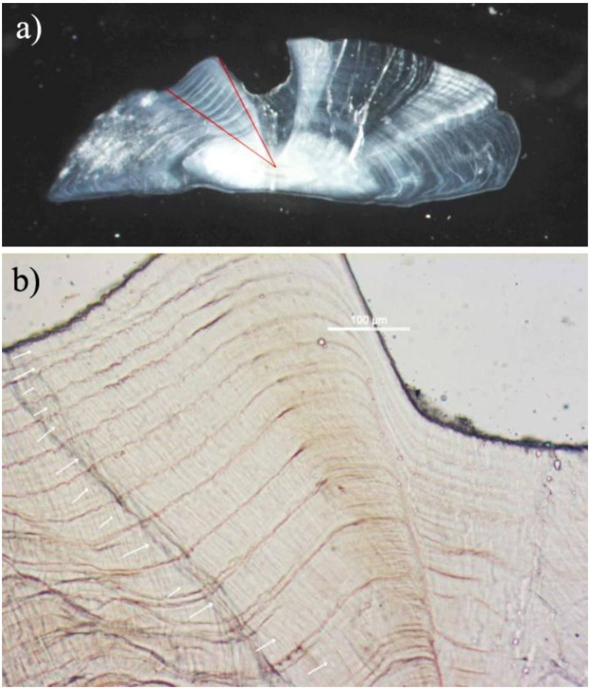

Fig. 2. Otolith transverse sections showing the selected zone for ageing and the nucleus (a, 40X under reflected light) and annual rings for an individual of 13 years (b, 100X under transmitted light).

The timing of annulus formation was examined by plotting the percentage occurrence of otoliths with a peripheral opaque band as a function of the sampling month (Morales-Nin 1992). January 1st (peak spawning; see results) was considered the birthdate, hence their annuli count was assigned to equal age. Finally, the von Bertalanffy growth equation was used to describe the growth of the species; it was fitted to the observed individual length-at-age data, rather than the frequently used mean length-at-age, to show individual growth variability:

$$L = L_{\infty}[1 - e^{-k(t - t_{o})}]$$

where L is the total length (cm), L_{∞} is the asymptotic length, k is the growth coefficient, t is the age (years) and t_0 is the hypothetical age at which length is zero. To better estimate growth parameters, ages of smallest individuals (undifferentiated) were used for both sexes (García-Mederos et al. 2010). Hotelling's T^2 test was used to compare growth parameters between males and females (Cerrato 1990, Gordo 1996).

A multiple linear regression model was used to evaluate whether age determination was predicted by otolith weight, otolith diameter and fish size (Boehlert 1985, Schwamborn and Ferreira 2002). All variables used in the multiple linear regression were log-transformed to conform the assumptions of linearity, i.e. normality and homogeneity of variances (Zar 1996).

2.4 Reproductive biology

The spawning pattern was assessed from monthly changes in the frequency of the maturity stages and the gonadosomatic index (West 1990):

$$GSI = 100\ (GNW / GW)$$

Size at first maturity was based on the examination of males and females in mature phases (phase III, phase IV, or phase V) and immature individuals collected during the spawning period. The total length of all individuals was used to estimate the size at first maturity (L_{50}), defined as the size at which 50% of all fish are at sexually mature phases. Maturity curves were adjusted using the logistic curve (Pope et al. 1975):

$$P = 100 / (1 + \exp\ (a + b\mathrm{TL}))$$

where P is the percentage of mature individuals as a function of size class (TL), and *a* and *b* are specific parameters which can change during the life cycle. A logarithmic transformation was initially applied to calculate the parameters *a* and *b* by means of linear regression. An Analysis of Covariance (ANCOVA) was used to compare the curves of maturity between sexes.

The sex ratio of the population (males: females), and the sex ratio by size intervals (10 mm), were determined. Sex ratios were tested statistically for significant deviations from the expected 1:1 ratio via chi-square tests (α = 0.05).

2.5 Abundance patterns

Spatial and temporal variation in the abundance of *S. lurida* was studied from visual censuses carried out, on a monthly basis between January and December 2012, at two randomly selected localities (Fig. 1). One locality is in the north-western (NW, Agaete, 28° 5' 57.58"N, 15°42' 33.48"W) and the other in the eastern of the island (E, Telde, 27°59' 21.68"N, 15°22' 12.96"W); visual counts were performed between 0.2 and 5.8 m depth. Only individuals >2 cm (TL) were counted to optimize the *in situ* identification. On each sampling occasion, n= 5 replicated 25 m transects were haphazardly surveyed during daylight hours. The abundance of fish within 2 m of either side of each transect (100 m^2) was recorded on waterproof paper by the same diver, according to standard procedures for the study region (Boyra et al. 2004, Tuya et al. 2004). Individuals were categorized as juveniles (TL<4 cm), sub-adults (TL 6-8 cm) and adults (TL>10 cm) based on morphological characteristics, fundamentally related to their coloration and body size (Mapstone and Wood 1975). This approach was subsequently endorsed by our data (see results). Concurrently, the diver counted on his way back the number of large (>1 m) and small (<1 m) topographic elements of the rocky substrate (i.e. cracks, crevices, caves, holes per 100 m^2), and visually estimated the percentage cover of algae, following standardized procedures via the

Linear Point Intercept (LPI) sampling technique (Ohlhorst et al. 1988). The type of substrate was recorded every meter along the 25 m long transect (i.e. 25 points per transect). Water temperature on the bottom was registered by using an underwater thermometer.

Differences in the total abundance of juveniles, sub-adults and adults among months (fixed factor) and localities (random factor) were tested through ANOVAs from square root transformed data; this was necessary to avoid heterogeneous variances. Multiple linear regressions tested whether the number of small and large topographic elements (100 m^{-2}), the type of substrate, and the algal cover (per transect) affected abundances of the damselfish through time. To retain variables with good explanatory power, the AIC routine was used as a selection criterion for each model (the smaller the value the better the model, Anderson and Legendre 1999), and the contribution of each independent variable to each model was described with partial-r^2 values. Collinearity diagnoses among independent (predictive) variables were carried out through Spearman-rank-correlations. All analyses were based on a 'forward' selection procedure.

3 RESULTS

3.1 Population structure

Fish ranged in size from 56 to 157 mm TL, and weighed between 3.9 and 76.6 g TW. A total of 419 males, 113 females and

110 immature specimens (gonads were characterized by small, thin and translucent filaments) were identified. Significant differences (Student *t*-test, $t = 11.22$, $p = 0.002$) were found between the mean sizes of sexes; males were larger than females (Table 1). The size and weight distributions differed significantly between males and females (Kolmogorov-Smirnov test, length: $d = 6.00$, $p<0.0001$; weight: $d = 5.67$, $p<0.0001$).

Table 1

Summary statistics of the size and weight for *S. lurida* according to sex. SD, standard deviation.

Variable	Males				Females			
	n	range	mean	SD	n	range	mean	SD
Total length (cm)	419	75-157	135.42	7.65	113	79-114	122.44	11.51
Total weight (g)	419	8.9-76.6	54.28	8.39	113	10.4-67.2	42.60	10.61

The overall ratio of males to females was 1:0.26; the hypothesis of uniformity between sexes was then rejected ($\chi^2 = 180.5$, $p<0.05$). Females were found in most size intervals; however, males were more abundant in the larger size interval (130–140 mm) (Table 2).

Table 2

Number of males and females of *S.lurida* by 10 mm size (total length) class intervals and chi-square statistic to test the sex ratio from the hypothetical 1:1 ratio. *, significant for p< 0.05.

TL (mm)	Males	Females	Sex-ratio	c^2	*p*
70	1	1	1:1.00	0	1.000
80	1	2	1:0.50	0.333	0.564
90	-	-	-	-	-
100	0	6	-	-	-
110	6	10	1:1.66	1.000	0.317*
120	58	65	1:1.12	0.389	0.528
130	216	20	1:0.09	162.780	0.000*
140	119	3	1:0.02	110.295	0.000*
150	6	0	-	-	-

3.2 Growth

The readings coincided for 171 otoliths (85%) and were dissimilar for the remaining 29 (15%). There was no significant difference in age estimation between readings (CV = 2.7%; $t = -0.094$, $p>0.05$). The growth rings, opaque and translucent, were usually well visible (Fig. 2). Marginal zone analysis showed a pattern of alternating narrow translucent zones and wide opaque zones, forming one annulus per year. Otoliths with an opaque edge (faster growth) were more abundant (52.9–87.5%) from November to March (spawning season, see below), while otoliths with a translucent edge (slower growth) were more common during the remaining months (Fig. 3).

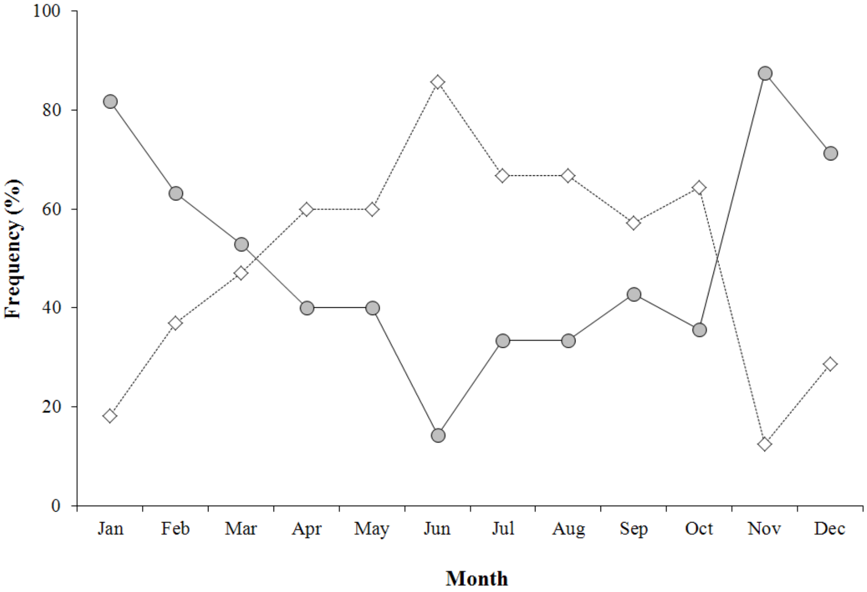

Fig. 3. Monthly changes in otolith frequency with opaque (—●—) and translucent (--◊--) edges.

Fish ranged in age from 0 to 18 years, being between 8 and 10 years the dominant age classes. Females reached higher maximum ages (18 years) than males (14 years). Significant differences in mean sizes between sexes were obtained from V and X-age classes (Table 3), where a great number of specimens were ageing. A considerable variability in the length-age relationship indicated considerable differences in individual growth. The growth curve obtained by age-at-length data was well described by a von Bertalanffy growth, attaining a determination coefficient (r^2) of 0.439 for males and 0.707 for females (Fig. 4, Table 4). Significant differences were found between the von Bertalanffy growth curves of both sexes (Hotelling's T^2-test, $T^2 = 68.654 > T_0{}^2{}_{0.05,3,181} = 8.515$).

Table S1. - Age-length key for *S. lurida* at Gran Canaria Island. n, number of individuals; SD, standard deviation; TL, total length; *, significant differences.

TL (mm)	Age classes (years)																		
	0	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
55	1																		
60																			
65		1	1																
70																			
75				1		1													
80			1	1															
85				1	1														
90				1															
95					1														
100		1				1	1	1		1									
105						1		1											
110						1	1												
115					2		1	3		1		2							
120				1		2	1	2	1	2	2	1		2	1				1
125				1		3		8	6	2	4	5	1	1	1				
130			1		1	4	5	2	2	3	4	3	3						
135				1	3	1	1	3	2	1	2	1	1	2	2	1			
140				1	1		4	2	2	4	2	2	2						
145				1			1	5	3	5	3			2	1				
150								1	2	1									
155															1				
Total	1	2	3	9	9	14	15	28	18	20	17	14	7	7	6	1	0	0	1
Males																			
n			1	5	7	9	11	18	10	13	8	7	3	4	2				
mean			133.0	125.0	126.9	128.6	134.7	136.6	142.1	142.5	139.4	131.7	137.0	135.8	152.0				
SD				28.84	18.82	5.20	8.68	9.94	7.20	6.47	7.33	9.76	6.00	9.77	7.07				
Females																			
n		1		3		5	4	9	8	7	9	6	4	2	4	1			1
mean		103.0		99.0		104.6	119.5	122.3	126.9	121.9	127.6	127.5	132.8	123.0	129.3	136.0			122.0
SD				19.16		17.18	16.54	10.32	2.85	9.55	4.67	2.59	5.56	4.24	6.95	-			-
																			-
Student *t*-test		-	-	1.368	-	3.988*	2.366*	3.481*	5.603*	5.755*	4.008*	1.018	0.958	1.694	3.755*	-			-

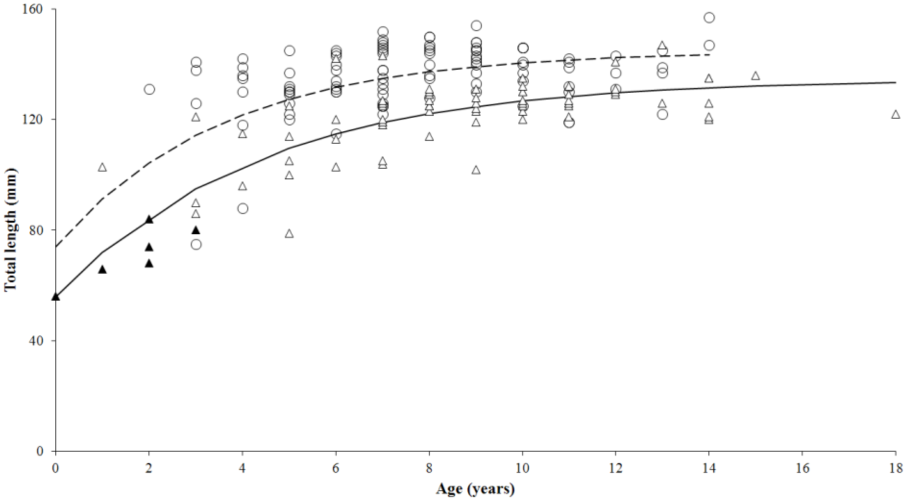

Fig. 4. Calculated von Bertalanffy growth curves for males (circle) and females (white triangle). Black triangles show the age for immature individuals.

Table 4

Von Bertalanffy growth parameters for males and females. CL, 95 % confidence limits for *L*; *K*, growth rate parameter (year^{-1}); *L*, asymptotic length (mm); n, number of individuals; t_0, time (year). Values in brackets are standard errors.

Sex	n	*L*	*K*	t_0	r^2	CL
Males	117	144.87 (4.12)	0.28 (0.06)	-2.55 (0.87)	0.439	136.70-153.04
Females	78	134.61 (4.27)	0.23 (0.05)	-2.32 (0.72)	0.707	126.08-143.14

Partial regression coefficients indicated that radius diameter (r^2-partial= 0.775, t= 13.728, p< 0.001) and otolith weight (r^2-partial= 0.5575, t= 6.367, p< 0.001) were significant predictors of fish age (Fig. 5). By contrast, fish length did not contribute to explain variation (r^2-partial= 0.338, t= -0.728, p= 0.338).

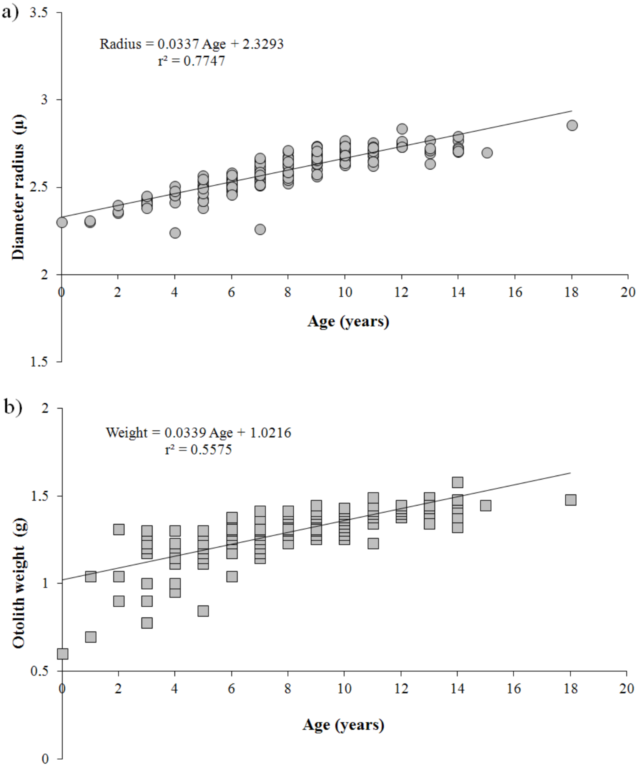

Fig. 5. Relationships between the age and weight (a) and diameter (b) of otoliths.

3.3 Reproduction

Males in phase III were observed from November to May, with a maximum peak in February (Fig. 6a). The maximum occurrence of spawning females (phase III) also occurred from November to March, including a peak in February (Fig. 6b). The presence of regressing females (phase IV) was observed from February to August. Females at immature, regressing and developing/regenerating phases (V, I and II, respectively) were found throughout the entire year. A slight increase in phase III females was observed in May, which would likely result in spawning activity during June, suggesting the possibility of a secondary breeding season (Fig. 6b). For males, the GSI increased from November to May, including a peak in January (0.258) (Fig. 6c). The GSI of females also increased from November to May, with a peak of maximum activity in February (3.897) (Fig. 6d). Overall, integration of EMS and GSI results with maturity phases throughout the year indicated a spawning season from November to May. The maturity curves were clear difference between males and females (ANCOVA, $F = 34.811$, $p<0.001$); the size at which 50% of individuals are mature was 103.44 mm TL for males and 84.71 mm TL for females (Fig. 7).

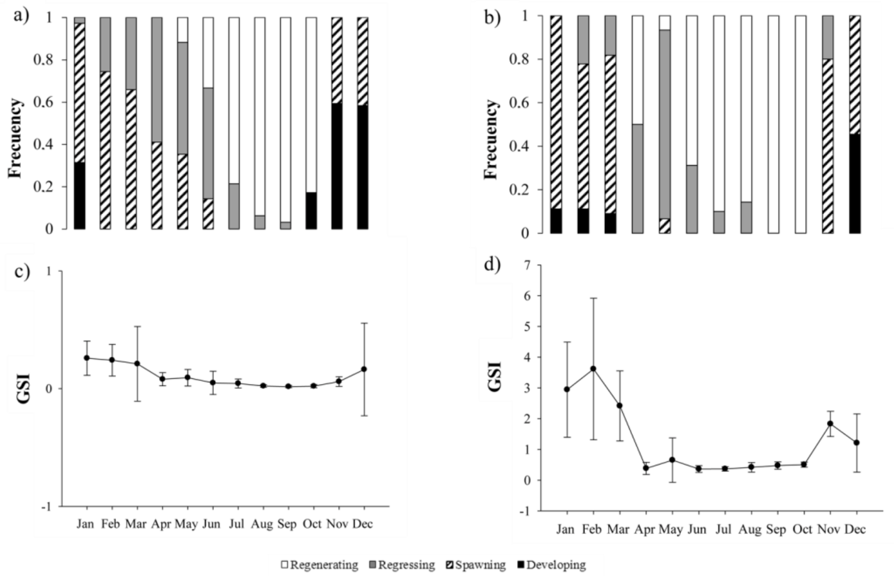

Fig. 6. Monthly variation of maturity stages and gonadosomatic index (GSI, mean ± standard deviation, SD) for males (a and c) and females (b and d).

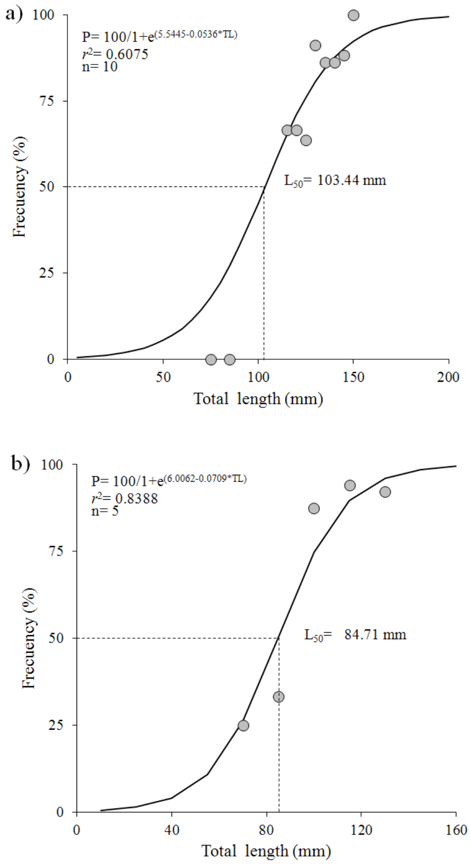

Fig. 7. Sexual maturity curves and sizes at first maturity ($L_{50\%}$) for males (a) and females (b).

3.4 Abundance and recruitment patterns

The abundance of juveniles, sub-adults and adults inconsistently varied through time between localities (ANOVA: Locality x Month, $p<0.05$, Table 4). However, juvenile abundances were significantly higher in April at both localities (9.0 ind 100 m^{-2} ± 2.6 at Agaete; 11.0 ind 100 m^{-2} ± 2.7 at Telde, Fig. 8a, b). The abundance of sub-adults attained higher mean values in July at Agaete (19.6 ind 100 m^{-2} ± 2.8), while the larger values were observed between November and January (14.2 ind 100 m^{-2} ± 0.7, 13.2 ind 100 m^{-2} ± 2.8, respectively) at Telde (Fig. 8c,d). Adults peaked in abundance at similar times at both localities; November (22.4 ind 100 m^{-2} ± 1.8) at Agaete and November-December (28.2 ind 100 m^{-2} ± 2.1, 23.8 ind 100 m^{-2} ± 1.7, respectively) at Telde (Fig. 8e, f).

Table 5

Results of 2-factor ANOVA testing for differences in the abundance of individuals between localities (fixed factor) and months (random factor). *df*: degree of freedom; MS: means squares; F: statistical value. Significant valor *P< 0.05.

	df	MS	*F*	*P*
Juveniles				
Locality	1	3.8101	7.3188	0.0076*
Month	10	5.9679	2.4785	0.0858
Locality x Month	10	2.4079	4.6253	0.0002*
Residual	88	0.5206		
Sub-adults				
Locality	1	4.7961	14.0104	0.0006*
Month	10	2.7779	0.4310	0.9102
Locality x Month	10	6.4447	18.8265	0.0002*
Residual	88	0.3423		
Adults				
Locality	1	65.7911	160.9795	0.0002*
Month	10	7.3129	4.3504	0.0166*
Locality x Month	10	1.6810	4.1130	0.0002*
Residual	88	0.4087		

The percentage of sandy cover in the case of juveniles and adults, and the percentage cover of algae for sub-adults, accounted for the largest contribution to variability in fish abundances at Agaete. However, the number of small topographic elements was the largest contributor to variation in the abundance of sub-adults and adults at Telde (Table S2). For the majority of specimens, the best models provided by the AIC routine included both the number of small topographic elements with algae and sandy cover, i.e. patterns of abundance were, in most cases, affected by these two descriptors of the habitat (Table S2). Juvenile abundance was significantly predicted by the presence of large topographic elements at Telde (Table S2), i.e. juveniles were particularly abundant on high relief areas.

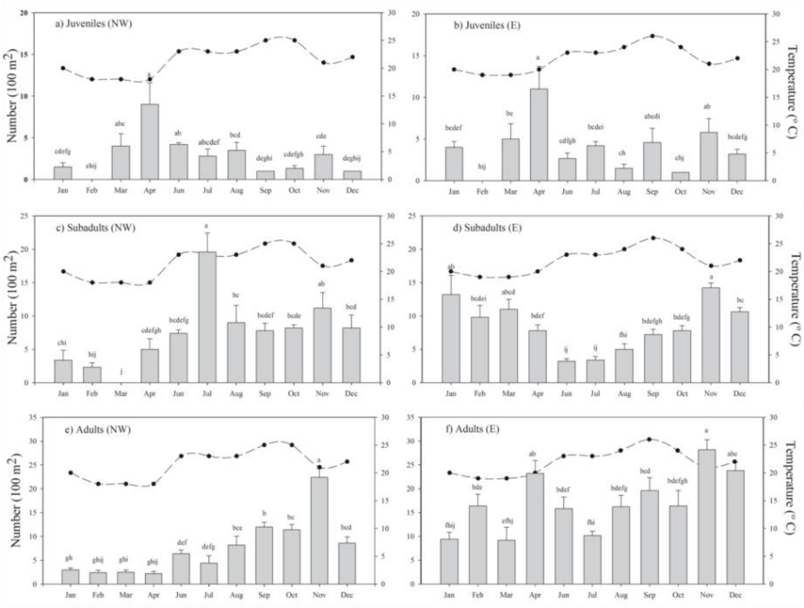

Fig. 8 Mean (± standard error, SE) abundance of individuals (100 m^2) and water temperature (─●─) throughout the study.

Table S2. - Results of multiple linear regression analyses testing for the relationship between the total abundances of juvenile, sub-adult and adult individuals and structural elements of the habitat for each locality. The AIC routine was used to retain variables with good explanatory power.

Total	Juveniles	Subadults	Adults
Agaete			
X_1= small topographical elements	X_1= Sandy cover	X_1= algal cover	X_1= Sandy cover
X_2= algal cover	X_2= large topographical elements	X_2= small topographical elements	X_2= small topographical elements
X_3= Sandy cover		X_3= Sandy cover	X_3= algal cover
$Y=-0.676+0.089X_1+ 0.399X_2+0.07X_3$	$Y=-0.536+0.117X_1+0.175X_2$	$Y=0.262+0.248X_1+0.034X_2+0.051X_3$	$Y=-0.401-0.097X_1+0.045X_2+0.167X_3$
$r^2=0.551$	$r^2=0.322$	$r^2=0.4771$	$r^2=0.446$
Telde			
X_1= small topographical elements with algae	-	X_1= small topographical elements with algae	X_1= small topographical elements with algae
$Y=49.77+0.254X_1$		$Y=0.99+0.153X_1$	$Y=28.887+0.202X_1$
$r^2=0.307$		$r^2=0.129$	$r^2=0.314$

4 DISCUSSION

The Canary damsel, *Similiparma lurida*, is somehow similar in size (157 mm TL) relative to other pomacentrids from the Macaronesian archipelagos, such as *C. limbata* (120 mm SL) and *S. hermani* (160 mm SL), but smaller than *A. saxatilis* (229 mm TL), *C. chromis* (250 mm TL) and *A. taurus* (250 mm TL) (Froese and Pauly 2015). Our findings clearly indicated this species is of early rapid growth, because it reached half of its asymptotic length within the first year. In pomacentrids, small-sized species seem to have a faster growth (Dulĉić and Kraljević 1995, Tzioumis and Kingsford 1999, Wilson and Meekan 2002), although it may be a response to unpredictable recruitment success (Longhurst 2006). Moreover, differences in growth were obtained between sexes; males grow faster (0.28 years^{-1}) than females (0.23 years^{-1}), what favours the presence of males in larger sizes. Although this is not uncommon for many fishes, this is particularly relevant for those fish species with nuptial behaviour, where males have to defend their territories and to care for their offspring (Breder and Rosen 1966, Dulčić and Kraljević 1995, Bracciali et al. 2014, Allen et al. 2006). Some studies have also indicated that fish size is correlated with social dominance, which additionally favours the acquisition of food, mate choice, retention and reproductive success (e.g. Hoffman 1985, DeMartini 1988, Folkvord 1991, Webster and Hixon 2000, Hobbs and Munday 2004, Fero and Moore 2008). From an ecological perspective, a sexual variability of certain life-history traits may represent a trade-off, the costs paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another

(Charnov and Krebs 1973, Stearns 1989, Lester et al. 2004). A fast growth may involve a cost in terms of reproduction, as early maturing occurs at a larger size; when growth is delayed, however, maturing occurs at a smaller size (Stearns and Koella 1986, Charnov 2008, this study).

Alterations in somatic growth are not always reflected in otolith morphometry, due to continuous growth and metabolic non-dependence between both processes (Reznick et al. 1989, Fowler and Doherty 1992, Secor and Dean 1992, Xiao 1996). Many studies have indicated that otolith thickness, or weight, can explain up to 80-95% variation in fish age (Fletcher 1991, Newman et al. 1996, Labropoulou and Papaconstantinou 2000). However, Pawson (1990) concluded that this technique have a limited application in ageing fish from wild population with highly variable growth rates. Schwamborn and Ferreira (2002) found a linear correlation (r^2-partial= 0.739) between otolith weight and age of the pomacentrid *Stegastes fuscus*, but they recommended that the high variability of otolith weight-at-age hampered the use of this variable for an accurate prediction of age. In our study, otolith thickness provided a better relationship with age than weight. This is most likely because the otolith weight may underestimate the age of older fish (Beckman et al. 1991, Wilson et al. 1991, Ferreira and Russ 1994, Worthington et al. 1995, Newman et al. 1996, Tuset et al. 2004).

There are many spawning strategies by marine fishes, including variation at daily, lunar and seasonal scales (Robertson 1991). Our results demonstrated that *S. lurida* has a large spawning period (ca. 7 months) that coincides with an increase in fish growth and the appearance of denser otolith rings. For pomacentrids, seasonal cycles of spawning and recruitment can be synchronized, particularly when one main spawning peak dominate the spawning period (Robertson 1990). This occurred for the population of *S. lurida* at Gran Canaria Island; recruitment of juveniles reached a maximum in April, immediately after the main peak of spawning (February). This outcome suggests that it takes about 2 months the duration between gametes release and the appearance of recruits>2 cm. This result sounds plausible, given the fact that larval dispersion in most pomacentrids is reduced (10-24 days, Thorrold and Milicich 1990, Nemeth 2005), and that males guard fertilized eggs only for some weeks (Thresher 1984, Asoh and Yoshikawa 2002, Bessa and Sabino 2012). Some authors have suggested that certain variability in the time of recruitment may arise as a result of several spawning acts, or that larval duration vary due to environmental uncertainty (Robertson 1990, Thorrold and Milicich 1990). The fact that recruitment patterns were studied in shallower waters (0.2-6 m) relative to collections of specimens via fishing traps (18-30 m) does not seem to disturb interpretations, as the habitat is the same: rocky reefs in infralittoral bottoms.

The present study also highlighted the importance of habitat structure on the spatial and temporal variability in the abundance of juveniles, sub-adults and adults of *S. lurida* on shallow-water bottoms. The paramount role of habitat structure (e.g. substratum composition) as a driver of fish distribution and abundance has been largely highlighted (Luckhurst and Luckhurst 1978, Friedlander and Parrish 1998, García-

Charton and Pérez-Ruzafa 2001, Tuya et al. 2009, Tuya et al. 2011). In general, our results suggest that rocky bottoms covered with algae interspersed with sandy patches seem as an ideal habitat for *S. lurida*. This pattern, however, varied between localities. At Agaete, different habitat elements contributed to explain variation in the abundances of sub-adults and adults, in particular the presence of small topographic elements and algal cover. A positive influence of algal cover may be explained as damselfish territories need to contain algae where females deposit their eggs (Knapp et al. 1995, Navarrete-Fernandez et al. 2014), which are further protected by males. Small-sized topographic elements, on the other hand, provide protection against predators. The presence of large topographic elements contributed to explain the presence of juveniles at this locality. Juveniles of a range of reef fish species tend to seek refuge after recruitment into the benthos, as way to avoid predation (Scharf et al. 2006, Leitão et al. 2008), including damselfishes (Almany 2004). Hence, large ledges and outcrops, what we here have included as large topographic elements, seem to provide an ideal habitat for juveniles, which tend to concentrate in these areas. The positive influence of sandy cover on juvenile abundances may be an artefact, as large ledges and outcrops typically reduce water flow and ease sedimentation in their surroundings. Taking together, these outcomes may be indicative of a change in habitat use by *S. lurida* with ontogeny (e.g. an ontogenetic niche shift, Wilbur 1980). Ontogenetic shifts in microhabitat preferences by juveniles and adults of another pomacentrid (*Stegastes planifrons*) have been also registered (Lirman 1994); in particular, adults exhibit a preference for foliose coral heads, whereas juveniles exhibit a preference for dead foliose coral heads. At Telde, however, the number of small topographic elements exclusively contributed to explain the abundances of sub-adults and adults. This fact may be explained by the presence of more homogenous bottoms at this locality. Therefore, the discrepancy in results between the two localities points out that between-location variation in habitat composition and structure may affect partitioning of habitat niches between juvenile and adult populations of reef damselfishes.

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CAPÍTULO / CHAPTER 4

IDENTIFYING INTRASPECIFIC AND INTERSPECIFIC VARIATION OF DAMSELFISHES FROM THE CANARY ISLANDS USING GEOMETRIC MORPHOMETRICAL AND FUNCTIONAL ANALYSES.

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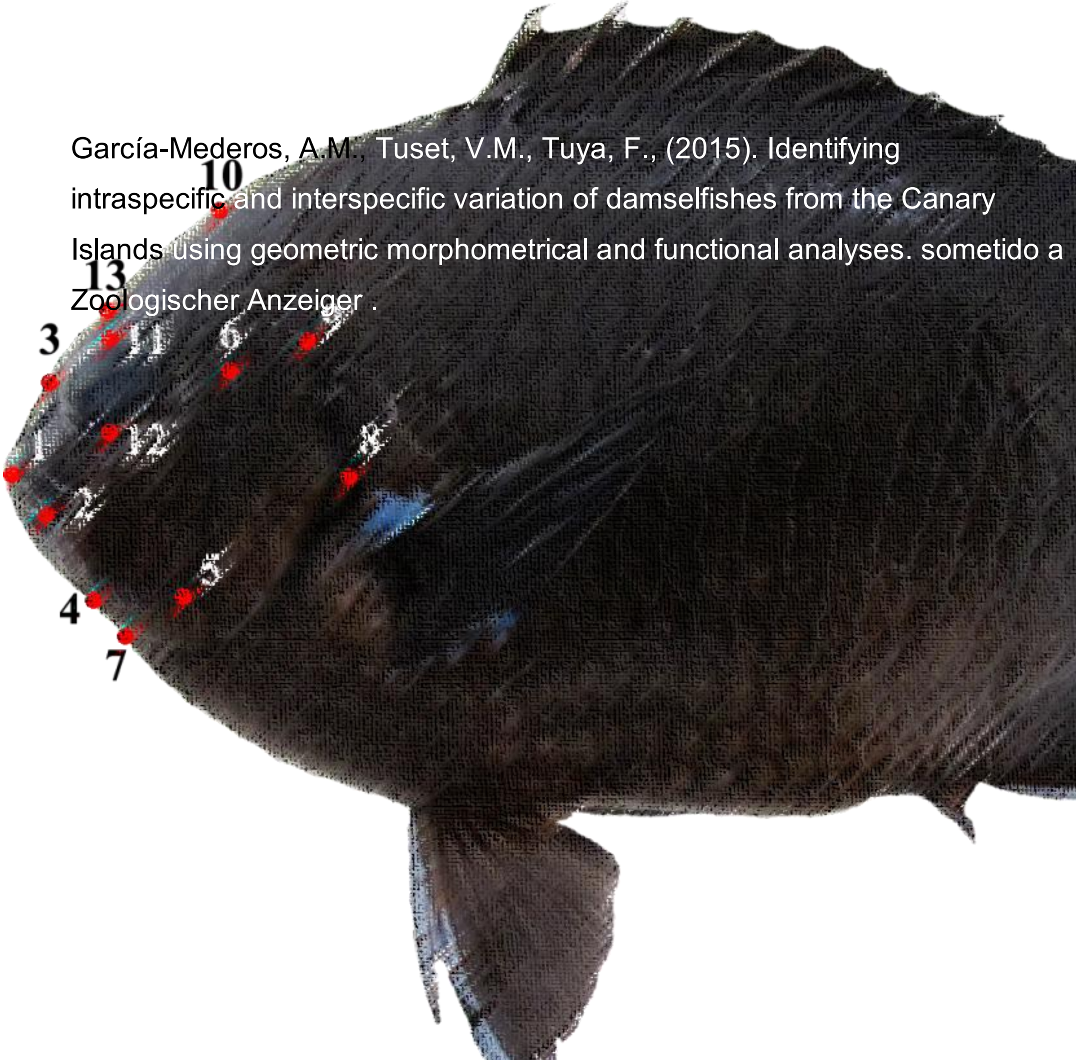

Identifying intraspecific and interspecific variation of damselfishes from the Canary Islands using geometric morphometrical and functional analyses.

INDEX

1 INTRODUCTION

Through evolution, species develop physiological, behavioural and morphological adaptations to improve their fitness and performance, hence defining species' ecological niches. The ecological niche use of marine fishes is typically reflected in variation in fish morphology, which is directly connected with a range of fish vital functions and/or activities (Karr and James, 1975; Gatz, 1979; Winemiller and Pianka, 1990; Motta et al., 1995; Frédérich et al., 2013). Variation in fish morphology is mainly reflected in variability in body and head shape. Body shape is related to multiple vital activities, such as swimming, searching for food, evading predators, courtship dances and territory defence (Schoener, 1971; Webb, 1984; Walker 2010). Head shape is mainly linked with foraging and prey selection (Snorrason et al., 1994; Wainwright and Richard, 1995; Adams et al., 1998). Feeding and locomotion have been, in particular, considered key functional abilities to understand niche partitioning among fishes and so their coexistence (Kneitel and Chase, 2004). In turn, the processes of evolutionary radiation involve a strong connection between both functional abilities (Collar et al., 2008).

At the level of species, niche variation can occur depending on the levels of intra and interspecific competition and predation, among other factors (Araujo et al., 2011). As a consequence, it is common to find morphological polymorphism within populations, including variation in head and body shape (Arruda, 1977; Duka and Shevchenko, 1980; Skulason and Smith, 1995; Hegrenes, 2001; Moe et al., 2004; Borcherding and Magnhagen, 2008). These local morphological variations have been described in genetically isolated populations and populations with high levels of gene flow (Rice and Hostert, 1993; Kawecki and Ebert, 2004; Marcil et al., 2006; Nosil, 2008; Elmer et al., 2010). It has been pointed out that phenotypic variation seems to be less accentuated for island relative to mainland populations (Ayala and Campbell, 1974; Frankam 1977), despite a very limited number of studies have focused in the identification of species' polymorphism at insular scales (Abaad et al., 2015).

Pomacentrids, popularly known as damselfishes, are a diverse fish family, including *ca*. 29 genera and 391 species distributed throughout tropical to temperate oceans of the world (Allen, 1991; Nelson, 2006; Robertson, 1998; Eschmeyer, 2015), representing one of the most successful evolutionary radiations of coral and rocky reef fishes (Bellwood and Hughes, 2001; Bellwood and Wainwright, 2002; Cooper and Westneat, 2009; Cooper et al., 2009; Frédérich et al., 2013). The external morphology of this group is rather uniform (Allen, 1991; Wainwright and Bellwood, 2002), despite clear morphological differences between species (Emery, 1973; Gluckmann and Vandewalle, 1998; Frédérich et al., 2008, 2013; Cooper and Westneat, 2009; Aguilar-Medrano et al., 2011; Copper et al., 2014). Environmental variation explains morphological differentiation among Pomacentrids (Piñeiros et al., 2015); for example, damselfishes from tropical waters are smaller and have higher feeding rates than their subtropical counterparts (Barneche et al., 2009). Most damselfishes are territorial, showing aggressive behaviour when defending their territories, and live in coastal habitats under regimes of high wave energy (Myers, 1989; Randall et al., 1997; Randall, 2005; Gordon et al., 2015). This has implications in terms of fish manoeuvrability and acceleration at low speeds, which also vary among species (Wainwright et al., 2002; Fulton et al., 2011).

In the Canary Islands, two species of damselfishes cohabit on shallow-water rocky reefs, *Similiparma lurida* (Cuvier, 1830), previously known as *Abudefduf luridus* (Cooper et al. 2014) and *Chromis limbata* (Valenciennes, 1833) (Froese and Pauly, 2015), both of which are found at high densities (Tuya et al. 2004). Recently, two other species have been described: *Abudefduf saxatilis* (Linnaeus, 1758) and *Chromis chromis* (Domingues et al, 2006; Leite et al., 2009; Froese and Pauly, 2015). In this study, we aimed at examining morphological and functional variation within and between populations of *S. lurida* and *C. limbata* at Gran Canaria Island (Canary Islands, north-western Atlantic). Furthermore, we determined the level of interspecific variability and tested the morphological and functional equivalence of the recently described damselfishes (*A. saxatilis* and *C. chromis*) for assessing their possible successful establishment in the waters of the Canary Islands. This is rather pertinent, since this archipelago is undergoing severe changes in the composition and abundance of its ichthyofauna due to seawater warming, overexploitation of nearshore fisheries, and the massive arrival of non-indigenous fishes via ballast waters, mainly associated with oil platforms (Brito et al. 2005, 2011; Freitas and Araújo, 2006; García-Mederos and Tuset, 2014).

2 MATERIAL AND METHODS

2.1 Collection of individuals

Specimens of *S. lurida* and *C. limbata* were collected through fish traps at two localities of Gran Canaria Island during 2014; one locality is situated in the north-western side of the island (Agaete), exposed to large oceanic swells (7 Kw per m of wave front of average annual power, Idae, 2015). The second locality is situated on the eastern side of the island (Telde), which is more sheltered from wave action (5 Kw/m, Idae, 2015) (Fig. 1). Differences in wave action between the northern and eastern sides of the Canary Islands have been shown to affect the composition of coastal assemblages, for example macroalgae (Tuya and Haroun, 2006). Additionally, we obtained material of the species *A. saxatilis* and *C. chromis* from the north-eastern (Las Palmas) and eastern (Telde) sides of the island, respectively (Fig. 1).

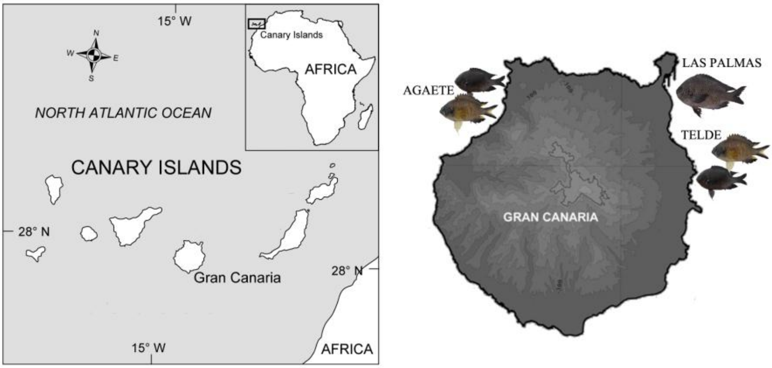

Fig. 1. Study area, including location of collections at Gran Canary Island (eastern Atlantic Ocean).

2.2 Functional analysis

Fifteen morpho-anatomical measures were taken from adult individuals (Fig. 2a) and recorded to the nearest 0.01 mm using Vernier callipers. Over 50 individuals of *S. lurida* and *C. limbata* were analysed from each locality, whereas 7 and 3 specimens were analysed for *A. saxatilis* and *C. chromis*, respectively (Table 1). Morpho-anatomical measures provided 9 functional traits related to the mode of food acquisition, position in the water column, swimming behaviour and preferred food type (Gatz, 1979; Webb 1984; Sibbing and Nagelkerke, 2001; Karpouzi and Stergiou, 2003; Dumay et al., 2004; Boyle and Horn, 2006; Albouy et al., 2011). We included (Fig.

2a): Oral gape surface (Osf= [Mw x Md]/[Bw x Bd]), which indicates the nature/size of items captured; Oral gape shape (Osh= Md/Mw), which describes the method to capture food items; Oral gape position (Ops= Mo/Hd), which denotes the feeding position in the water column; Eye size (Edst= Ed/Hd), which helps to prey detection; Eye position (Eps= Eh/Hd), which displays the vertical position in the water column; Body transversal shape (Bsh= Bd/Bw), which denotes the vertical position in the water column and the level of hydrodynamism; Body transversal surface (Bsf= $\frac{\ln[\left(\frac{\pi}{4} \mathrm{x}\ \mathrm{Bw}\ \mathrm{x}\ \mathrm{Bd}\right)+1]}{\ln(\mathrm{B}+1)}$), which also provided information on hydrodynamism; Pectoral fin position (PFps= PFi/PFb), which represents the pectoral fin use in terms of manoeuvrability; and Caudal peduncle throttling (CPt= CFd/CPd), which explains the caudal propulsion efficiency through reduction of drag. For the intraspecific analyses, functional traits were standardized to avoid an allometric effect. The biomass was selected because of the robust relationship between morphological attributes and body mass (Dumay et al., 2004). Since the exponent of relationship between a trait (x) and body mass (M) (x=aM^b) is invariant for each attribute, the transformation [log (x+1)]/[log (M+1)] was then applied (Dumay et al., 2004). For the interspecific analysis, residuals of the relationships were used, since the slopes varied among species.

Table 1

Mean ± SD of functional attribues of pomacentrids from Gran Canaria Island. n: number of individuals; Bd: body depth; Bl: body standard length; Bw: body width; CFd: caudal fin depth; CPd: caudal peduncle minimal depth; Ed: eye diameter; Eh: distance between the bottom of the head and the eye center along the head depth axis; Hd: head depth along the vertical axis of the eye; Mo: distance bottom of head-mouth; Md: mouth depth; Mw: mouth width; PFb: body depth at the level of the pectoral fin insertion; PFI: pectoral fin length; PFi: distance between the insertion of pectoral fin and the bottom of the body.

Functional traits	*Similiparma lurida*		*Chromis limbata*		*Abudefduf saxatilis*	*Chromis chromis*
	North-western	Eastern	North-western	Eastern	North-eastern	Eastern
Weight (g)	49.91 ± 5.96	49.80 ± 7.25	41.13 ± 5.85	48.88 ± 6.23	197.18 ± 28.90	44.87 ± 11.05
BI (mm)	101.76 ± 4.16	100.02 ± 6.11	96.32 ± 4.83	98.84 ± 4.37	152.71 ± 6.45	87.33 ± 4.93
Bd (mm)	47.45 ± 2.63	44.98 ± 3.26	42.22 ± 2,51	46.48 ± 2.44	84.23 ± 1.23	42.83 ± 4.90
Bw (mm)	18.95 ± 1.09	19.43 ± 1.62	17.60 ± 0.99	19.41 ± 1.06	23.60 ± 0.98	19.64 ± 1.99
Ed (mm)	6.50 ± 0.24	6.41 ± 0.29	9.32 ± 0.32	8.82 ± 0.40	12.51 ± 0.51	7.57 ± 0.53
Eh (mm)	17.60 ± 1.34	17.73 ± 1.37	16.58 ± 1.35	17.24 ± 1.39	28.53 ± 1.18	15.73 ± 2.52
Hd (mm)	27.14 ± 1.60	28.63 ± 2.00	27.41 ± 1.53	27.19 ± 1.49	46.05 ± 2.64	25.70 ± 2.60
Mo (mm)	15.61 ± 1.69	15.84 ± 1.54	14.97 ± 1.19	16.72 ± 1.77	28.71 ± 2.95	14.06 ± 3.15
Md (mm)	4.52 ± 0.26	4.42 ± 0.36	4.40 ± 0.26	4.49 ± 0.30	6.39 ± 0.20	3.91 ± 0.19
Mw (mm)	8.52 ± 0.32	7.34 ± 0.56	8.64 ± 0.49	9.10 ± 0.50	14.43 ± 0.78	7.57 ± 0.31
PFI (mm)	25.75 ± 1.45	25.25 ± 1.86	29.93 ± 1.72	30.17 ± 1.98	47.05 ± 3.94	25.89 ± 2.03
Pfi (mm)	20.57 ± 1.11	20.51 ± 1.23	18.15 ± 1.32	19.93 ± 1.10	30.84 ± 1.25	19.09 ± 1.88
PFb (mm)	48.66 ± 2.19	49.27 ± 2.91	43.43 ± 2.66	46.87 ± 2.84	87.45 ± 3.91	45.73 ± 5.89
CPd (mm)	15.60 ± 0.74	14.88 ± 1.07	14.27 ± 0.87	14.98 ± 0.78	25.62 ± 1.28	13.05 ± 1.18
CFd (mm)	32.10 ± 3.21	32.11 ± 4.28	32.43 ± 3.04	30.82 ± 2.18	58.89 ± 5.65	41.66 ± 3.51

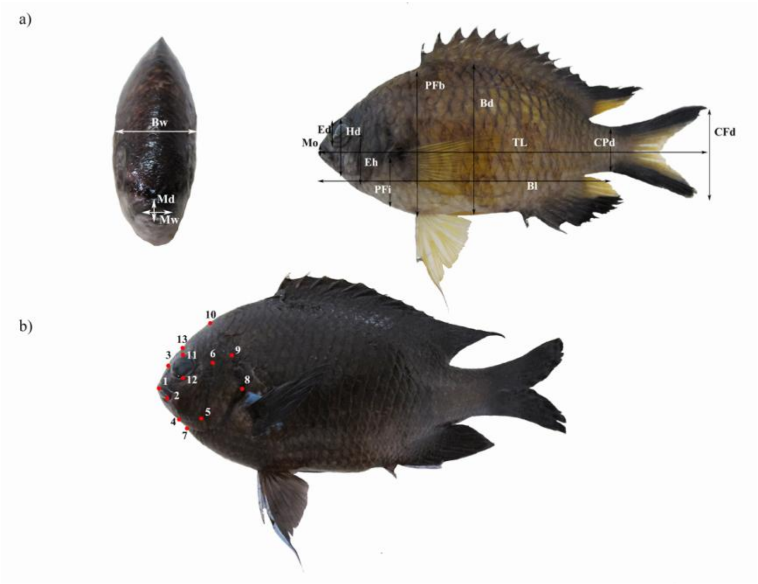

Fig. 2. Morpho-anatomical measures (a), and localization of landmarks (b) measured on Pomacentrids off Gran Canary Island. Bd: body depth; Bl: body standard length; Bw: body width; CFd: caudal fin depth; CPd: caudal peduncle minimal depth; Ed: eye diameter; Eh: distance between the bottom of the head and the eye center along the head depth axis; Hd: head depth along the vertical axis of the eye; Mo: distance bottom of head-mouth; Md: mouth depth; Mw: mouth width; PFb: body depth at the level of the pectoral fin insertion; PFI: pectoral fin length; PFi: distance between the insertion of pectoral fin and the bottom of the body.

2.3 Geometric morphometrical analysis

The head shape of each individual was analysed using a landmark-based approach (Rohlf and Marcus, 1993). We selected 13 landmarks (LM) on the left side of the head (Fig. 2b) (Copper et al., 2014; Olivier et al., 2015), including: (1) dorso-rostral tip of the pre-maxillary bone; (2) distal point of the maxillary bone; (3) anterior part of neurocranium between the LM 11 and 12; (4) the ventral point of the pre-opercular; (5) the corner of the pre-opercular; (6) operculo-hyomandibular articulation; (7) the cauda-ventral point of the operculum; (8) maximum length of the head in the anterior-posterior axis; (9) limit dorsal of the operculum; (10) dorsal margin of head directly above; (11 and 12) lie at the extreme of the orbit along the antero-posterior head axis; (13) most dorsal point of the skull at the level of the eye with respect to the line connecting LM 11 and LM 12. These landmarks were obtained, for each individual, using the TPSDIG2 software (Rohlf, 2004). The TPS Small 1.28 software package (Rohlf, 2002) was used to evaluate the approximation of the distribution of the specimens in the Kendall's shape space relative to the linear tangent space for each analysed view (Dryden and Mardia, 1998). The correlation coefficient between tangent distances and the Procrustes distances was high in all cases ($r^2 > 0.995$, $P < 0.0001$), indicating that the amount of shape variation was small enough to allow statistical analyses exclusively using the Procrustes distances. A Generalized Procrustes Analysis (GPA) (Rohlf and Slice, 1990; Dryden and Mardia, 1998) on the raw landmarks data was performed to superimpose all specimens to a common location and remove the effects of size and orientation from landmark coordinates. A Principal Component Analysis (PCA) was performed on the matrix data. The resulting PCs are often termed 'relative warps' (RWs). This is mathematically equivalent to computing a PCA using the Procrustes coordinates of each specimen after GPA when a= 0 (Rohlf, 1993; Meloro et al., 2008) and was generated through the MorphoJ software (Klingenberg, 2011).

2.4 Statistical analysis

Two multivariate analyses were performed for the identification of morpho-types and successful classification of populations (intraspecific analysis) or species (interspecific analysis). The morphs were identified using a Ward's cluster analysis from squared Euclidean distances derived from functional or morphological data. To test for differences between morphs, we performed a multivariate analyses of variances (MANOVA) using individual scores on functional variables, or the PC scores as dependent variables. Significance levels were corrected for multiple testing by using the Bonferroni adjustment factor (Sokal and Rohlf, 1995).

Intra- and interspecific variations in head shape and centroid size were explored by analysis of variance (One-way ANOVA). The centroid size is computed as the square root of the sum of squared distances of a set of landmarks from their centroid (CS) (Frost et al., 2003), and it is correlated with overall body size (Bookstein, 1991).

Significance was evaluated by using a permutation test against the null hypothesis of independence (10,000 iterations). If the relationship between centroid and fish size is significant, linear regressions of each PC scores on centroid size were performed using TPSREGR v.1.37 (Rohlf, 2009) to determine which variables affected and the percentage of explained variance by the model. Since the allometric effect was very low in all cases (<5%, see results), the PC scores were not standardized (Leysen et al., 2011).

Multivariate analysis of variance (MANOVA) was used to test the hypothesis of intraspecific and interspecific variability using functional and morphological data. This procedure was explored using a linear discriminate analysis (LDA). This technique allows evaluating the significance of differences between groups using several discriminant variables. The first step was to carry out a single factor ANOVA to find out which variables discriminate between species, using the *F* statistics to rank the potential predictors. To avoid multi-collinearity, a matrix correlation was obtained to eliminate from the LDA analysis those correlated variables. Stepwise linear discriminant analysis was used to guide selection of variable sets used in each function. This procedure chooses variables to be included in the model on the basis of the significance level of an *F*-test by ANOVA (Tuset et al., 2006). The classification accuracy of each LDA was evaluated by means of leave-one-out cross-validation estimates (Nishimoto et al., 2010). All statistical analyses were performed in XLStat 2012, a statistical plug-in for MS Excel 2011 and PAST

(PAlaeontological STatistics, version v1.81) (Hammer et al., 2001). The significance level was set at the 0.05 type I error rate for all statistical tests.

3 RESULTS

3.1 Insular populations and degree of polymorphism

Significant differences were observed in the body mass of *C. limbata* between localities (Student-*t* test, $t= -6.407$, $P< 0.0001$), so all functional traits were standardized. All functional traits showed significant differences between the north-western and the eastern populations (Table 2); however, multi-collinearity was observed between variables (Table S1). Thus, only CPt and Ops were retained in the final LDA model (Table 3), which performed well in discriminating local populations (Wilks' $\lambda= 0.442$, $F_{2,97}= 61.181$, $P< 0.0001$). There was a higher accuracy in predicting individual assignment to the north-western population (90%) than to the eastern population (82%, Table 4). The results indicated that the north-western specimens had greater values for CPt and smaller values for Ops relative to specimens from the eastern side of the island. This insular variation was reflected in the three types of morphs detected from the Ward's cluster analysis (Fig. 3a). The first and third morphotypes were mainly composed by north-western and eastern specimens, respectively; the second morphotype, however, was a combination of both populations. The MANOVA test showed significant difference between morphs (Wilks' $\lambda= 0.111$, $F_{18,178}=$

19.830, $P < 0.0001$), and the Bonferroni-corrected test indicated that the three morphs differed significantly ($P < 0.0001$, for all cases). These phenotypic variations were mainly due to the CPt and Bsf traits, which were greater in the morph-1 and smaller in the morph-3 (Fig. 4a). This indicated that the north-western specimens were characterized by higher caudal propulsion efficiency and a higher level of hydrodynamism.

Table 2
Results of ANOVAs testing for differences in functional attributes within (north-western versus eastern populations) and between species.

Variables	Wilks' lambda	*F*	d.f. 1	d.f. 2	*P*
Chromis limbata					
Osh	0.828	20.307	1	98	0.000
Ops	0.903	10.539	1	98	0.002
Cpt	0.575	72.463	1	98	0.000
Bsh	0.796	25.186	1	98	0.000
PFps	0.928	7.571	1	98	0.007
Bsf	0.724	37.267	1	98	0.000
Edst	0.706	40.726	1	98	0.000
Similiparma lurida					
Osf	0.817	21.912	1	98	0.000
Ops	0.962	3.829	1	98	0.053
Edst	0.895	11.499	1	98	0.001
Eps	0.928	7.609	1	98	0.007
Bsh	0.843	18.230	1	98	0.000
PFps	0.991	0.905	1	98	0.344
Cpt	0.944	5.851	1	98	0.017
Bsf	1.000	0.023	1	98	0.880
Chromis limbata versus *Similiparma lurida*					
Osf	0.560	51.333	3	196	0.000
Osh	0.540	55.622	3	196	0.000
Ops	0.838	12.616	3	196	0.000
Edst	0.159	346.480	3	196	0.000
Eps	0.915	6.072	3	196	0.001
Bsh	0.817	14.606	3	196	0.000
PFps	0.958	2.868	3	196	0.038
Cpt	0.820	14.315	3	196	0.000
Bsf	0.922	5.557	3	196	0.001
Among all species					
Osf	0.454	49.162	5	204	0.000
Osh	0.484	43.479	5	204	0.000
Ops	0.788	10.999	5	204	0.000
Edst	0.102	359.329	5	204	0.000
Eps	0.860	6.616	5	204	0.000
Bsh	0.358	73.123	5	204	0.000
PFps	0.614	25.598	5	204	0.000
Cpt	0.655	21.522	5	204	0.000
Bsf	0.261	115.528	5	204	0.000

Table S1
Correlation matrix of LDA discriminant analysis for functional indexes. Osf: Oral gape surface; Osh: Oral gape shape; Ops: Oral gape position; Edst: Eye size; Eps: Eye position; Bsh: Body transversal shape; Bsf: Body transversal surface; PFps: Pectoral fin position; CPt: Caudal peduncle throttling.

Chromis limbata

Variable	Osh	Ops	Bsh	PFps	Cpt	Bsf	Edst
Osh	1.000						
Ops	**0.008**	1.000					
Bsh	0.357	**0.039**	1.000				
PFps	0.414	0.274	0.591	1.000			
Cpt	0.453	0.079	0.551	0.541	1.000		
Bsf	0.521	0.100	0.778	0.758	0.754	1.000	
Edst	0.490	0.139	0.633	0.680	0.668	0.849	1.000

Similiparma lurida

	Osf	Osh	Ops	Edst	Eps	Bsh	PFps	Cpt	Bsf
Osf	1.000								
Osh	**0.001**	1.000							
Ops	0.136	**0.003**	1.000						
Edst	0.336	**0.002**	0.182	1.000					
Eps	0.152	**0.000**	0.399	0.355	1.000				
Bsh	0.357	**0.000**	**0.039**	0.297	0.208	1.000			
PFps	0.212	0.063	0.109	0.402	0.263	0.165	1.000		
Cpt	**0.000**	**0.032**	**0.032**	0.081	0.063	**0.010**	0.058	1.000	
Bsf	0.250	0.098	0.064	0.516	0.196	0.356	0.594	0.120	1.000

Chromis limbata versus *Similiparma lurida*

	Ops	Edst	Eps	PFps	Cpt
Ops	1.000				
Edst	0.283	1.000			
Eps	0.480	**-0.007**	1.000		
PFps	0.259	0.076	0.254	1.000	
Cpt	0.047	0.133	-0.011	**-0.076**	1.000

All species

	Cpt	Ops	Eps	Bsh	PFps	Bsf	Edst
Cpt	1.000						
Ops	**-0.007**	1.000					
Eps	-0.068	0.497	1.000				
Bsh	-0.112	-0.071	0.046	1.000			
PFps	-0.128	0.289	0.318	-0.194	1.000		
Bsf	**0.001**	**-0.021**	**0.025**	**-0.007**	**-0.011**	1.000	
Edst	0.175	0.228	-0.082	0.201	-0.053	0.169	1.000

For *S. lurida*, both populations (from the north-western and the eastern side of the island) presented a similar body mass (t= 0.084, P= 0.933). Only Osh did not conform to the premise of homogeneity of variances, being eliminated for further analyses. The functional traits Osf, Edst, Eps, Bsh and Cpt showed significant differences between north-western and eastern populations (Table 2); significant multi-collinearity was, however, detected (Table S1). Thus, only Osf, Eps and CPt were included in the final LDA model (Table 3), keeping a low correlation among them (r< 0.400). Significant variation was observed between both populations (Wilks' λ= 0.724, $F_{3,96}$= 12.209, P< 0.0001). Total classification success was 69%; the north-western population displayed a higher accuracy (72%) than the eastern population (66%, Table 4). Specimens from the north-western side of the island showed greater values for Eps and Osf and smaller for CPt relative to specimens from the eastern side. Although the cluster analysis also distinguished three morphs (Wilks' λ= 0.201, $F_{16,180}$= 13.813, P< 0.0001, Fig 3b) that significantly differed (Bonferroni corrected, P< 0.0001), there was not a well-defined correspondence with localities. The morph-1 was majorly composed (66.7%) by specimens from the north-western, the morph-2 was a fair mixture between localities (51.9%), and the morph-3 was dominated by specimens from the eastern side of the island (17.6%). Most functional traits from the morph-3 attained lower values. The traits that most contributed to separation among morphs were CPt, Bsf and Bsh. Again, functional traits related to locomotion were linked with the identification of morphs (Fig. 4b).

Head shape differences between north-western and eastern populations of both *C. limbata* and *S. lurida* were significant ($F= 5.59$, $P< 0.0001$ and $F= 4.61$, $P< 0.0001$, respectively). This variability was not due to differences in size, accounted by the log CS, for *C. limbata* ($F= 2.06$, $P= 0.1544$). However, significant differences were noted for *S. lurida* ($F= 7.79$, $P= 0.0063$). The PCA analysis extracted sixteen and fourteen eigenvalues that explained 96.9% and 95.4% of the total variance for *C. limbata* and *S. lurida*, respectively (Table S2).

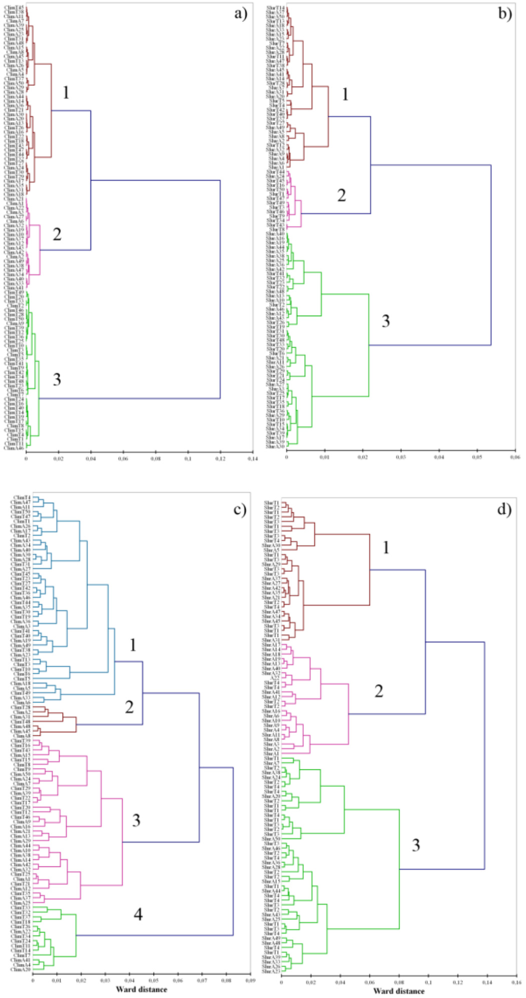

Fig. 3. Fish phenotypes obtained from functional analysis and geometric morphological analysis through the Ward's cluster for *Chromis limbata* (a, c) and *Similiparma lurida* (b, d).

For both species, the first fourth axes of the PCA reached values over 10% (see Table S2). For both species, PC1 was driven by differences in length and height in the head, whereas the anterior-dorsal head shape (more rounded or angled) mainly influenced PC2 (Fig. 5). PC3 was induced by head height, eye and pre-operculum position for *C. limbata*, and by the head, pre-operculum position, and the posterior-ventral head shape (more or lesser angled) for *S. lurida* (Fig. 5). PC4 was affected in both species by the posterior-ventral head shape (more or lesser angled) (Fig. 5). Again, and for both species, the morphospace generated from PC1 and PC2 showed a clear differentiation between localities, especially along the PC1-axis (Fig. 6).

Table S2
Eigenvalues and associated explained variance from the Principal Component Analysis for the geometric morphologic analysis of head shape of pomacentrids off Gran Canaria Island.

PC components	Eigenvalues	Variance (%)	Cumulative Variance (%)
Chromis limbata			
1	0.001054	16.917	16.917
2	0.000921	14.786	31.703
3	0.000711	11.415	43.118
4	0.000632	10.146	53.264
5	0.000500	8.024	61.288
6	0.000374	6.008	67.297
7	0.000328	5.265	72.562
8	0.000269	4.310	76.872
9	0.000255	4.093	80.965
10	0.000230	3.699	84.663
11	0.000177	2.840	87.503
12	0.000151	2.416	89.920
13	0.000133	2.128	92.047
14	0.000113	1.810	93.857
15	0.000101	1.626	95.483
16	0.000090	1.437	96.920
Similiparma lurida			
1	0.001076	18.362	18.362
2	0.000949	16.198	34.560
3	0.000713	12.162	46.721
4	0.000624	10.643	57.365
5	0.000529	9.026	66.391
6	0.000399	6.815	73.206
7	0.000304	5.184	78.391
8	0.000219	3.730	82.121
9	0.000200	3.410	85.531
10	0.000190	3.241	88.772
11	0.000116	1.974	90.746
12	0.000103	1.759	92.505
13	0.000095	1.628	94.133
14	0.000072	1.225	95.358

Table S2. Continued

Chromis limbata versus Similiparma lurida				
	1	0.0042442	43.054	43.054
	2	0.0009348	9.483	52.538
	3	0.0009078	9.209	61.747
	4	0.0006227	6.316	68.063
	5	0.0005486	5.566	73.629
	6	0.0004339	4.401	78.030
	7	0.0003718	3.772	81.803
	8	0.0003436	3.485	85.288
	9	0.0002326	2.359	87.647
	10	0.0002115	2.145	89.792
	11	0.0001857	1.883	91.676
	12	0.0001546	1.568	93.244
	13	0.0001256	1.274	94.518
	14	0.0001228	1.246	95.764
	15	0.0001062	1.077	96.841
All species				
	1	0.0040839	40.428	40.428
	2	0.0009779	9.681	50.109
	3	0.0009646	9.549	59.658
	4	0.0007315	7.241	66.899
	5	0.0005598	5.542	72.440
	6	0.0004711	4.663	77.104
	7	0.0004218	4.176	81.279
	8	0.0003634	3.598	84.877
	9	0.0002414	2.390	87.267
	10	0.0002258	2.235	89.502
	11	0.0001940	1.921	91.423
	12	0.0001654	1.637	93.059
	13	0.0001325	1.311	94.371
	14	0.0001305	1.291	95.662
	15	0.0001048	1.037	96.700

Table 3
Results of MANOVA associated with the stepwise procedure of LDA discriminant analysis for functional attributes. Bsh; Body transversal shape; Cpt: Caudal peduncle throttling; Eps: Eye position; Edst: Eye size; Ops: Oral gape position; Osh: Oral gape surface. Partial R^2 coeficients indicates the percentage of variation explained by each predictor.

Attributes	partial R^2	F	P	Wilks' lambda
Chromis limbata				
1. Cpt	0.425	72.463	< 0.0001	0.575
2. Ops	0.231	29.112	< 0.0001	0.442
Similiparma lurida				
1. Osf	0.183	21.912	< 0.0001	0.817
2. Cpt	0.074	7.748	0.006	0.757
3. Eps	0.044	4.374	0.039	0.724
Chromis limbata versus Similiparma lurida				
1. Edst	0.814	867.503	< 0.0001	0.186
2. Eps	0.049	10.114	0.002	0.177
All species				
1. Edst	0.895	585.425	< 0.0001	0.105
2. Cpt	0.205	17.603	< 0.0001	0.083
3. Eps	0.103	7.836	< 0.0001	0.075
4. Bsh	0.074	5.386	0.001	0.069

For *C. limbata*, the LDA extracted nine canonical variables (Table 5), contributing to significant differentiation between insular populations (Wilks' λ= 0.483, $F_{9,90}$= 10.715, P< 0.0001). PC1 and PC3 were the first variables introduced in the LDA that showed higher significant differences between populations (Table 5). North-western individuals were mainly differentiated by the enlarger and narrower head (Fig. 6). On average, 77% of the specimens were correctly classified to their locality, being 76 and 78% of accuracy for north-western and eastern individuals, respectively (Table 4). The Ward's cluster analysis differentiated four morphs, which did not correspond with the geographical locality. A MANOVA test indicated significantly differences among them (Wilks' λ= 0.06651, $F_{48,214.7}$= 7.491, P< 0.0001; Fig. 3c); however, morph-2 and -4 did not differ due to the low number of contained specimens (Fig. 3c). The morph-1 was characterized by specimens with larger and pointed heads, the morph-2 by rounded heads, the group-3 by larger and deeper heads and the morph-4 by deeper heads (Fig. 4c).

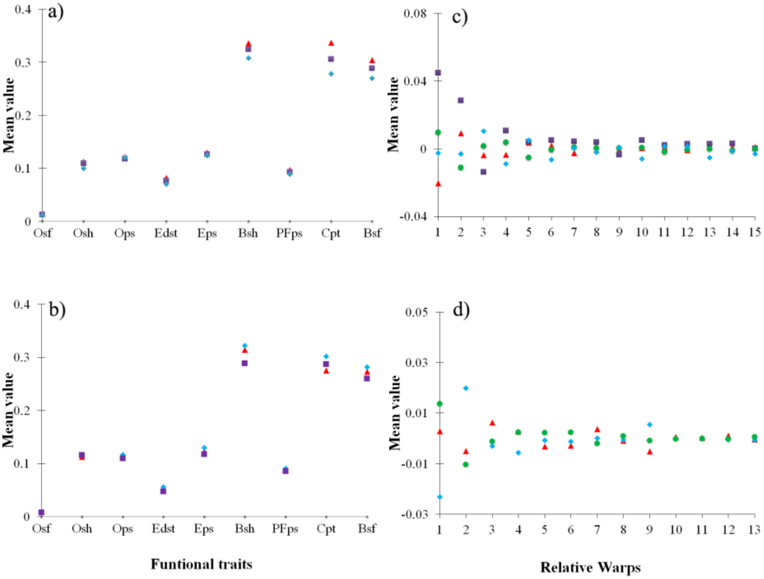

Fig. 4. Mean values of functional traits and relative warps of each phenotypic morph (in color) of *Chromis limbata* (a, c) and *Similiparma*

lurida (b, d). Morph 1, triangle in red; Morph 2, diamond in blue; Morph 3, circle in green; Morph 4, quadrate in purple.

For *S. lurida*, the linear regressions of PCs scores onto CS were significant (Goodall *F*-test, $F_{22,2156}$= 3.1278, P< 0.0001); however, the percentage of unexplained variance in this model (96.9%) demonstrated no relationship between size and shape. Therefore, PCs scores were directly used for the LDA analysis. Only four canonical variables were used to build the discriminant model (Table 5) allowing to separate populations from the north-western and the eastern side of the island (Wilks' λ= 0.602, $F_{4,95}$= 15.731, P< 0.0001). PC1 was the variable with more variance to discriminate the populations (Table 5), where the north-western individuals presented shorter and deeper heads than eastern specimens (Fig. 6). The specimens from the eastern side classified better (88% of accuracy) than those from the north-western (72%) (Table 4). The Ward's cluster analysis differentiated three morphs; only the group-1 was clearly discriminated geographically, whereas the morph-2 and -3 were mixed with over 60% of eastern specimens and 40% of north-western individuals. Significant differences were detected (Wilks' λ= 0.1197, $F_{28,168}$= 11.34, P< 0.0001; Fig. 3d) and the Bonferroni-corrected test indicated that the three morphs significantly differed (P< 0.0001 for all cases). The morph-1 was characterized by specimens with larger and pointed heads, the morph-2 by rounded heads and the morph-3 by shorter and height heads (Fig. 4d).

The Mantel test indicated that the distance matrices between functional and morphological data were correlated (*C. limbata*, $r = 0.190$, $P < 0.0001$; *S. lurida*, $r = 0.171$, $P < 0.0001$). Therefore, the identification and assignation of specimens within morphs did not depend on the method.

Table 4
Results (correct percentage of classification) of linear discriminant analysis (LDA) using functional and geometric morphological data. In bold, the method providing the best result.

Species/Localities	Functional traits	Geometric morphology
Chromis limbata		
North-western	90%	76%
Eastern	82%	78%
Total	**86%**	77%
Similiparma lurida		
North-western	72%	72%
Eastern	66%	88%
Total	69%	**80%**
Chromis limbata versus Similiparma lurida		
Similiparma lurida	98%	100%
Chromis limbata	99%	100%
Total	99%	**100%**
All species		
Similiparma lurida	100%	100%
Chromis limbata	81%	67%
Abudefduf saxatilis	100%	98%
Chromis chromis	100%	100%
Total	91%	**99%**

3.2 Interspecific variability

In the functional analysis, the standardized residuals of the functional variables in relation to body mass were used to discriminate the species. In the first analysis, which aimed at separating the common species inhabiting the island (*C. limbata* and *S. lurida*), only two (Edst and Eps) of the five functional variables (Edst, Eps, Ops, PFps and CPt) presented significant differences (Table 3), which did not correlate between them (r= -0.007; Table S1); hence they were used in the LDA model. These variables were related with the detection of preys (Edst) and the vertical position in the water column (Eps). Thus, *C. limbata* presented a larger lateral eye size characterising nektonic fishes. Total classification success was 99%; for both species, the accuracy percentage was very high, 98% for *C. limbata* and 99% for *S. lurida* (Table 4). In contrast, when the analysis included the occasional species (*C. chromis* and *A. saxatilis*), the LDA model was constructed with Edst, Eps, Cpt and Bsh (Table 3). Significant differences were displayed between species (Wilks' λ= 0.069, $F_{12,537}$= 78.014, P< 0.0001), where the first function explains 96.5% of the variance and was strongly correlated with Edst (canonical r= 0.994), and the second function explains the 2.6% with CPt as the most important variable (canonical r= 0.975). The discriminant analysis demonstrated that 91% of all individuals were correctly classified, reaching 100% for cases, except for *C. limbata* (81%, Table 4). The species closer in the functional space were *C. limbata* and *A. saxatilis*, which have a greater eye in relation to the head (Edst). In contrast, *C. chromis* and *S. lurida* occupied distant zones relative to other species, being *C. chromis* more influenced by the size of caudal peduncle (CPt) and *S. lurida* by a smaller eye (Edst) (Fig. 7a).

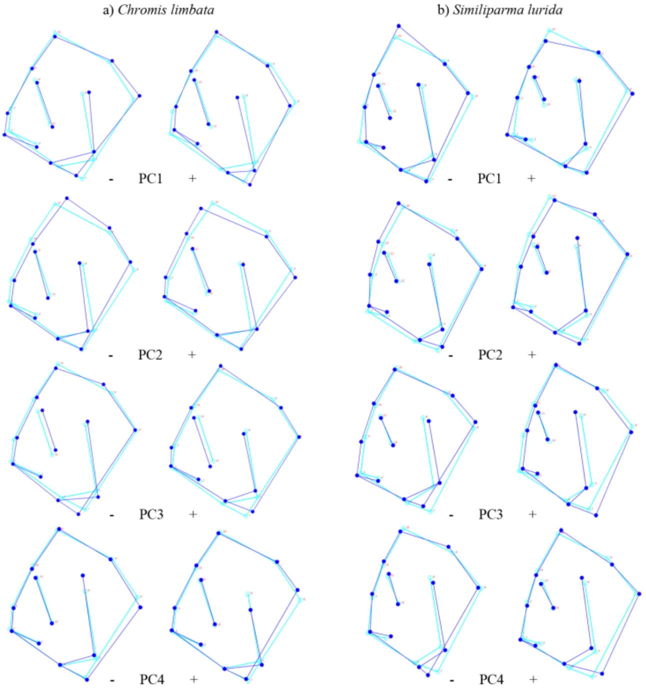

Fig. 5. Head shape changes at the positive (+) and negative (-) extremes of the distribution of the first four PC components using geometric morphometric analysis for *Chromis limbata* (a) and *Similiparma lurida* (b). The dark blue indicates these changes, while the light blue shows head shape at the *x*= 0 and *y*= 0 position.

In the geometric morphological analysis, the comparative study of head shape between *C. limbata* and *S. lurida* revealed significant differences in the Procrustes distances ($F_{22,4356}$= 121.29, P< 0.0001) and head size ($F_{1,198}$= 6.23, P= 0.0134). Fifteen eigenvalues were obtained in the PCA analysis, explaining 96.8% of the total variance (Table S2). Although the linear regressions of PCs scores onto CS were significant ($F_{22,4356}$= 2.2527, P< 0.0001), only size explained the 1.1% of variance, showing a weak relation between size and shape. The PC1 attained a 43.1% of variance and differentiated clearly the head shape of both species. The individuals of *S. lurida* presented a shorter head, as well as the eye and mouth, an angled shape in the anterior zone, and a narrower and more height pre-operculum (Fig. 8a). Specimens of *C. limbata* exhibited a larger head, including eye and mouth, a rounded shape and wider and shorter pre-operculum (Fig. 8b). PC2 was mainly related with head height for both species (Fig. 8b). MANOVA test (Wilks' λ= 0.074, $F_{9,190}$= 263.700, P< 0.0001) indicated significant differences in nine variables. These variables separated both species with an accuracy of 100% (Table 4). When data of the recently described species (*C. chromis* and *A. saxatilis*) were added, no changes were noted in size ($F_{22,4576}$= 2.3942, P< 0.0001; and 1.1% of total variance), and the meaning of PC scores. The discriminant analysis showed significant variability between species (Wilks' λ= 0.032, $F_{36,577}$= 35.605, P< 0.0001, Table 5) from twelve PC scores used in the model. The first two canonical discriminant functions explained 99.7% of variance, clustering

Chromis spp. and clearly separating *S. lurida* and *A. saxatilis* (Fig. 7b). The overall accuracy in discrimination among species reached 98% (Table 4). Except for *C. chromis* (67%, n=3), the other species were highly separated in the model; hence the head shape was showed as a clearly specific character.

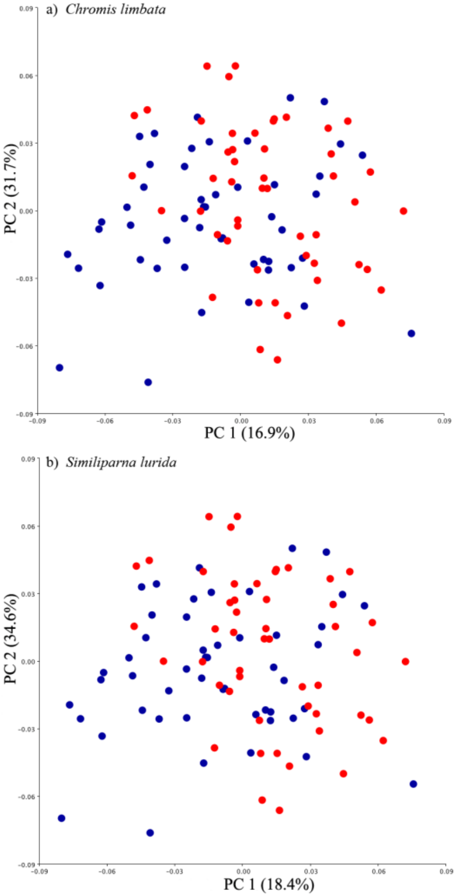

Fig. 6. Variation in the spatial distribution of specimens by locality along the PC1 and PC2 components using geometric morphometric analysis for *Chromis limbata* (a) and *Similiparma lurida* (b). In blue, individuals from the north-western side of the island; in red, individuals from the eastern side.

Table 5
Results of MANOVA performed during the stepwise procedure of LDA discriminant analysis for geometric morphological data. RWs are the relative warps; Partial R^2 coefficients indicate the percentage of variation explained by each predictor.

Order of variables	partial R^2	F	P	Wilks' lambda
Chromis limbata				
1. RW 1	0.146	16.731	< 0.0001	0.854
2. RW 3	0.114	12.448	0.001	0.757
3. RW 4	0.076	7.869	0.006	0.700
4. RW 7	0.075	7.649	0.007	0.648
5. RW 9	0.079	8.048	0.006	0.596
6. RW 11	0.059	5.874	0.017	0.561
7. RW 12	0.051	4.968	0.028	0.532
8. RW 16	0.048	4.596	0.035	0.507
9. RW 2	0.047	4.466	0.037	0.483
Similiparma lurida				
1. RW 7	0.165	19.318	< 0.0001	0.835
2. RW 1	0.150	17.182	< 0.0001	0.710
3. RW 8	0.077	7.963	0.006	0.655
4. RW 11	0.082	8.483	0.004	0.602
Chromis limbata versus Similiparma lurida				
1. RW 1	0.878	1424.403	< 0.0001	0.122
2. RW 6	0.206	51.041	< 0.0001	0.097
3. RW 13	0.061	12.797	0.000	0.091
4. RW 15	0.064	13.397	0.000	0.085
5. RW 5	0.041	8.296	0.004	0.082
6. RW 9	0.026	5.151	0.024	0.080
7. RW 8	0.024	4.658	0.032	0.078
8. RW 4	0.024	4.656	0.032	0.076
9. RW 11	0.022	4.281	0.040	0.074
Interspecific for all species				
1. RW 1	0.877	491.597	< 0.0001	0.123
2. RW 7	0.223	19.590	< 0.0001	0.095
3. RW 4	0.192	16.136	< 0.0001	0.077
4. RW 2	0.166	13.432	< 0.0001	0.064
5. RW 6	0.190	15.809	< 0.0001	0.052
6. RW 15	0.084	6.110	0.001	0.048
7. RW 9	0.073	5.233	0.002	0.044
8. RW 10	0.073	5.200	0.002	0.041
9. RW 3	0.070	4.971	0.002	0.038
10. RW 12	0.070	4.919	0.003	0.035
11. RW 5	0.071	4.956	0.002	0.033
12. RW 14	0.043	2.956	0.034	0.032

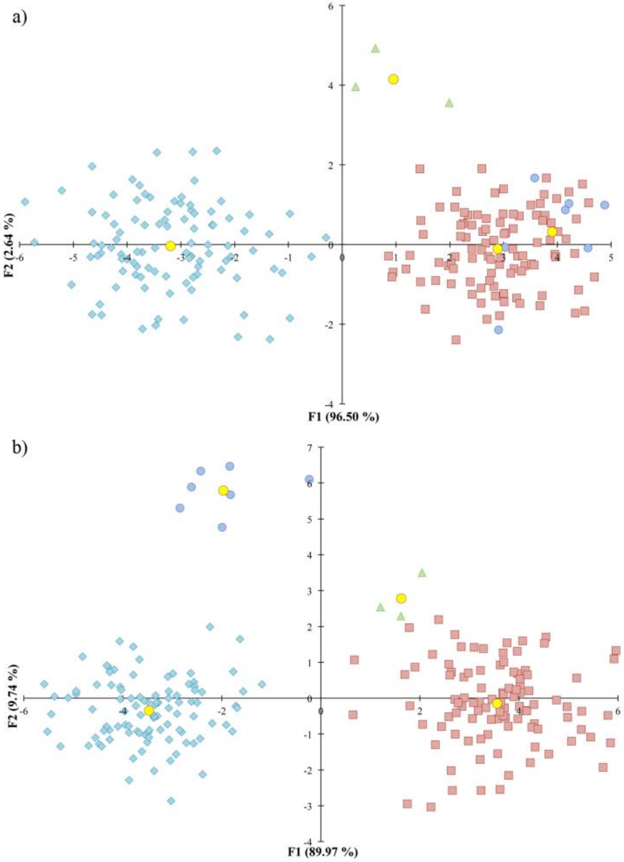

Fig. 7. Linear discriminant scores for the classification of pomacentrids from Gran Canaria Island for functional (a) and geometric morphological (b) analyses. *Abudefduf saxatilis*, circle in dark blue; *Chromis chromis*, triangle in green; *Chromis limbata*, squared in red; *Similiparma lurida*, rhomboid in light blue; Yellow circle indicates the centroid for each species.

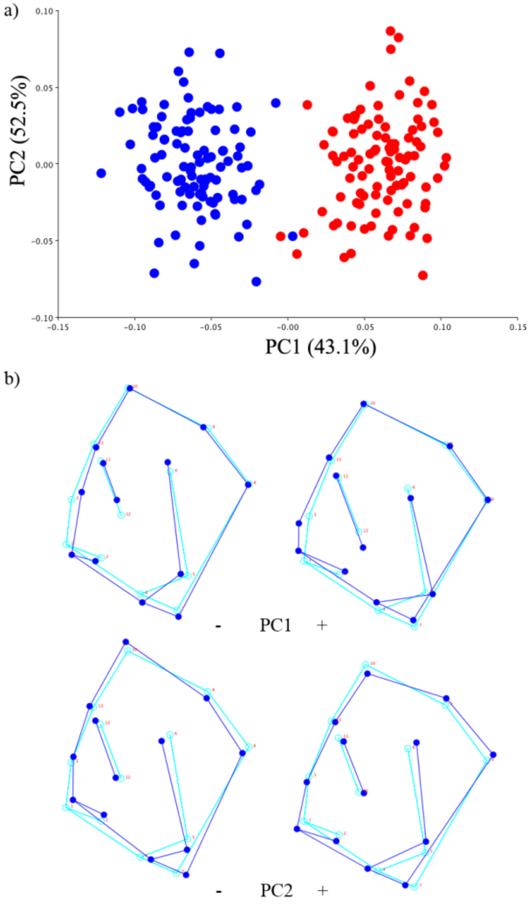

Fig. 8. Comparison of the head shape between *Chromis limbata* (red) and *Similiparma lurida* (blue) along the PC1 and PC2 axes using geometric morphometric analysis (a), and their changes at the positive (+) and negative (-) extremes along the PC components (b). The dark blue indicates these changes, while the light blue shows the head shape at the *x*= 0 and *y*= 0 position.

4 DISCUSSION

Our results revealed that morpho-functional adaptations explain intra and interspecific diversity of damselfishes living in an oceanic island of the North-eastern Atlantic, similarly as it has been reported for species inhabiting coral reefs (Frédérich et al., 2008; Farré et al., 2015). Moreover, we demonstrated a correspondence between head shapes and functional attributes; hence the degree of phenotype diversity (polymorphism) seems to affect whole body shape and associated vital functions. Therefore, both morphological and functional approaches suggest a clear evolutionary divergence of lineages (Frédérich et al., 2013; Cooper and Westneat, 2009), favouring the identification and separation of species.

Several studies have consistently shown that environmental factors affect fish morphology (Kingsolver and Huey, 2008; Sfakianakis et al, 2011, Ramler et al, 2014). For example, fishes occurring in wave-swept habitats with high water motion need to maintain high swimming speeds, or at least to manoeuvre at high speeds (e.g., Bellwood and Wainwright, 2002; Bellwood et al., 2002; Langerhans and Reznick 2010; Fulton and Bellwood, 2005; Yan et al., 2013). Water flow velocity is, in turn, a key environmental factor influencing phenotypic differentiation within species. Species in habitats with strong water flows tend to present more robust bodies, acquiring a fusiform shape, and so modifying traits related with manoeuvrability and velocity during swimming (e.g., Pakkasmaa and

Pironen, 2001; Blake 2004, Fulton et al., 2005; Ohlberger et al., 2006; Langerhans 2008). For damselfishes, recent studies have shown a phenotypic divergence in pectoral fin morphology and swimming performance across water flow gradients at both regional and local scales (Fulton et al., 2013; Binning et al., 2014). Our findings confirmed a local adaptation to hydrodynamic differences between the north-western and eastern sides of Gran Canaria Island. In particular, the population of *C. limbata* from the north-western side of the island (a more energetic environment) displayed a higher swimming capacity, as reflected by CPt and Bsf traits and a more pointed head to favour hydrodynamics. This is particularly pertinent for this species in the study region, as it usually occurs a few meters above the bottom (Espino et al, 2006). In contrast, *S. lurida* is a species that lives closer to the rocky bottom, where exposition to water flow is not as relevant to affect key daily activities. This fact may help out to explain the lower percentage of correct identifications for this species (69% for the functional approach) and, therefore, that phenotypic plasticity was not directly linked with the geographical locality for both approaches. The pectoral fin morphology has a clear influence on locomotion of this species; other behavioural and physiological adaptations are also responsible for enabling the persistence of some species across a range of flow regimes (Binning and Roche, 2015). Intra-species divergences in fin and body shape can be linked to the type of habitat, in particular between 'open water' and bottom dwelling morphs. For example, bottom dwelling morphs of bluegill sunfish (*Lepomis* *macrochirus*) have deeper bodies and longer, more posterior-situated pectoral fins than 'open water' morphs (Ehlinger and Wilson 1988).

Morphological variations have been described for our target species at both local and regional scales; for example, Molina et al. (2006) found that Brazilian populations of *A. saxatilis* show significant differences in body size and shape, suggesting a connection with the intensity of oceanic currents. Although at a major spatial scale, Arruda (1977) showed morphological differences between specimens of *C. chromis* from the Mediterranean and those from the oceanic archipelagos of Azores and Madeira, while Duka and Shevchenko (1980) reported differences in morphology between populations from the Mediterranean and the Black Sea.

The family of damselfishes include several types of feeding types, including planktivorous, herbivores, coral predators and omnivores (Emery, 1973; Kuo and Shao, 1991; Gluckmann and Vandewalle, 1998; Frédérich et al., 2008; 2009; Olivier et al., 2015). There is a high correlation between head shape and the ecological and functional diversity of damselfishes (Emery, 1973; Gluckmann and Vandewalle, 1998; Frédérich et al., 2008; Frédérich and Vandevalle, 2011). In this context, our results indicated a certain relationship between functional variability and fish habits. In particular, *C. chromis*, *C. limbata* and *A. saxatilis* have eyes located closer to the dorsal side of their heads, facilitating the vision in the water column. Furthermore, *C. chromis* have a higher swimming capacity (higher

Cpt), whereas *C. limbata* and *A. saxatilis* have a better hydrodynamism (higher Bsf). This implies that *C. chromis* has more options in its ecological adaptations, living in the interface between a rock dwelling and a mid-water fish. Frédérich et al. (2008) suggested that *Chromis* spp., as omnivorous species, are suckers (*versus* ram feeders for zoo-planktivorous) showing a similar head shape relative to omnivorous damselfishes of the genus *Dascyllus*, which could correspond to a change in the strategy of prey capture in the water column during evolution. Partially, it may explain why the morphological and functional head approaches provided a similar pattern. Both *Chromis* species have similar morphological patterns in the head due phylogenetic similarities (Frédérich and Vandevalle, 2011), but from a functional perspective these two species noticeable differ in their swimming capability. In contrast, *S. lurida* have bigger eyes close to the mouth, adapted to capture benthic invertebrates directly associated with the bottom (Mapstone and Wood, 1975; Tuya et al., 2004). Moreover, the high hyomandibular and short maxilla of *S. lurida* denote an adaptation for grazing (Frédérich and Vandevalle, 2011). This suggests that this species has an omnivorous diet, as occurs for other Pomacentrids (Frédérich et al., 2008).

In the last decades, the arrival of non-native fish species in the Macaronesian region has notoriously increased, which has been associated with ocean warming and increased marine shipping, leading to a tropicalization of the littoral fish faunas (e.g. Brito et al., 2005; Perry et al., 2005; Freitas and Araújo, 2006; Machado and

Barreiros, 2006). Since fish morphology is a proxy for a species' ecological niche within a community (Azurro et al., 2014), *A. saxatilis* and *C. chromis* have morpho-functional adaptations relative to the native species; this may suggest their successful establishment in the Canary Islands. According to the limiting-similarity hypothesis (MacArthur and Levins 1967), species that are dissimilar relative to native conspecifics are predicted to persist due to relaxed interspecific competition. This fact stresses the importance of morpho-functional studies to predict the establishment of species outside their common distribution ranges (Gratwicke and Speight, 2005; Price et al., 2011; Montaña et al., 2014; Farré et al 2015).

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CAPÍTULO 5

CONCLUSIONES

CONCLUSIONES.

1. Las especies que proporcionaron rendimientos de pesca relativamente altos, en términos de biomasa fueron: *Sparisoma cretense*, *Dentex gibbosus*, *Diplodus* spp, *Mullus surmuletus*, *Pagrus* spp., *Pagellus* spp. y *Sarpa salpa*.

2. Tres especies de pequeño tamaño son importantes, en términos de abundancia: *Stephanolepis hispidus*, *Chromis limbata* y *Similiparma lurida*.

3. Se detectaron variaciones en la estructura y abundancia de la comunidad de peces entre las zona NO y NE de Gran Canaria.

4. Para doce especies de peces costeros (*Dentex gibbosus, Diplodus sargus, Diplodus vulgaris Pagellus acarne, Pagellus erythrinus Pagrus auriga Pagrus pagrus Sarpa salpa, Spondyliosoma cantharus, Sparisoma cretense, Mullus surmuletus y Stephanolepis*

hispidus) la talla media de la capturas está por debajo de la talla de primera madurez.

5. A la luz de estos resultados y estudios previos en la región de estudio, se recomienda una gestión eficaz de los recursos, lo que implica una reducción de la presión pesquera (profesional y, sobre todo, recreativa).

6. *La fula negra (S. lurida) puede* alcanzar 157 cm de longitud y 18 años edad.

7. Los machos crecen más rápido y son más grandes (K= 0.28 years^{-1}, L_{∞}= 144.87 cm TL) que las hembras (K= 0.23 years^{-1}, L_{∞}= 134.61 cm TL), lo que afecta a la sex ratio de machos y hembras (1:0.26).

8. La talla de primera madurez sexual fue 103.44 mm (LT) para los machos y 84.71 mm (LT) para las hembras.

9. El crecimiento es lento durante la temporada de desove, que ocurre de noviembre a marzo, incluyendo un máximo reproductivo en febrero. Dos meses después

de este pico (abril), los juveniles alcanzaron abundancias máximas en zonas de gran relieve.

10. Los ejemplares adultos, muestran una preferencia hacia los fondos rocosos cubiertos de algas intercaladas con parches de arena, lo que sugiere cambios ontogenéticos en las preferencias de micro-hábitat cuando los juveniles se desarrollan en adultos.

11. Las adaptaciones morfo-funcionales explican la diversidad intra e interespecíficas de pomacéntridos en Gran Canaria. Esta diferenciación morfo-funcional es parcialmente el resultado de la variación filogenética, pero puede también estar relacionada con la variabilidad ambiental, como los regímenes hidrodinámicos locales.

12. La población de *Chromis limbata* de un entorno más energético muestra una mayor capacidad de natación y una cabeza más puntiaguda para facilitar la hidrodinámica. Sin embargo, *Similiparma lurida* no siguió este patrón; los especimenes que se encuentran

en un ambiente energético ocupan una posición "más expuesta" en la columna de agua.

13. Existe una alta variabilidad morfo-funcional de especies de peces damisela recién citados en relación con damiselas nativas. Esto podría explicar el éxito de *Abudefduf saxatilis* en las aguas costeras de Canarias, lo que demuestra el valor de los estudios morfo-funcionales para abordar el posible establecimiento de especies no nativas.

14. Los resultados confirman que el nicho ecológico de los peces damisela se refleja típicamente en la morfología de los peces, que está conectado con un rango de rasgos funcionales.

En Canarias, existe una gran biodiversidad marina debido a sus características topográficas e hidrográficas; más de 100 especies son explotadas por la pesca artesanal. Entre esas especies se encuentran los pomacéntridos, o peces damisela, que son mayormente pescados como captura accidental. Aunque su interés comercial es limitado, tienen una gran importancia ecológica. *Similiparma lurida* y *Chromis limbata* son las dos principales especies que se pueden encontrar en el archipiélago Canario.

A pesar de ser muy abundantes en toda la costa, apenas existen estudios sobre la biología y ecología de los peces damisela de Canarias. En esta tesis, se abordan cuestiones sobre la ecología y biología de los principales pomacéntridos que se pueden encontrar en aguas canarias.

ULPGC

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