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ORIGINAL ARTICLE

Ichthyofauna of the Selvagens Islands. Do small coastal areas show high species richness in the northeastern Atlantic?

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Abstract

The Selvagens Islands are located in the northeastern Atlantic between the Canary Islands and Madeira Island. As a result of their small size, remote location and harsh sea conditions only a few studies have been conducted to describe their marine species diversity. We were able to identify 29 new coastal fish species, an increase of 33% in the ichthyofauna described for these islands (n = 88). There is a prevalence of species with tropical affinities and only 2.3% (n = 2) are endemic to Macaronesia. Considered a stepping-stone colonization vector from the nearest continental shore, as proposed by other authors for this region, the Selvagens Islands host 34.1% of the ichthyofauna described for the much larger Canary Islands (n_{species} = 258, submerged area $n_{\text{SelvagensIs.}}$ = 2.3%) and 47.3% of the ichthyofauna described for the more distantly located Madeira Island (n_{species} = 186, submerged area $n_{\text{SelvagensIs.}}$ = 17.9%). Interestingly, 6.8% (n = 6) of the species failed to bridge the gap between the Selvagens Islands and Madeira Island. Data collected so far showed no trend toward an increasing number of species with high dispersal capability. The Selvagens Islands are an example of a high coastal species diversity occurring even in very small areas of the northeastern Atlantic Ocean.

Key words: *Biogeography, dispersal capability, ichthyofauna, Macaronesia, Selvagens Islands*

Introduction

The warm temperate northeastern Atlantic Ocean is punctuated by a number of archipelagos and seamounts. This region known as Macaronesia includes the Canary Islands, located near the north African coast and, in a northwestward offshore direction, the archipelagos of Madeira, Selvagens and the Azores (Lloris et al. 1991; Brito et al. 2007). According to several authors the ichthyogeography of Macaronesia has mainly been influenced by the tropical west African coast, the Mediterranean Sea and to a lesser extent the western European continental shores (Almada et al. 2001; Briggs & Bowen 2012). Recently, Almada et al. (2013) have shown the

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distinctiveness of the Macaronesia ichthyofauna compared with the continental African and European regions at the same latitude and its close affinity with west African tropical communities. These affinities were already noted by Santos et al. (1995), who suggested that the colonization of Macaronesia by warm-water fish followed a route from west African continental shores along progressively distant clusters of islands in a stepping-stone process. But how is it possible to support this hypothesis if the Canary Current, the main current in this region, flows in the opposite direction southward along the southwestern European and northwestern African coasts? Stramma (1984) showed that the transport of eggs and larvae to the north was possible through gyres and eddies that frequently flow northward, forming a complex two-way system of connection among these archipelagos. Additionally this northward colonization trend was also detected by molecular studies that analysed the phylogeography of Macaronesian warm-water species (e.g. Domingues et al. 2006).

The Selvagens Islands (Lat. 30°08′45″N, Long. 15°51′51″W; Lat. 30°01′59″N, Long. 16°01′00″W) are located south of Madeira Island and north of the Canary Islands (Figure 1). They form an isolated group of small islands and reefs that may have played (or may play) an important role for some fish species, allowing them to bridge the gap between those larger archipelagos.

Although the Selvagens Islands have been a marine protected area for more than 40 years, their remoteness and the rough oceanographic conditions usually found in this region of the Atlantic Ocean are probably the reasons why only one paper has addressed their ichthyofaunal richness. Falcón et al. (2000) described the ichthyofauna around these islands, reporting a total of 60 coastal fish species. More surveys are still needed to provide a better description of the species composition at the Selvagens Islands. This is of major importance to understanding the forcing agents underlying the colonization patterns presented above.

The ichthyogeography of the northeastern Atlantic may have been shaped significantly by climatic events. Macaronesia is included in the Lusitania Province which encompasses the warm and temperate waters of the northeastern Atlantic, that extend from the southern British Isles in the north to southern Morocco in the south and eastwards through the Mediterranean (Briggs 1995; Spalding et al. 2007; Briggs & Bowen 2012). This province is

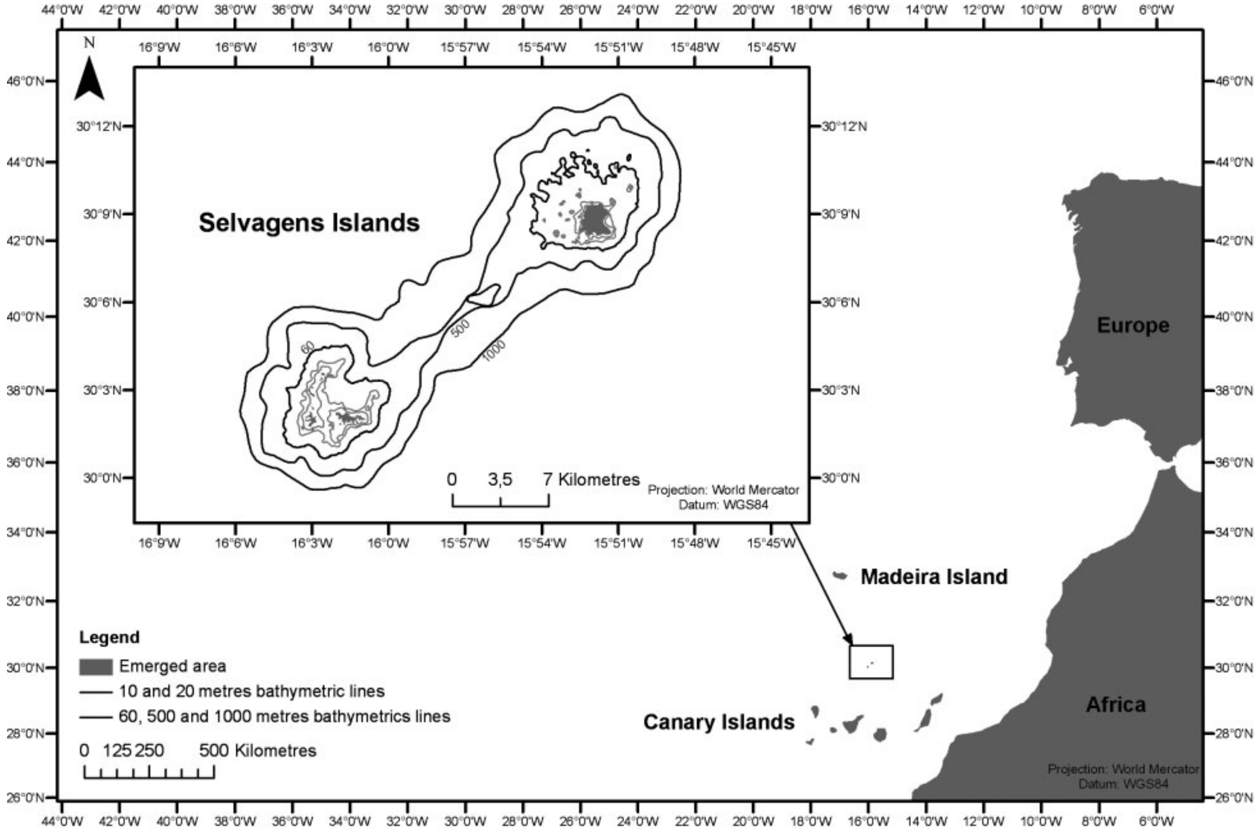

Figure 1. Map showing the location of the Selvagens Islands in the northeastern Atlantic between Madeira and the Canary Islands. Bathymetric data of these small remote islands are also presented.

one of the poorest regions on the planet in terms of fish species diversity, a fact probably related to the climatic deterioration that has been evolving since the Miocene (Briggs 1995) and that became especially severe with the Pleistocene glaciations (CLIMAP 1981; Hayes et al. 2005). During the glacial maxima much of the habitat for warm-water species ceased to be available on the western European shores. In the last glacial peak the polar front advanced to the south, possibly reaching the west Iberian coast (Dias et al. 1997).

While the continental shores of west Africa and Europe experienced a severe cooling (Briggs 1995), Macaronesia maintained milder conditions together with some warmer water pockets that persisted in the Mediterranean (Thiede 1978; Briggs 1995; Almada et al. 2001). Indeed, the Macaronesian archipelagos were affected differently by the glaciations. While the Azores, in the north, experienced a moderate drop in sea surface temperature (2–3°) in the last glacial maximum (LGM), Madeira seems to have been almost unaffected while in the Canaries, the islands nearer the African shore were more affected than those located offshore (Crowley 1981).

During the LGM the average sea level was approximately 130 m lower than at the present time (Dias et al. 1997). These eustatic changes led to an increase in the coastal area available for most inshore fish both in the present northeastern Atlantic Islands and on several seamounts in this region that are currently submerged (e.g. Gorringe Bank). This fact may have favoured stepping-stone processes along the Macaronesian islands by inshore fish fauna during the regression of the polar front in the last 11,000 years. This hypothesis is also supported by the low number of endemic species in the Macaronesian archipelago (Briggs 1966; Santos et al. 1997).

In this paper we provide an updated checklist and abundance data of fish species from the Selvagens Islands. We discuss the biogeographic affinities of the ichthyofauna of the Selvagens Islands reported so far and also analyse the role of some ecologically relevant features traditionally related to the dispersal ability of fish species in an attempt to further understand the factors shaping the ichthyofaunal richness of these islands.

Materials and methods

The Selvagens Islands are small, uninhabited islands of volcanic origin dating from the Oligocene (24.2 to 29.5 Ma) (Mata et al. 2010). The largest islands, Selvagem Grande (2.5 km^2) and Selvagem Pequena (0.16 km^2), are approximately 18 km from each other and are surrounded by small islets. The largest island, Selvagem Grande, is mostly flat and surrounded by abrupt cliffs, about 80 m high, with scarce intertidal platforms. The smaller island, Selvagem Pequena, rises just a few metres above sea level, with large areas of intertidal rocky platforms that lead into a shallow subtidal area connecting small rocks and islets. The shallow seascape is mostly rocky. The calculation of available submerged areas between 0 and 60 m depth and distances between groups of islands was obtained using the ArcGIS Desktop 9.3 (ESRI) software and the method described by Vincenty (1975). The coordinate system used in this work was the WGS84 Gebco (08-Grid, version 20100927) bathymetry data with 30 arc-second (IOC et al. 2003) and CAOP (version 2011) coastline data.

The EMEPC/M@rbis/Selvagens expedition in June–July 2010 involved more than 80 investigators and had the larger objective of sampling the marine communities of this poorly known archipelago including algae, invertebrates, fish and marine birds. No additional sampling was made in the remaining seasons due to the remoteness of these islands and the rough sea conditions which can almost completely submerge some islands of this archipelago and make sampling in these coastal areas a difficult or dangerous task. Ichthyofauna censuses included non-destructive sampling methods like underwater scuba diving visual census, photography and video surveys, snorkelling surveys, intertidal censuses during low tide and additional sampling methods described below. Photos and videos of the species observed during the campaign are available from EMEPC (2010). Specimens of some species were euthanized with MS-222 and preserved in ethanol (marked with an (S) in Table I) for later molecular studies. Species names follow Eschmeyer (2014) and specific literature on the taxonomy of some fish families (Blenniidae: Almada et al. (2005a, 2005b), Muss et al. (2001); Diodontidae: Leis (2006); Gadidae: Roa-Varón & Ortí (2009); Gobiesocidae: Almada et al. (2008), Henriques et al. (2002); Labridae: Almada et al. (2002), Hanel et al. (2002)) was also considered.

Intertidal specimens were captured with hand nets and released at the same site. Large pools were also visually sampled by snorkelling. Subtidal sampling involved groups of two to four divers who performed six snorkelling and 39 scuba diving censuses (including five nocturnal dives) around Selvagem Grande, and 18 snorkelling and 35 scuba diving censuses (including three nocturnal dives) around Selvagem Pequena. A strip transect technique was adopted (Brock 1954) and transects were established along isobaths and allocated to pre-established depth strata between 0 and 30 m. A fixed transect area of 50 × 4 m was sampled following the recommendations of Fowler (1987). Under-estimation of cryptobenthic

Table I. Species list for the Selvagens Islands. N, new records for Selvagens Islands (species highlighted in bold); S, specimens collected and preserved. Abundance levels: 1, single observation (one individual); 2, rare (2–10); 3, common (11–100); 4, abundant (>100); (a), species sampled by coastal angling, (b), species identified in fresh stomach contents of *Calonectris diomedea*; C, species reported for the Canary Islands but absent from Madeira Island; asterisks mark species previously reported by Falcón et al. (2002), whose valid name has changed due to recent taxonomic updates. Biogeographic affinities: TAS, tropical west African species; WTS, warm-temperate species; TES, temperate species; EAS, eurythermic eastern Atlantic species; AAS, amphiatlantic species; WAS, west Atlantic species; COS, Cosmopolitan species and END, endemic Macaronesian species; MED, distribution range includes the Mediterranean. Habitats: B, benthic, D, demersal, BP, benthopelagic, P, pelagic. Adult mobility: s, sedentary, m, mobile, vm, very mobile. Reproductive functional group: v, viviparous; w, ovoviviparous; oviparous with pelagic eggs (op) and with adhesive eggs attached to substrata (ov); og, species in which one or the other parent guards externally; os, species that shed their eggs and protect them in a part of their body; ob, species that produce eggs which settle on the substratum (see Materials and methods section for more information).

Species	Common name	Abundance level (no. of independent observations)	Falcón et al. (2000)	EMEPC/ M@rbis/ Selvagens (2010)	Main biogeographic affinities	Water column habitat	Adult mobility	Reproductive functional group	Recent taxonomic updates and references
Subclass Elasmobranchii									
CARCHARHINIDAE									
Prionace glauca **(Linnaeus, 1758)**	Blue shark	1 (1)		N	COS	P	vm	v	
DASYATIDAE									
Dasyatis pastinaca (Linnaeus, 1758)	Common stingray	2 (3)	√	√	EAS/MED	B	m	w	
Taeniura grabata **(Geoffroy Saint-Hilaire, 1817)**	Round stingray	1 (1)		N	COS	B	m	w	
MYLIOBATIDAE									
Myliobatis aquila (Linnaeus, 1758)	Common eagle ray	2 (2)	√	√	EAS/MED	B	m	w	
Pteromylaeus bovinus **(Geoffroy Saint-Hilaire, 1817)**	Bull ray	1 (1)		N	COS	B	m	w	
TORPEDINIDAE									
Torpedo marmorata **Risso, 1810**	Spotted torpedo	1 (1)		N	EAS/MED	B	s	w	
Class Actinopterygii									
ANTENNARIIDAE									
Antennatus nummifer **(Cuvier, 1817)**	Spotfin frogfish	1 (1)		N	COS	B	s	ov	
APOGONIDAE									
Apogon imberbis (Linnaeus, 1758)	Cardinal fish	3 (43)	√	√	TAS/MED	D	s	os	
ATHERINIDAE									
Atherina presbyter Cuvier, 1829	Sand smelt	4 (5)	√	√	TES	P	vm	op	
AULOSTOMIDAE									
Aulostomus strigosus **Wheeler, 1955**	Atlantic cornetfish	3 (17)		N	TAS	D	m	op	
BALISTIDAE									
Balistes capriscus Gmelin, 1789 (S)	Grey triggerfish	3 (23)	√	√	AAS/MED	BP	vm	og	
Canthidermis sufflamen (Mitchill, 1815)	Ocean triggerfish	3 (19)	√	√	WAS	BP	vm	og	
BELONIDAE									
Belone belone **(Linnaeus, 1761)**	Garfish	1 (1)		N	TES/MED	P	vm	ov	
BLENNIIDAE									
Coryphoblennius galerita (Linnaeus, 1758) (S)	Montagu's blenny	3 (14)	√	√	TES/MED	B	s	og	
Lipophrys pholis (Linnaeus, 1758) (S)	Shanny	2 (2)	√	√	TES/MED	B	s	og	Almada et al. (2005a)
Lipophrys trigloides (Valenciennes, 1836)* (S)	N/A	1 (1)	√	√	WTS/MED	B	s	og	Almada et al. (2005a)
Ophioblennius atlanticus (Valenciennes, 1836)	Redlip blenny	3 (69)	√	√	AAS	B	s	og	Muss et al. (2001)
Parablennius incognitus (Bath, 1968)	N/A	0	√		WTS/MED	B	s	og	
Parablennius parvicornis (Valenciennes, 1836) (S)	Rock-pool blenny	4 (57)	√	√	TAS	B	s	og	Almada et al. (2005b)
Scartella cristata (Linnaeus, 1758) (C)	Molly miller	2 (2)	√	√	COS	B	s	og	
BOTHIDAE									
Bothus podas (Delaroche, 1809)	Wide-eyed flounder	1 (1)	√	√	TAS/MED	B	s	op	

Table I. (Continued)

Species	Common name	Abundance level (no. of independent observations)	Falcón et al. (2000)	EMEPC/ M@rbis/ Selvagens (2010)	Main biogeographic affinities	Water column habitat	Adult mobility	Reproductive functional group	Recent taxonomic updates and references
CARANGIDAE									
Caranx crysos (Mitchill, 1815)	Blue runner	3 (19)	√	√	AAS/MED	BP	vm	op	
***Naucrates ductor* (Linnaeus, 1758)**	Pilot fish	(b)		N	COS	P	vm	op	
Pseudocaranx dentex (Bloch & Schneider, 1801)	White trevally	4 (24)	√	√	COS	BP	vm	op	
Seriola dumerili (Risso, 1810)	Greater amberjack	3 (14)	√	√	COS	BP	vm	op	
Seriola fasciata (Bloch, 1793)	Lesser amberjack	2 (2)	√	√	AAS/MED	BP	vm	op	
Seriola rivoliana Valenciennes, 1833	Longfin yellowtail	4 (43)	√	√	COS	BP	vm	op	
Trachinotus ovatus (Linnaeus, 1758)	Pompano, Derbio	3 (13)	√	√	EAS/MED	P	vm	op	
CLUPEIDAE									
***Sardinella maderensis* (Lowe, 1838)**	Madeira sardinella	4 (1)		N	TAS/MED	P	vm	op	
CONGRIDAE									
***Conger conger* (Linnaeus, 1758)**	Conger eel	2 (5)		N	EAS/MED	B	s	op	
DIODONTIDAE									
Chilomycterus reticulatus (Linnaeus, 1758)*	Spotfin burrfish	2 (6)	√	√	COS	D	m	op	Leis (2006)
***Diodon eydouxii* Brisout de Barneville, 1846**	Pelagic porcupinefish	1 (1)		N	COS	BP	vm	op	Leis (2006)
EXOCOETIDAE									
***Cheilopogon exsiliens* (Linnaeus, 1771)** (C)	Bandwing flyingfish	(a)		N	WAS	P	vm	op	
***Cheilopogon pinnatibarbatus* (Bennett, 1831)**	Bennett's flyingfish	(a)		N	COS	P	vm	op	
***Exocoetus volitans* Linnaeus, 1758**	Tropical two-wing flyingfish	(a)		N	COS	P	vm	op	
GADIDAE									
***Gaidropsarus guttatus* (Collett, 1890)**	Macaronesian rockling	1 (1)		N	WTS	B	s	op	Roa-Varón & Ortí (2009)
GOBIESOCIDAE									
***Apletodon dentatus* (Facciolà, 1887)** (C)	Sea-urchin clingfish	1 (1)		N	TES/MED	B	s	og	
***Apletodon pellegrini* (Chabanaud, 1925)**	Chubby clingfish	2 (2)		N	TAS	B	s	og	
Lepadogaster candolii Risso, 1810*	Connemarra clingfish	2 (6)	√	√	TES/MED	B	s	og	But see Almada et al. (2008)
Lepadogaster lepadogaster (Bonnaterre, 1788)* (S)	Shore clingfish	3 (11)	√	√	WTS/MED	B	s	og	Henriques et al. (2002)
GOBIIDAE									
***Gnatholepis thompsoni* Jordan, 1904**	Goldspot goby	2 (2)		N	AAS	B	s	og	
***Gobius niger* Linnaeus, 1758** (C)	Black goby	2 (2)		N	EAS/MED	B	s	og	
Gobius paganellus Linnaeus, 1758	Rock goby	2 (8)	√	√	EAS/MED	B	s	og	
***Gobius xanthocephalus* Heymer & Zander, 1992** (C)	Yellow-headed goby	1 (1)		N	WTS/MED	B	s	og	

Table I. (Continued)

Species	Common name	Abundance level (no. of independent observations)	Falcón et al. (2000)	EMEPC/ M@rbis/ Selvagens (2010)	Main biogeographic affinities	Water column habitat	Adult mobility	Reproductive functional group	Recent taxonomic updates and references
Mauligobius maderensis (Valenciennes, 1837) (S)	Madeira rock goby	4 (72)	√	√	END	B	s	og	
Thorogobius ephippiatus (Lowe, 1839)	Leopard-spotted goby	0	√		TES/MED	B	s	og	
HAEMULIDAE									
Parapristipoma octolineatum (Valenciennes, 1833)	African striped grunt	2 (2)	√	√	TAS/MED	D	m	op	
KYPHOSIDAE									
Kyphosus sectatrix (Linnaeus, 1758)*	Bermuda sea chub	4 (21)	√	√	AAS/MED	BP	vm	op	Eschmeyer (2014)
LABRIDAE									
Bodianus scrofa (Valenciennes, 1839)	Barred hogfish	3 (61)	√	√	TAS	D	m	op	
Coris julis (Linnaeus, 1758)	Mediterranean rainbow wrasse	3 (16)	√	√	TES/MED	D	m	op	
Symphodus trutta (Lowe, 1834)*	Atlantic wrasse	3 (16)	√	√	END	D	m	og	Almada et al. (2002), Hanel et al. (2002)
Thalassoma pavo (Linnaeus, 1758)	Ornate wrasse	4 (534)	√	√	TAS/MED	D	m	op	
Xyrichtys novacula (Linnaeus, 1758)	Pearly razorfish	2 (4)	√	√	AAS/MED	D	m	op	
LABRISOMIDAE									
***Labrisomus nuchipinnis* (Quoy & Gaimard, 1824)**	Hairy blenny	2 (9)		N	AAS	B	s	og	
MUGILIDAE									
Chelon labrosus (Risso, 1827)	Thicklip grey mullet	4 (26)	√	√	EAS/MED	BP	m	op	
***Liza aurata* (Risso, 1810)** (S)	Golden grey mullet	4 (46)		N	EAS/MED	BP	m	op	
Mugil cephalus Linnaeus, 1758 (C)	Flathead grey mullet	0	√		COS	BP	m	op	
MULLIDAE									
***Mullus surmuletus* Linnaeus, 1758**	Striped red mullet	2 (2)		N	TES/MED	B	m	op	
MURAENIDAE									
Enchelycore anatina (Lowe, 1838)	Fangtooth moray	3 (11)	√	√	WAS	B	s	op	
Gymnothorax unicolor (Delaroche, 1809)	Brown moray	3 (33)	√	√	TAS/MED	B	s	op	
Muraena augusti (Kaup, 1856) (S)	Black moray	3 (69)	√	√	TAS	B	s	op	
***Muraena helena* Linnaeus, 1758**	Mediterranean moray	1 (1)		N	EAS/MED	B	s	op	
PHYCIDAE									
Phycis phycis (Linnaeus, 1766)	Forkbeard	2 (5)	√	√	EAS/MED	D	m	op	
POMACENTRIDAE									
Abudefduf luridus (Cuvier, 1830) (S)	Canary damsel	4 (343)	√	√	TAS	D	m	og	
Chromis limbata (Valenciennes, 1833)	Azores chromis	4 (117)	√	√	AAS	BP	m	ov	
PRIACANTHIDAE									

Table I. (Continued)

Species	Common name	Abundance level (no. of independent observations)	Falcón et al. (2000)	EMEPC/ M@rbis/ Selvagens (2010)	Main biogeographic affinities	Water column habitat	Adult mobility	Reproductive functional group	Recent taxonomic updates and references
Heteropriacanthus cruentatus (Lacepède, 1801)	Glasseye	3 (22)	√	√	COS	D	m	op	
SCARIDAE									
Sparisoma cretense (Linnaeus, 1758)	Mediterranean parrotfish	4 (243)	√	√	TAS/MED	D	m	op	
SCOMBRIDAE									
***Katsuwonus pelamis* (Linnaeus, 1758)**	Skipjack tuna	(a)		N	COS	P	vm	op	
***Sarda sarda* (Bloch, 1793)**	Atlantic bonito	2 (4)		N	AAS/MED	P	vm	op	
***Scomber colias* Gmelin, 1789**	Atlantic chub mackerel	(b)		N	AAS/MED	P	vm	op	
SCORPAENIDAE									
Scorpaena maderensis Valenciennes, 1833 (S)	Madeira rockfish	4 (254)	√	√	TAS/MED	B	s	ov	
***Scorpaena notata* Rafinesque, 1810**	Small red scorpionfish	2 (2)		N	TAS/MED	B	s	ov	
SERRANIDAE									
***Anthias anthias* (Linnaeus, 1758)**	Swallowtail seaperch	2 (1)		N	TAS/MED	D	m	op	
Epinephelus marginatus (Lowe, 1834)	Dusky grouper	3 (26)	√	√	COS	D	m	op	
Mycteroperca fusca (Lowe, 1838)	Island grouper	3 (14)	√	√	TAS	D	m	op	
Serranus atricauda Günther, 1874 (S)	Blacktail comber	4 (135)	√	√	TAS/MED	D	m	op	
SPARIDAE									
Boops boops (Linnaeus, 1758)	Bogue	4 (34)	√	√	EAS/MED	P	vm	op	
Diplodus cervinus (Lowe, 1838)	Zebra seabream	3 (13)	√	√	TAS/MED	D	m	op	
Diplodus sargus (Linnaeus, 1758)	White seabream	3 (16)	√	√	TAS/MED	D	m	op	
Diplodus vulgaris (Geoffroy Saint-Hilaire, 1817)	Common two-banded seabream	3 (8)	√	√	TAS/MED	D	m	op	
Oblada melanura (Linnaeus, 1758)	Saddled seabream	4 (22)	√	√	EAS/MED	BP	vm	op	
Sarpa salpa (Linnaeus, 1758)	Salema	4 (27)	√	√	EAS/MED	D	m	op	
SPHYRAENIDAE									
Sphyraena viridensis Cuvier, 1829	Yellowmouth barracuda	3 (7)	√	√	TAS/MED	P	vm	op	
SYNODONTIDAE									
Synodus saurus (Linnaeus, 1758)	Atlantic lizardfish	3 (11)	√	√	AAS/MED	B	s	op	
Synodus synodus (Linnaeus, 1758)	Diamond lizardfish	3 (28)	√	√	WAS	B	s	op	
TETRAODONTIDAE									
Canthigaster capistrata (Lowe, 1839)	Macaronesian sharpnose puffer	4 (131)	√	√	TAS/MED	D	m	og	
Sphoeroides marmoratus (Lowe, 1838)	Guinean puffer	3 (18)	√	√	TAS/MED	D	m	og	
TRIPTERYGIIDAE									
Tripterygion delaisi Cadenat & Blache, 1970	Black-faced blenny	3 (47)	√	√	WTS/MED	B	s	og	

reef fish species (see Willis 2001) was minimized with the implementation of the method proposed by Beldade & Gonçalves (2007) following each transect: an interference visual census technique was applied to an additional 25 × 1 m cryptobenthic-focused transect. Additionally, all new species were recorded with no distance-to-observer limit.

Abundances in the Selvagens Islands were estimated following the scale suggested by Gonçalves et al. (2002): 1, Single observation (one individual); 2, Rare (2–10 individuals); 3, Common (11–100 individuals); 4, Abundant (>100 individuals). The number of independent observations of each species was also recorded in order to discriminate between isolated observations of a few individuals and large schools of a given species.

Traditional trawl surveys were not used due to the rough bottom structure but the sampling of fast-swimming pelagic species was partially bridged by obtaining fish from a small number of licensed fishermen working within the marine reserve. Additionally, from 2008 to 2011 very detailed studies of the diet and foraging ecology of Cory's shearwater *Calonectris diomedea* (Scopoli, 1769) have taken place at the colony on Selvagem Grande. While much of the prey captured by these birds comes from far away, some fish species consistently appeared in regurgitated samples in large numbers and in a very fresh state. This, combined with information on the movements of birds obtained by GPS tracking, allowed us to be confident that these species must be present in the immediate vicinity of the Selvagens Islands.

The relative contributions of each biogeographic region to the Selvagens Islands were defined according to species distribution data provided by Froese & Pauly (2012) and Almada et al. (2013). The biogeographic units follow the classification provided by Henriques et al. (2007): tropical west African species (TAS); warm-temperate species (WTS); cold-temperate species (CTS); temperate species (TES). Species with a widespread geographic range from tropical waters to the Bay of Biscay or boreal waters were classified as eurythermic eastern Atlantic species (EAS). Species that occur on both sides of the Atlantic and are well represented along American and African/European continental coasts were classified as amphiatlantic species (AAS). Species reported in the Selvagens Islands that are absent along African/European continental coasts but are widely distributed along the East American coast were considered of west Atlantic origin (WAS). Species whose distribution encompasses the Atlantic and other oceanic basins were classified as cosmopolitan species (COS). Endemic species (END) were those whose distribution is restricted to Macaronesia (*sensu* Almada et al. 2001; Wirtz 2011), being absent along the continental coasts of Europe and Africa. Whenever the distribution range of one species includes the Mediterranean (MED) that information is also provided.

Species-specific attributes that may be related to the ability to disperse, such as the reproductive functional group and the mobility of adult fish, followed the categories already defined by other authors (Elliott et al. 2007; Claudet et al. 2010) and are referred to in Table I. Larval dispersion and pelagic larval duration was not included because there is no information available for many species presented in this study. Fish were also classified according to the degree of dependence on the substrate as: strict benthic species (almost always in close contact with the substrate, e.g. blennies); demersal species (highly dependent on the substrate but are not strictly benthic, e.g. groupers); benthopelagic species (active swimmers that are almost always in the water column but occasionally use the substrate to feed, e.g. jacks, or for spawning, e.g. triggerfish); or pelagic species (long-distance swimmers always found in the water column, e.g. tuna).

Results and discussion

The 29 additional species found for the Selvagens Islands (see Table I) in the current study represent an increase of 33% compared with what had previously been reported by Falcón et al. (2000). Some specimens were only identified to the genus level because they are fast-swimming pelagic fish that were observed for a very short period: *Sphyrna* sp., *Decapterus* sp. and *Trachurus* sp. Although we report here their presence in the Selvagens Islands we did not include them in subsequent analysis.

Differences between fish assemblages in Selvagem Grande and Selvagem Pequena islands were assessed calculating the Jaccard index of similarity. A value of 72% indicates that the fish assemblages from both islands are very similar. This index was not higher due to the number of rare species with one single report from one of the islands (see Table I). In fact, only 20.5% ($n = 18$) of the species were considered abundant, which reflects the relative contribution to the fish community of rare and common taxa, with 47.7% ($n = 42$) and 31.8% ($n = 28$), respectively. This similarity is further emphasized by the fact that no differences were found between the number of times each species was reported from each island (Wilcoxon test, $n = 88$, $Z = 0.99$, $P = 0.32$). The Spearman rank correlation between abundances at the two islands was 0.73 ($n = 88$, $P < 0.05$). Taken together, these results suggest that the variation of abundances of species follows a similar pattern in the two islands and that none of them displays higher levels of abundance. In view of these findings and due to the very close proximity of those islands, they will be treated as a single entity.

The species reported for the Selvagens Islands are a subgroup (34.1%) of the coastal ichthyofauna described for the much larger Canary Islands (n_{species} = 258), meaning that all species reported for the Selvagens Islands are also present in the Canaries. It is also remarkable that the species richness of the Selvagens Islands represents almost half (47.3%) of the ichthyofauna described for the much larger Madeira Island (n_{species} = 186). This last figure retains its interest even if we take into consideration that 6.8% (n = 6) of the Selvagens Islands species (*Apletodon dentatus* (Facciolà, 1887); *Cheilopogon exsiliens* (Linnaeus, 1771); *Gobius niger* Linnaeus, 1758; *Gobius xanthocephalus* Heymer & Zander, 1992; *Mugil cephalus* Linnaeus, 1758 and *Scartella cristata* (Linnaeus, 1758)) are not reported for Madeira and Porto Santo Islands.

The biogeographic relationships of the Selvagens Islands with the surrounding regions must be considered provisional because, although involving a significant and diversified sampling effort, this campaign was limited to one season as reported above. Additionally, the increase of 33.0% in the cumulative number of fish species identified between the survey of Falcón et al. (2000) and the present one probably implies that the species richness of these islands may be greater than the one currently recorded.

Taking into consideration these limitations there are some patterns that emerge from the data currently available. In a decreasing order of importance the ichthyofauna of the Selvagens Islands is composed of eastern Atlantic tropical species (27.3%, n = 24), temperate species (10.2%, n = 9) and warm-temperate species (6.8%, n = 6). The remaining taxa: widespread eurythermic eastern Atlantic species (15.9%, n = 14), cosmopolitan (19.3%, n = 17) and amphiatlantic species (13.6%, n = 12) provide no biogeographic information. Two Macaronesian endemisms were also detected: *Mauligobius maderensis* (Valenciennes, 1837) and *Symphodus trutta* (Lowe, 1834). It is also interesting to note that 3.4% (n = 3) of the fish species reported for the Selvagens Islands are widespread along the western Atlantic coast, being absent from the European and African continental coasts. In fact, *Canthidermis sufflamen* (Mitchill, 1815), *Enchelycore anatina* (Lowe, 1838) and *Synodus synodus* (Linnaeus, 1758) have their centres of distribution along the eastern American coast.

In an attempt to find a pattern that could explain the presence of some species at the Selvagens Islands we analysed the water column habitat, adult mobility and reproductive functional group of each species. The degree of dependence on the substrate revealed that most species are benthic (42.0%, n = 37) or demersal (26.1%, n = 23), and only a small proportion are benthopelagic (15.9%, n = 14) or pelagic (15.9%, n = 14) fish. Furthermore, sedentary (37.5%, n = 33) and mobile species (35.2%, n = 31) clearly outnumber very mobile species (27.3%, n = 24). The type of eggs produced by each species revealed that the majority spawn pelagic eggs (58%, n = 51), followed by oviparous species with adhesive eggs with or without parental care of the eggs (34.1%, n = 30). The remaining reproductive functional groups represent a minority (7.9%, n = 7) of the total number of species.

Compared with other archipelagos the species richness reported for the Selvagens Islands is remarkable when one considers that the submerged area with depths less than 60 m (Table II) is much smaller than that available in larger Macaronesian archipelagos: 43 times smaller than the Canaries, 11 times smaller than the Azores and six times smaller than Madeira (differences in species richness are addressed below). This conclusion is further supported by the fact that the species list presented here probably represents an under-estimation of the species richness at these islands.

A similar pattern, even more extreme than the present one, was previously reported by Abecasis et al. (2009) for the Gorringe Bank with an estimated submerged area above 60 m of approximately 0.8 km^2 (71 times smaller than that of the Selvagens

Table II. Pairwise distances (km) calculated for island groups and Gorringe Bank in the Macaronesian region and estimated area (km^2) between 0 and 60 m depth for each location.

	Azores	Gorringe Bank	Madeira, Porto Santo	Selvagens	Canaries
Azores Is.	–	1174.2	838.4	1126.9	1112.6
Gorringe Bank		–	572.0	807.6	805.9
Madeira, Porto Santo Is.			–	251.3	417.6
Selvagens Is.				–	153.1
Submerged area 0–60 m (km^2)	584.8	0.8	308.6	55.2	2392.2

Islands). The summit of Gorringe is at 30–40 m depth (Alteriis et al. 2003), which means that this seamount has no habitat for shallow subtidal fishes. Despite the very small area and reduced number of habitat types, the estimated species richness of Gorringe was 42, about half of that for the Selvagens Islands. These results strengthen the conclusion that in Macaronesia islands or seamounts of small or very small size may harbour a substantial fraction of the species richness of this region.

It is likely that both the Selvagens Islands and the Gorringe Bank are within the dispersal range of many fish species that can be exported from other locations, in particular those that are at a shorter distance. The closest land masses to the Selvagens Islands are the Canary Islands (153 km) and the closest land mass to the Gorringe Bank is that of mainland Portugal (228 km). It remains unclear, however, whether the Selvagens Islands and the Gorringe seamounts sustain their own populations or if they are supplied from other sources and act as sinks *sensu* Pulliam (1988). In 2010 we found 57 of the 60 species described by Falcón et al (2000), but if colonization is frequent the finding of the same species in a given area in different years does not demonstrate that populations are self-recruiting. Also, we failed to detect three species: *Mugil cephalus* (Mugilidae), *Parablennius incognitus* (Bath, 1968) (Blenniidae) and *Thorogobius ephippiatus* (Lowe, 1839) (Gobiidae). Either these species were present in low numbers and we have failed to detect them during the campaign (because the fish assemblages are dominated by a small number of species and species richness is highly influenced by rare or very rare species), or there are changes in the community structure of the Selvagens Islands from year to year. Additional surveys of the Selvagens Islands ichthyofauna and fine-scale molecular studies may eventually answer this question in the future.

When comparing data from the Selvagens Islands ichthyofauna with similar data from the Canary Islands (Brito et al. 2002), Madeira (Wirtz et al. 2008) and the Azores (Porteiro et al. 2010), the high affinity between the first two regions becomes clear. Indeed, all species listed for the Selvagens Islands are also reported for the Canary Islands, while the corresponding numbers for Madeira are smaller. This is to be expected when we consider that the Canaries are the nearest neighbour to the Selvagens Islands (153 km) while Madeira and the Azores are at a distance of 251 km and 1127 km, respectively. Also, the Canary Islands are the largest and the oldest of the Macaronesian archipelagos and have the highest species richness, yielding 258 coastal fish species, while Madeira has 186 species and the Azores 148 species (Almada et al. 2013).

The high species richness of the Canary Islands is also likely to favour this archipelago as the dominant source of fish propagules (e.g. eggs and larvae) reaching the Selvagens Islands. Although the Canaries Current (north to south) and northwest winds are predominant, other current patterns that may transport these propagules from the Canary Islands northward to the Selvagens Islands are also common in this region (Stramma 1984; Morton et al. 1998). These results are congruent with the colonization of the Macaronesian Islands through a stepping-stone process, as proposed by Santos et al. (1995) and Almada et al. (2001). Overall, the high affinity between the ichthyofauna of the Macaronesian Islands and the west African coast parallels the biogeographic patterns found with other taxonomic groups (see Morton & Britton 2000; Tuya & Haroun 2009).

Excluding cosmopolitan species, some species reported for the Selvagens Islands are widely distributed along the western Atlantic coast but are not reported for the eastern Atlantic continental coast. These species only reach the archipelagos of the eastern Atlantic, including Cape Verde, São Tomé and Principe. Although they represent a small percentage of the total number of fish species from these islands, we must bear in mind that this transatlantic route is more than 10 times (closest American continental coast: 3669 km) the distance between the west African coast and the Selvagens Islands (353 km). This presumptive eastward colonization process could be favoured by the North Equatorial Countercurrent (see Fonseca et al. 2004).

When considering the potential capability of each species to colonize remote regions over long stretches of oceanic waters, no trend toward highly mobile pelagic fish can be found. In fact, most species reported for the Selvagens Islands are benthic or demersal and sedentary fish. Even considering that a few benthopelagic species may be found offshore associated with floating objects, e.g. *Balistes capriscus* Gmelin, 1789 and *Canthidermis sufflamen* (Mitchill, 1813), only a small number of species are able to cross the oceanic barrier between the west African coast or the Canary Islands and the Selvagens Islands.

On the other hand, when considering reproductive biology, most species reported for the Selvagens Islands spawn pelagic eggs or are viviparous and ovoviviparous, mobile or very mobile species (63.6%, n = 56). These fish may cross oceanic barriers, since there are no apparent barriers to the transport of eggs or breeding fish by marine currents. The high number of species that spawn pelagic eggs could represent a particularity of the fish communities of small and isolated islands.

The complexity of fish distribution patterns in Macaronesia is exemplified by the blenniids (the adults being sedentary and unable to cross deep water), with different species occurring in particular combinations of island groups but being absent in others which, judging by distance alone, seem to be accessible to eggs and larvae coming from the nearest island group. For instance, *Salaria pavo* (Risso, 1810) and *Parablennius pilicornis* (Cuvier, 1829), which occur in the Canary Islands and the shores of southwest Europe and northwest Africa, do not reach the Selvagens Islands. On the contrary, *Scartella cristata* (Linnaeus, 1758) shows a distribution that includes the Mediterranean, northwest Africa, both shores of the South Atlantic, the Canary Islands and the Selvagens Islands but not Madeira or the Azores. *Parablennius ruber* (Valenciennes, 1836), a very common blenniid at the Azores, occurs in western Europe, Madeira and Gorringe, but does not reach the Selvagens Islands and the Canaries. This diversity of distribution patterns in a single family suggests that interspecific differences in life history patterns, larval behaviour, ecology or even stochastic events may constrain each species to cope differently with transport to and survival at these islands (see Cowen 2002; Cowen & Sponaugle 2009). In a paper comparing reef fish communities across the Atlantic Ocean, Floeter et al. (2008) concluded that examples of recent dispersal outnumber those of historical events, although both factors have a strong influence on Atlantic fish diversity and biogeographic patterns.

In the scenario outlined above it is not surprising that no endemic fishes are known for the Selvagens Islands or the much larger Canary Islands. Macaronesian endemic species reported for other islands (e.g. *Scorpaena azorica* Eschmeyer, 1969 for the Azores) are considered doubtful reports because they are based on the description of a single specimen (Santos et al. 1997).

In the future, additional surveys are essential to improve our knowledge of the ichthyofauna of the Selvagens Islands in order to better understand fish dispersion in this geographic area. Additional data on the pelagic larval development and behaviour, together with a comprehensive phylogeographic study of the ichthyofauna from the Macaronesian islands, will improve our understanding of fish distribution patterns and processes in the north-eastern Atlantic and Mediterranean.

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