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Fishes of Clipperton Atoll, Eastern Pacific: Checklist, endemism and analysis of completeness of the inventory

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Abstract

This paper presents an updated checklist of cartilaginous and bony fishes from reefs and nearby areas around Clipperton Atoll (eastern Pacific). The register was compiled from field surveys between 1997 and 2012, an exhaustive literature review, and the consultation of museum collections and databases. The records were then used to assess the completeness of the local fish inventory using six non parametric rarefaction formulations. A total of 197 species in 62 families were recorded, and of these, 106 correspond to reef fishes; most of these are immigrants from the eastern and central Pacific, and only seven species were identified as endemics of the atoll. The estimated level of endemism in reef species (6.6%) is high for the eastern Pacific as a whole, but intermediate when compared with the figures for other oceanic islands of the same region. From the non parametric tests it was estimated that the expected number of reef fishes present at Clipperton is 110 $\pm$ 4 species, and as the difference from the reported figure from this new checklist was not significant, we suggest that the current listing is practically complete. Comparisons of the completeness of the inventory at Clipperton (~95%) to that reported for the fish fauna of the eastern Pacific and worldwide, revealed that the quality of the current inventory is remarkably high, even in spite of the geographic isolation of the atoll and the still limited scientific data.

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Introduction

Clipperton Island is a very isolated coral atoll located at the western edge of the tropical eastern Pacific region, and it zoogeographically belongs to the Oceanic Island Province (*sensu* Robertson and Cramer 2009). This volcanic headland rising only 29 m above sea level at its highest point, is located 1,280 km off west Mexico, at 10º18' N and 109º 13' W (Fig. 1). The atoll has a unique interior lagoon with no outlet, low topographic relief (Trichet 2009; Calmant et al. 2009), and is surrounded by well-cemented coral reefs that extend beyond a depth of 40 m and are composed predominantly of corals of the genera *Porites*, *Pavona* and *Pocillopora* (Glynn et al. 1996; Carricart--Ganivet and Reyes--Bonilla 1999).

Formal ichthyofaunal surveys of Clipperton reefs have been conducted since the early twentieth century (Snodgrass and Heller 1905) and have reported between 104 and 115 species of fishes (Allen and Robertson 1997; Robertson and Cramer 2009). However, the isolation and hence difficulties in accessing the island have resulted in relatively few scientific expeditions and a dearth of data on the marine communities. More recently, Robertson and Allen (2011) recorded 172 probable species, but only confirmed 130 of them. Collectively these communications have illustrated that the fish fauna at the atoll consists of a mixture of species from different biogeographic origins, including taxa from the Panamic Province, of circumtropical distribution, a very high percentage of transpacific species (Robertson et al. 2004), and more prominently, a relatively high proportion of endemics (Béarez and Séret 2009).

Clipperton Atoll is at the border of two major provinces in the Pacific Ocean, and may represent a key stepping stone for colonization of fishes into and from the tropical Americas (Allen and Robertson 1997). Because of its biogeographic relevance and with the aim of improving our knowledge about the local fish fauna, this paper presents an updated checklist of fishes observed or reported for the island, taking advantage of the availability of data collected on field trips conducted by the authors (1997--2012), and combining these with data from published records and museum collections.

Materials and Methods

The process followed to construct the fish checklist of Clipperton Atoll encompassed three steps. First, we conducted field surveys in the island in 1997, 2005, 2010 and 2012. Second, we gathered information from electronic and in--house scientific collections from institutions in three countries (France, Mexico and the United States), including records of specimens collected from the nineteenth century onward. Third, we conducted an extensive literature review on the fish fauna of Clipperton Atoll.

For our field survey, we visited several sites around the atoll in November 1997, March 2005, March 2010 and March 2012. At each site, we performed underwater visual censuses using SCUBA diving equipment, along belt transects of 25 x 4 m (12 transects in 1997, and 15 in 2012) and 25 x 2 m (25 transects in 2005), surveying at each visit an area between 1,200 m^2 and 2,500 m^2. Transects were run at two depths at each site: 0–15 m, on the first slope of the island (see Robertson and Allen 1996, and van Soest et al. 2009 for physiographic details), and from 16–40 m, where the reef bottom inclination becomes steeper. In addition, during the four visits we conducted observation dives in which the occurrence of all fish species was recorded. In all cases, the identification of species observed in the field was done on the basis of illustrations in Allen and Robertson (1994), Gotshall (1998), Humann and De Loach (2004), and Robertson and Allen (2013).

Figure 1 near here

In the case of museum data, we performed internet searches in databases of collections housed in México, the United States and France. From these inquiries we located records of fishes collected at Clipperton or in an area of 50 km around the central point of the island, which were deposited at the following institutions: California Academy of Sciences (San Francisco), National Museum of Natural History, Smithsonian Institution (Washington), Los Angeles Natural History Museum (Los Angeles), Scripps Institution of Oceanography (San Diego; SIO) and Musée National d'Histoire Naturelle (Paris; MNHN). The selection of specimens was independent of the fishing method, depth or year, in order to have a more inclusive listing of the species present at or nearby the atoll. Also, in case of doubt about the identity of the species, the curators of the collections were contacted directly for confirmation. It is important to note that most of the museum records for reef species had a counterpart in scientific publications or were visually confirmed during our field surveys, reinforcing their validity. Current nomenclature of the taxa was confirmed with the Catalog of Fishes of the California Academy of Sciences (Eschmeyer 2013) and FishBase (Froese and Pauly 2013).

To complete the checklist, we performed a literature review of refereed journals, formal scientific reports and technical books. We only took into consideration those species that were explicitly mentioned as seen or collected at Clipperton Atoll or its surroundings (50 km away). To eliminate synonyms and generate a systematic list consisting only of valid names, we also checked each taxonomic name in the Catalog of Fishes (Eschmeyer 2013).

Species identified from museums, field surveys and literature (20 different sources; Table 1 and 2) were divided among two lists: one for reef taxa and another for pelagic and deep-water fishes. This differentiation was due to the fact that the quality of the information is very dissimilar, as records of non-reef species are usually limited or imprecise, and collections are scarce (Eschmeyer et al. 2010), while data for reef fishes are much more abundant and identification is more accurate. Subsequent to this step and considering the limitation imposed by the insufficient information on pelagics and deep water fishes, we took only the data of reef species to build a matrix of species versus data source, and from there conducted numerical analyses to estimate the completeness of the inventory of reef fishes in the atoll and of the total richness per family present in Clipperton (equivalent to its gamma diversity; Magurran 2004). To do so, we used the cited sources as sampling units and from there we calculated the expected richness (total and of the 16 families with more than 3 species present in the checklist), using the software Primer ver. 6.0, and the non parametric rarefaction methods of Chao 1, Chao 2, Jacknife 1, Jacknife 2, Michaelis--Menten and Bootstrap (with 1,000 permutations; further details of these techniques are provided in Magurran 2004). These procedures were selected as they are suitable for application with information of species presences and absences, and have been demonstrated to be accurate estimators of richness in marine taxa, including fishes (Magurran et al. 2011; Drew et al. 2012); also, similar methods such as curves of species accumulation have been applied to examine potential richness for the entire eastern Pacific reef fish fauna (Zapata and Robertson 2007) and worldwide (Mora et al. 2008).

With the resulting values obtained by the six rarefaction methods, we calculated the average and standard deviation of the expected richness in total and for each reef fish family (16 in total), and statistically analyzed the difference between these expectations and the observed species richness. For that, we applied two procedures; one was described by Sokal and Rohlf (2012) and is based on a modified Student's t--test used to compare individual values of estimated parameters against a series of projected values, under the expectation that data follow a normal distribution. In addition we conducted another non parametric comparison involving resampling to generate 1,000 expected values of the total and per family gamma diversity obtained from the results of the six used methods. From those numbers we considered that the difference was significant if the known species richness has a probability of less than 5% in the resampled distribution (Dixon 2001).

Results

We confirmed the occurrence of 197 species of marine fishes off Clipperton Atoll, from 141 genera, 62 families, 20 orders, and 2 classes (Tables 1 and 2). Of these, we observed 76 species in the field while the literature review yielded 186 species reported for the island, and 107 records came from museums. The most speciose families were the Muraenidae (15), Exocoetidae (15), Carangidae (11), Acanthuridae (10), Labridae (8), Serranidae (8), Carcharhinidae (8), Echeneidae (7), Holocentridae (6) and Balistidae (5).

Table 1 and 2 near here

Considering a subdivision by habitat, 91 species (46.2%) are typically from deep (> 50 m) or pelagic waters, while the remaining 106 (53.8%) are reef fishes. On the other hand, according to the updated information, Clipperton Atoll has only 7 endemic fishes (3.6 % of the total, and 6.6% of the reef taxa): *Holacanthus limbaughi* Baldwin, 1963, *Myripristis gildi* Greenfield, 1965, *Ophioblennius clippertonensis* Springer, 1962, *Pseudogramma axelrodi* Allen and Robertson, 1995, *Stegastes baldwini* Allen and Woods, 1980, *Thalassoma robertsoni* Allen, 1995, and *Xyrichtys wellingtoni* Allen and Robertson, 1995.

When using only previously unpublished information (data from collections and field work), Table 1 and 2 include a total of 12 new records of fish species for Clipperton Atoll, from 12 genera, 9 families, 8 orders, and 2 classes. Among the newly registered species are typical reef taxa like *Aulorhynchus flavidus* Gill, 1861, *Chilomycterus reticulatus* (Linnaeus, 1758) and

Triaenodon obesus (Ruppell, 1837), *Upeneus xanthogrammus* Gilbert, 1892, but also pelagic or deep water species including *Bathophilus filifer* (Garman, 1899), *Diogenichthys lanternatus* (Garman, 1899), *Gonichthys tenuiculus* (Garman, 1899), *Myctophum aurolanternatum* Garman, 1899, *Sudis atrox* Rofen, 1963, and *Vinciguerria lucetia* (Garman, 1899). Finally, in the collections we located unidentified specimens of a species of the genus *Diaphus* (Myctophidae) and another of *Ichthyapus* (Ophichthidae) that require further examination by specialists for clear identification, but nevertheless it is noteworthy that those genera have not been reported for Clipperton before. From these records, we add five families (Phosichthydae, Stomiidae, Paralepididae, Myctophidae, and Aulorhynchidae) that have not previously been reported for the atoll.

Robertson and Allen (2011) mentioned 42 species as potentially present in the area, but with no confirmed records (Table 2). Of these, we corroborated the presence of 12 species from museum collections: *Carcharhinus longimanus* (Poey, 1861), *Manta birostris* (Walbaum, 1792), *Cheilopogon spilonotopterus* (Bleeker, 1866), *Cheilopogon xenopterus* (Gilbert, 1890), *Exocoetus monocirrhus* Richardson, 1846, *Exocoetus volitans* Linneaus, 1758, *Fodiator rostratus* (Gunther, 1866), *Oxyporhamphus micropterus* (Valenciennes, 1847), *Remora osteochir* (Cuvier, 1829), *Cubiceps pauciradiatus* Gunther, 1872, *Psenes sio* Haedrich, 1970, and *Lagocephalus lagocephalus* (Linnaeus, 1758); most of these are pelagic like elasmobranchs and flying fishes (Exocoetidae).

Estimates obtained by non--parametric rarefaction methods indicate that the expected richness for reef fishes is higher than the observed (106 species; Table 1), with expectations ranging between 118 species (Michaelis--Menten) and 107 species (Chao 1 and 2), with an average of 110 ± 4.0 (s.d.) species. This assessment suggests that the local inventory is still not complete, that it currently represents about 96% of the expected total richness, and that probably less than 10 reef fish species that occur around the atoll may still be unreported. Analyzing the data at a different taxonomic level, the total richness recognized for each family of reef fishes having three of more species was usually lower than the figure proposed by the models (except 3 of 16 families; Figure 2). On the other hand, the currently reported number of species within the Acanthuridae, Balistidae, Blenniidae, Holocentridae, Kyphosidae, Labridae, Muraenidae, Pomacanthidae and Pomacentridae is comparable to the average species richness derived from the estimates (less than 3% in difference; Fig. 2, Table 3); this suggests that at least for those families the checklist may be complete. In contrast, the current species roster for Antennariidae, Diodontidae, Mullidae, Tetraodontidae, Scorpaenidae, Serranidae, and Ophichthidae apparently underestimate the true richness by 5% to 15% (Fig. 2, Table 3); notwithstanding, the difference between expected and observed richness is less than one species in all these cases.

Figure 2 near here

Finally, the statistical analyses using the Student t--test and the bootstrap, point out that of the 16 analyzed reef fish families, only three had significant differences between the expected and observed richness: Serranidae, Mullidae and Tetraodontidae (the latter only for the parametric test; Table 3). For all of them the tests indicate an underestimation of the true richness, although the actual discrepancies (measured in number of species observed vs. expected) are negligible: less than one in each case.

Table 3 near here

Discussion

The comprehensive fish checklist of Clipperton Atoll presented here (197 species; Tables 1 and 2) is almost 35% higher than the number of species reported in previous inventories (104 species: Robertson and Cramer 2009, 115 species: Robertson and Allen 1996 and Allen and Robertson 1997, and 130 species: Robertson and Allen 2011). One reason for the increase in the total species richness is the inclusion of deep water and pelagic taxa in our review (Table 2), many of those not previously considered in the cited checklists and other papers referred to the atoll (Béarez and Séret 2009). We decided to take account of them because isolated individuals and even schools of many species of sharks, flyingfishes, myctophids, jacks and others, have been observed near the reefs; however, acknowledging the difference in quality of available information, we decided to separate these records (Table 2) from those of the typical reef species (Table 1). In spite of that, even when we only pay attention to reef taxa (families included in Table 1), our total species richness count adds up to 106 species, against a maximum of 95 cited in the most recent reference (Robertson and Allen 2013). We suggest that the rise in number of reported species in our study is due to the natural improvement in the existing data as a result of more frequent visits to the atoll in the last decade, as well as for the increase in the amount of technical papers devoted to the area (Béarez and Séret 2009), and finally, the possibility to locate and retrieve information about specimens collected in the atoll in the twentieth century that are now deposited in scientific collections.

The total gamma diversity of 197 species at Clipperton (Table 1 and 2), of which only 106 are typical residents of rocky or coral reefs, is low compared with that reported by Robertson and Cramer (2009), Robertson and Allen (2011) and Fourriére (2012) for other oceanic islands of the eastern Pacific including Galápagos, Ecuador (363 species), Revillagigedos, México (over 350 species) and Cocos, Costa Rica (259 species), but very similar to the one known at Malpelo

Island, Colombia (203). It appears likely that in conformity to principles of island biogeography, the reduced size of the atoll diminishes the probability for larvae or vagrant adults to arrive to the area from other regions, and the homogeneity in the coral reef habitat limits local recruitment. These two factors might be playing a relevant role in determining local fish species richness in Clipperton, as suggested previously by Robertson and Allen (1996) and, Béarez and Séret (2009).

One of the most interesting findings of this study was the confirmation of the number of species reported exclusively for Clipperton: a total of seven, equivalent to 6.6% of the reef fish fauna (Table 1). This level of local endemism is much lower to that calculated for the atoll by Robertson and Allen (1996; 14% endemism), but slightly higher compared to more recent information presented for the locality by Mora et al. (2003; 6.0%), Allen (2008; 5.8%) and Robertson and Cramer (2009; 5.8%), and corroborating observations by Béarez and Séret (2009) point out a high level of endemism in the reef fish fauna of Clipperton Atoll.

According to data presented by the latter authors, the figure of 6.6% in endemism is relatively high for a typical location of the eastern Pacific, but intermediate among oceanic islands: lower than Galápagos and Revillagigedos (over 8%), and higher than at Cocos (4.6%), and Malpelo islands (2.5%). In addition, Allen (2008) mentioned that according to his data, Clipperton island has the highest number of reef fish endemics per coral reef habitat area in the entire Indo Pacific (at the time, 6 taxa in 1.5 km^2). The current figure (seven endemics) has changed this value in a positive sense, so the consideration of Allen (2008) holds and highlights the relevance of this area from the perspective of conservation.

The first comprehensive species lists for the study location, by Robertson and Allen (1996, 1997), identified nine endemic fish species, which at that time added up to over 10% of the known local assemblage. The proportion of endemics has subsequently been cut down as the total number of species recorded from the atoll increased, and also because two species originally identified as local endemics have either been synonymized or have a wider geographic range than originally thought. In the first case, the goby *Bathygobius arundelii* Garman, 1899, is currently considered a synonym of *B. lineatus* (Jenyns, 1841), a common species in Clipperton that is also found in the Galápagos, Gorgona Island, Colombia, and Lobos Afuera Island, Peru (Robertson and Allen 2011). In the second instance, *Epinephelus* sp. is now *E. clippertonensis* Allen and Robertson, 1999. The species was noted by Robertson and Allen (2011) not to be an endemic, as it also occurs in the Revillagigedo Islands and Alijos Rocks, México.

Taking a wider perspective, our results are noteworthy considering that Hobbs et al. (2012) indicated that endemism in reef fishes of other remote islands like the Christmas Island and Cocos--Keeling Archipelago (Indian Ocean) do not exceed 3%. In the case of Clipperton, although there is a high percentage of endemism in reef fishes (6.6%) and decapod crustaceans (6.3%; Poupin *et al*. 2009), actually the figures for other marine taxa are not prominent; for mollusks, endemism is only 2.6% (Kaiser 2007), there is only one endemic barnacle (Zullo 1969) and no exclusive reef corals (Carricart--Ganivet and Reyes--Bonilla 1999). This pattern of reduced endemism in many groups at Clipperton illustrate that even taking into account the isolation of the atoll, speciation has not occurred so often, or the new demes have not been successful enough to remain in the island. In concordance to this idea, Bellwood and Meyer (2009) show how isolation in itself is not always sufficient for speciation to occur, as of 91 Indo Pacific reef fish species for which the origination age is known, 66 (73%) are over 4 million years old and many date from the Miocene, thus indicating that this group requires a long time for speciation.

Another possible cause for the low level of endemism in many taxa resident of Clipperton Atoll might be a relatively frequent larval flow of immigration of adults, in this case, from the

American mainland and the central Pacific. Genetic information of the coral *Porites lobata* point out that larval exchange of that species between Clipperton and the central Pacific islands is common to the point of being included in a single metapopulation (Baums et al. 2012). Also, LaJeunesse et al. (2011) showed that zooxanthellae associated with *Pocillopora* spp. from Clipperton and the eastern Pacific coast coincide in their haplotype composition, except for one particular combination which is not found in the atoll but not elsewhere along the region. Finally, Lessios and Robertson (2006) demonstrated with molecular data that several reef fishes have maintained connectivity between the east Pacific (including Clipperton) and the central Pacific, possibly by larval transportation back and forth during the Pleistocene and Recent.

Focusing on the analysis of completeness of the species inventory, the non parametric tests point out that the current figure of 106 species is very similar, and not significantly different to the expected one (Table 3); this result means that probably we are already informed about 95% or more of the total reef fish diversity of Clipperton Atoll. This percentage is very high, considering that the thorough study by Zapata and Robertson (2007) propose that the list of marine shorefishes of the eastern Pacific is 85% to 88% complete, and that the publication by Mora et al. (2008) predicts that we have documented 79% of the world inventory of marine fishes. The latter authors note that at a small scale (quadrats of 3 x 3 degrees in latitude and longitude), less than 5% of the world oceans are sampled well enough to have an inventory that is 80% complete, and that finding contrasts with the high quality of the survey effort that has been conducted at Clipperton, even with all the limitations associated with study of a very isolated area.

Restricting the analyses of completeness of the inventory to 16 reef fish families with three or more species, most of these seem to be very well sampled as the expected richness in 13 of them is not significantly different from the currently reported (Fig. 2, Table 3). It is probable that as the reef physiography at the atoll is relatively homogeneous below 15 m (mostly composed of continuous reef framework with abundant live coral colonies and small patches of free reef rock; Glynn et al. 1996), the surveys have been able to locate most of the taxa present. On the other hand, the small size of the island and limited number of habitats must restrict the local richness, as suggested by Robertson and Allen (1996), and makes easier to have a full recollection of the assemblage. Finally, for the three families for which expected and observed figures differ significantly (Mullidae, Serranidae and Tetraodontidae), the discrepancy in actual richness is quite small (less than one species in any case).

In conclusion, thanks to the abundant new information available for this research, the present checklist of the fish fauna of Clipperton Atoll includes 197 species. This represents almost 70 species more than the previous checklists for the atoll, and includes 11 new species records for this location. The assemblage has seven endemics (about 6% of the total reef fish fauna), a high value when compared with other areas of the eastern Pacific, but not unusual in relation to endemism of fishes in oceanic islands of that region. A series of rarefaction methods, applied to determine the completeness of the reef fish species inventory, indicated that the expected number of fishes is a little higher than the one observed; nevertheless, the difference is not significant both for most families and when analyzing the full checklist, and in consequence, the catalogue of local reef fishes seems to be almost complete; this is an important feat given the isolation and difficulty in accessing Clipperton Atoll.

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TABLE 1. Taxonomic list of reef fishes species from Clipperton Atoll.
Key to museums: **USNM)** National Museum of Natural History, Smithsonian Institution; **SIO)** Scripps Institution of Oceanography, San Diego; **MNHN)** National Museum of Natural History, Paris; **LACM)** Natural History Museum of Los Angeles.
References: **1)** Snodgrass and Heller 1905; **2)** Schmitt and Schultz 1940; **3)** Ehrhardt and Plessis 1972; **4)** Robertson and Allen 1996; **5)** Allen and Robertson 1997; **6)** Victor and Wellington 2000; **7)** Adjeroud and González--Salas 2005; **8)** Béarez and Séret 2009; **9)** IOC of UNESCO 2010; **10)** Robertson and Allen 2011 (* unconfirmed species); **11)** Froese and Pauly 2013; **12)** Eschmeyer 2013.
Key to bathymetric range (data from Robertson and Allen 2013, and Froese and Pauly 2013): **S**: Shallow water species (resident from surface to 50 m deep); **D**: Deep water species (bathymetric midpoint limit higher than --50 m, or deeper).

	Field observation (1997)	Field observation (2005)	Field observation (2010)	Field observation (2012)	Museum records	References	Bathymetric distribution
Phylum CHORDATA							
Class CHONDRICHTHYES							
Family Carcharhinidae							
Triaenodon obesus (Rüppell, 1837)	+		+				D
Class ACTINOPTERYGII							
Order ANGUILLIFORMES							

Table 1, cont'd

Family Muraenidae						
Anarchias galapagensis (Seale, 1940)				USNM, MNHN, LACM	4, 5, 9, 10	S
Echidna nebulosa (Ahl, 1789)				USNM, SIO, MNHN, LACM	3, 4, 5, 8, 9, 10, 11	S
Echidna nocturna (Cope, 1872)			+	USNM	4, 5, 8, 9, 10, 11	S
Enchelycore octaviana (Myers and Wade, 1941)		+			4, 5, 7, 9, 10	S
Enchelynassa canina (Quoy and Gaimard, 1824)				USNM, SIO, LACM	4, 5, 8, 9, 10	S
Gymnomuraena zebra (Shaw, 1797)			+	SIO, LACM	4, 5, 9, 10	S
Gymnothorax buroensis (Bleeker, 1857)				USNM	4, 5, 8, 9, 10	S
Gymnothorax dovii (Günther, 1870)	+	+	+	USNM, SIO, LACM	4, 5, 8, 9	S
Gymnothorax flavimarginatus (Rüppell, 1830)		+	+	USNM, LACM	4, 5, 9, 10	S
Gymnothorax panamensis (Steindachner, 1876)				USNM, LACM	4, 5, 9, 10	S
Gymnothorax pictus (Ahl, 1789)				USNM, SIO, MNHN, LACM	3, 4, 5, 8, 9, 10, 11	S

Table 1, cont'd

Uropterygius macrocephalus (Bleeker, 1864)	USNM, SIO, MNHN	2, 3, 4, 5, 9, 10, 11	S
Uropterygius supraforatus (Regan, 1909)	USNM, LACM	9, 10, 12	S
Uropterygius versutus Bussing, 1991	USNM	4, 5, 9, 10	S
Scuticaria tigrina (Lesson, 1828)		4, 9, 10	S
Family Ophichthidae			
Apterichtus equatorialis (Myers and Wade, 1941)	MNHN	4, 5, 9, 10	D
Ichthyapus sp.	USNM		S
Myrichthys pantostigmius Jordan and McGregor, 1898	USNM, MNHN	4, 5, 8, 9, 10, 11	S
Phaenomonas pinnata Myers and Wade, 1941		4, 5, 9, 10	S
Order OPHIDIIFORMES			
Family Ophidiidae			
Petrotyx hopkinsi Heller and Snodgrass, 1903		9, 10	S
Order LOPHIIFORMES			
Family Antennariidae			
Antennatus coccineus (Lesson, 1831)		4, 5, 9, 10	S
Antennatus sanguineus (Gill, 1863)		4, 5, 9, 10	S

Table 1, cont'd

Antennatus strigatus (Gill, 1863)					SIO	4, 5, 9, 10	S
Order MUGILIFORMES							
Family Mugilidae							
Chaenomugil proboscideus (Günther, 1861)						4, 5, 9, 10	S
Order BERYCIFORMES							
Family Holocentridae							
Myripristis berndti Jordan and Evermann, 1903	+	+	+		SIO, MNHN	4, 5, 8, 9, 10, 11	D
Myripristis clarionensis Gilbert, 1897					USNM, MNHN, LACM	3, 4, 5, 9, 10, 11, 12	S
Myripristis gildi Greenfield, 1965					USNM	3, 4, 5, 9, 10, 11, 12	S
Myripristis murdjan (Forsskål, 1775)					USNM	3, 5, 7	S
Plectrypops lima (Valenciennes, 1831)					MNHN	4, 5, 9, 10, 12	S
Sargocentron suborbitale (Gill, 1863)	+			+	USNM, SIO, MNHN, LACM	4, 5, 8, 9, 10, 11	S
Order GASTEROSTEIFORMES							
Family Syngnathidae							

Table 1, cont'd

Doryrhamphus excisus Kaup, 1856					USNM, MNHN	4, 5, 10	S
Family Aulostomidae							
Aulostomus chinensis (Linnaeus, 1766)	+	+	+	+	USNM, MNHN	4, 5, 7, 8, 9, 10, 11	D
Family Fistulariidae							
Fistularia commersonii Rüppell, 1838					SIO, MNHN, LACM	4, 5, 9, 10	D
Order SCORPAENIFORMES							
Family Scorpaenidae							
Pontinus vaughani Barnhart and Hubbs, 1946					USNM, SIO	4, 5, 9, 10, 11, 12	D
Scorpaena histrio Jenyns 1840						3	D
Scorpaenodes xyris (Jordan and Gilbert, 1882)	+		+		USNM, SIO, MNHN, LACM	4, 5, 8, 9, 10	S
Order PERCIFORMES							
Family Serranidae							
Dermatolepis dermatolepis (Boulenger, 1895)	+	+	+	+	SIO, MNHN, LACM	4, 5, 7, 8, 9, 10	S

Table 1, cont'd

Epinephelus analogus Gill, 1863						11	S
Epinephelus clippertonensis Allen and Robertson, 1999			+		USNM, SIO, MNHN, LACM	8, 10, 11, 12	S
Epinephelus labriformis (Jenyns, 1840)	+	+		+	SIO	1, 3, 4, 5, 7	S
Liopropoma fasciatum Bussing, 1980						9, 10	D
Paranthias colonus (Valenciennes, 1846)	+	+	+	+	SIO, MNHN, LACM	4, 5, 7, 8, 9, 10, 11	S
Pseudogramma axelrodi Allen and Robertson, 1995					USNM	4, 5, 9, 10, 11	S
Rypticus bicolor Valenciennes, 1846					USNM, MNHN	4, 8, 9, 10	S
Family Priacanthidae							
Heteropriacanthus cruentatus (Lacepède, 1801)	+					9, 10	D
Family Apogonidae							
Apogon atricaudus Jordan and McGregor, 1898					MNHN	4, 5, 8, 9, 10	S
Family Echeneidae							
Echeneis naucrates Linnaeus, 1758	+					9, 10	S
Family Lutjanidae							
Lutjanus viridis (Valenciennes, 1846)	+	+	+	+	USNM, SIO, MNHN, LACM	3, 4, 5, 8, 9, 10	S

Table 1, cont'd

Family Mullidae							
Mulloidichthys dentatus (Gill, 1862)	+	+	+	+	USNM	4, 5, 7, 8, 9, 10	S
Mulloidichthys vanicolensis (Valenciennes, 1831)						9, 10	D
Upeneus xanthogrammus Gilbert, 1892					LACM		S
Family Kyphosidae							
Kyphosus analogus (Gill, 1862)		+	+	+		3, 4, 5, 7, 8, 9, 10	S
Kyphosus elegans (Peters, 1869)	+	+	+	+	LACM	4, 5, 7, 8, 9, 10	S
Sectator ocyurus (Jordan and Gilbert, 1882)		+	+			4, 5, 8, 9, 10	S
Family Chaetodontidae							
Forcipiger flavissimus Jordan and McGregor, 1898	+	+	+	+	USNM	4, 5, 8, 9, 10	D
Johnrandallia nigrirostris (Gill, 1862)	+	+	+	+	USNM	4, 5, 7, 8, 9, 10	S
Family Pomacanthidae							
Holacanthus clarionensis Gilbert, 1890						4, 5, 9, 10	S
Holacanthus limbaughi Baldwin, 1963	+	+	+	+	USNM, SIO,	3, 4, 5, 7, 8,	D

Table 1, cont'd

					MNHN, LACM	9, 10, 12	
Pomacanthus zonipectus (Gill, 1862)					LACM	10	S
Family Kuhliidae							
Kuhlia mugil (Forster, 1801)					SIO, MNHN, LACM	3, 4, 5, 8, 9, 10	S
Family Cirrhitidae							
Cirrhitichthys oxycephalus (Bleeker, 1855)	+	+	+	+	USNM, SIO, MNHN, LACM	4, 5, 7, 8, 9, 10	S
Cirrhitus rivulatus Valenciennes, 1846	+	+	+	+	USNM, SIO, MNHN, LACM	3, 4, 5, 7, 8, 9, 10	S
Family Pomacentridae							
Abudefduf troschelii (Gill, 1862)						6, 10	S
Chromis alta Greenfield and Woods, 1980						4, 5, 6, 9, 10	D
Stegastes baldwini Allen and Woods, 1980	+	+	+	+	USNM, SIO, MNHN, LACM	4, 5, 6, 7, 8, 9, 10, 11	S
Family Labridae							
Bodianus diplotaenia (Gill, 1862)	+	+	+	+	USNM, MNHN, LACM	1, 3, 4, 5, 6, 7, 8, 9, 10, 11	S

Table 1, cont'd

Novaculichthys taeniourus (Lacepède, 1801)		+			USNM	4, 5, 6, 8, 9, 10	S
Stethojulis bandanensis (Bleeker, 1851)					USNM, MNHN	4, 5, 6, 7, 8, 9, 10, 11, 12	S
Thalassoma grammaticum Gilbert, 1890	+	+	+	+		4, 5, 6, 7, 8, 9, 10	S
Thalassoma purpureum (Forsskål, 1775)		+			USNM, MNHN	4, 5, 6, 7, 8, 9, 10	S
Thalassoma robertsoni Allen, 1995		+	+	+	USNM, MNHN	4, 5, 6, 7, 8, 9, 10, 11, 12	S
Thalassoma virens Gilbert, 1890		+				4, 5, 6, 7, 9, 10, 11	S
Xyrichtys wellingtoni Allen and Robertson, 1995		+			USNM	4, 5, 6, 7, 9, 10, 11, 12	S
Family Scaridae							
Scarus rubroviolaceus Bleeker, 1847	+	+	+	+	USNM	4, 5, 7, 8, 9, 10	S
Family Blenniidae							

Table 1, cont'd

Entomacrodus chiostictus (Jordan and Gilbert, 1882)					USNM, SIO, MNHN, LACM	3, 4, 5, 8, 9, 10, 11	S
Ophioblennius clippertonensis Springer, 1962					USNM, MNHN	3, 4, 12	S
Ophioblennius steindachneri Jordan and Evermann, 1898	+	+	+	+	SIO, MNHN, LACM	7, 9, 10	S
Family Gobiidae							
Bathygobius lineatus (Jenyns, 1841)		+			MNHN	3, 4, 5, 8, 9, 10, 11, 12	S
Family Zanclidae							
Zanclus cornutus (Linnaeus, 1758)	+	+	+	+	USNM, MNHN, LACM	3, 4, 5, 7, 8, 9, 10	D
Family Acanthuridae							
Acanthurus achilles Shaw, 1803		+			LACM	4, 5, 7, 8, 9, 10, 11	S
Acanthurus guttatus Forster, 1801					MNHN	8, 9, 10	S
Acanthurus japonicus (Schmidt, 1931)						1, 7	S
Acanthurus nigricans (Linnaeus, 1758)	+	+	+	+	USNM, MNHN	3, 4, 5, 7, 8, 9, 10	S

Table 1, cont'd

Acanthurus triostegus (Linnaeus, 1758)	+	+	+		USNM, SIO, MNHN, LACM	2, 3, 4, 5, 7, 8, 9, 10, 11	S
Acanthurus xanthopterus Valenciennes, 1835	+	+				4, 5, 7, 9, 10, 11	S
Ctenochaetus marginatus (Valenciennes, 1835)		+	+	+	USNM, MNHN, LACM	4, 5, 7, 8, 9, 10, 11	S
Naso annulatus (Quoy and Gaimard, 1825)						4, 5, 9, 10, 12	S
Naso hexacanthus (Bleeker, 1855)						4, 5, 9, 10	D
Naso lituratus (Forster, 1801)						4, 5, 9, 10, 11	S
Order PLEURONECTIFORMES							
Family Bothidae							
Bothus mancus (Broussonet, 1782)		+	+		USNM, SIO, MNHN, LACM	3, 4, 5, 8, 9, 10, 11	D
Order TETRAODONTIFORMES							
Family Balistidae							
Balistes polylepis Steindachner, 1876			+		SIO	4, 5, 9, 10	D
Melichthys niger (Bloch, 1786)	+	+	+	+	USNM, SIO, MNHN, LACM	2, 3, 4, 5, 7, 8, 9, 10, 11	S

Table 1, cont'd

Melichthys vidua (Richardson, 1845)						9, 10	S
Sufflamen verres (Gilbert and Starks, 1904)	+	+	+	+	USNM, SIO, MNHN, LACM	1, 3, 4, 5, 7, 8, 9, 10, 11	S
Xanthichthys mento (Jordan and Gilbert, 1882)	+					4, 5, 9, 10, 11	S
Family Monacanthidae							
Aluterus scriptus (Osbeck, 1765)			+		USNM	4, 5, 9, 10	D
Cantherhines dumerilii (Hollard, 1854)	+		+	+	USNM, MNHN, LACM	4, 5, 8, 10	S
Family Ostraciidae							
Ostracion meleagris Shaw 1796	+	+	+	+	USNM, SIO, MNHN, LACM	1, 3, 4, 5, 8, 9, 10, 12	S
Family Tetraodontidae							
Arothron hispidus (Linnaeus, 1758)						2, 3	S
Arothron meleagris (Anonymous, 1798)	+	+	+	+	USNM, SIO, MNHN, LACM	1, 3, 4, 5, 7, 8, 9, 10	S
Canthigaster punctatissima (Günther, 1870)	+	+	+	+	USNM, SIO, MNHN	4, 5, 8, 9, 10	S
Family Diodontidae							

Table 1, cont'd

Chilomycterus reticulatus (Linnaeus, 1758)		+			S
Diodon eydouxii Brisout de Barneville, 1846			SIO	9, 10	S
Diodon holocanthus Linnaeus, 1758	+	+		4, 5, 9, 10	S
Diodon hystrix Linnaeus, 1758		+		4, 5, 9, 10	S

TABLE 2. Taxonomic list of non reef fishes species from Clipperton Atoll.
Key to museums: **USNM)** National Museum of Natural History, Smithsonian Institution; **SIO)** Scripps Institution of Oceanography, San Diego; **MNHN)** National Museum of Natural History, Paris; **LACM)** Natural History Museum of Los Angeles.
References: **1)** Snodgrass and Heller 1905; **2)** Schmitt and Schultz 1940; **3)** Ehrhardt and Plessis 1972; **4)** Robertson and Allen 1996; **5)** Allen and Robertson 1997; **6)** Victor and Wellington 2000; **7)** Adjeroud and González--Salas 2005; **8)** Béarez and Séret 2009; **9)** IOC of UNESCO 2010; **10)** Robertson and Allen 2011 (*unconfirmed species); **11)** Froese and Pauly 2013; **12)** Eschmeyer 2013.
Key to bathymetric range (data from Robertson and Allen 2013, and Froese and Pauly 2013): **S**: Shallow water species (resident from surface to 50 m deep); **D**: Deep water species (bathymetric midpoint limit higher than --50 m, or deeper).

	Field observation (1997)	Field observation (2005)	Field observation (2010)	Field observation (2012)	Museum records	References	Bathymetric distribution
Phylum CHORDATA							
Class CHONDRICHTHYES							
Order ORECTOLOBIFORMES							
Family Rhincodontidae							
Rhincodon typus Smith, 1828					LACM	8, 9, 10, 11	D
Order LAMNIFORMES							
Family Lamnidae							
Isurus oxyrinchus Rafinesque, 1810						10*	D
Order CARCHARHINIFORMES							
Family Carcharhinidae							
Carcharhinus albimarginatus (Rüppell, 1837)			+		SIO, MNHN	1, 3, 4, 5, 8, 9, 10, 11	D
Carcharhinus falciformis (Müller and Henle, 1839)			+		MNHN	4, 5, 8, 9, 10, 11	D
Carcharhinus galapagensis (Snodgrass and Heller, 1905)			+		SIO, MNHN, LACM	3, 4, 5, 8, 9, 10, 11	D
Carcharhinus limbatus (Müller and Henle, 1839)			+		LACM	3, 4, 5, 9, 10	S
Carcharhinus longimanus (Poey, 1861)						10*, 11	D
Galeocerdo cuvier (Péron and Lesueur, 1822)						8, 9, 10	D
Prionace glauca (Linnaeus, 1758)					USNM	9, 10	D

Table 2, cont'd

Family Sphyrnidae					
Sphyrna lewini (Griffith and Smith, 1834)	+	+		4, 5, 8, 9, 10	D
Order MYLIOBATIFORMES					
Familia Dasyatidae					
Pteroplatytrygon violacea (Bonaparte, 1832)				10*	D
Family Myliobatidae					
Manta birostris (Walbaum, 1792)	+			3, 8, 10*	S
Mobula japanica (Müller and Henle, 1841)				10*	S
Mobula tarapacana (Philippi, 1892)				10*	S
Mobula thurstoni (Lloyd, 1908)				8	S
Class ACTINOPTERYGII					
Order GONORYNCHIFORMES					
Family Chanidae					
Chanos chanos (Forsskål, 1775)				4, 5, 9, 10	S
Order STOMIIFORMES					
Family Phosichthyidae					
Vinciguerria lucetia (Garman, 1899)			USNM, SIO, LACM		D
Family Stomiidae					
Bathophilus filifer (Garman, 1899)			SIO		D
Order AULOPIFORMES					
Family Paralepididae					
Sudis atrox Rofen, 1963			USNM, SIO		D
Order MYCTOPHIFORMES					
Family Myctophidae					
Diaphus sp.			SIO		D
Myctophum aurolaternatum Garman, 1899			SIO		D
Diogenichthys laternatus (Garman, 1899)			SIO		D

Table 2, cont'd

Gonichthys tenuiculus (Garman, 1899)		SIO		D
Order GADIFORMES				
Family Bregmacerotidae				
Bregmaceros bathymaster Jordan and Bollman, 1890			10*	D
Order OPHIDIIFORMES				
Family Ophidiidae				
Brotula multibarbata Temminck and Schlegel, 1846			9, 10	D
Order LOPHIIFORMES				
Family Linophrynidae				
Linophryne sp.			12	D
Order BELONIFORMES				
Family Exocoetidae				
Cheilopogon californicus (Cooper, 1863)			3	S
Cheilopogon dorsomacula (Fowler, 1944)			10*	S
Cheilopogon heterurus (Rafinesque, 1810)			4, 5	S
Cheilopogon papilio (Clark, 1936)			10*	S
Cheilopogon spilonotopterus (Bleeker, 1865)		SIO	4, 5, 9, 10*, 11	S
Cheilopogon xenopterus (Gilbert, 1890)		SIO	10*	S
Exocoetus monocirrhus Richardson, 1846		SIO	10*	S
Exocoetus volitans Linnaeus, 1758		SIO	3, 10*	S
Fodiator rostratus (Günther, 1866)	+	SIO	4, 5, 10*, 11	S
Hirundichthys marginatus (Nichols and Breder, 1928)			10*	S
Hirundichthys rondeletii (Valenciennes, 1847)			10*	S
Hirundichthys speculiger (Valenciennes, 1847)			10*	S
Oxyporhamphus micropterus (Valenciennes, 1847)		SIO	3, 4, 5, 10*	S
Parexocoetus brachypterus (Richardson, 1846)			10*	S
Prognichthys sealei Abe, 1955			10*	S
Family Hemiramphidae				

Table 2, cont'd

Euleptorhamphus viridis (Van Hasselt, 1823)					SIO, MNHN	4, 5, 8, 9, 10, 11	S
Hemiramphus saltator Gilbert and Starks, 1904	+					9, 10	S
Family Belonidae							
Ablennes hians (Valenciennes, 1846)						10	S
Platybelone pterura (Osburn and Nichols, 1916)			+			9, 10, 11	S
Strongylura strongylura (Van Hasselt, 1823)						3	S
Tylosurus melanotus (Bleeker, 1850)	+		+			4, 5, 9, 10, 11	S
Order GASTEROSTEIFORMES							
Family Aulorhynchidae							
Aulorhynchus flavidus Gill, 1861					LACM		S
Order PERCIFORMES							
Family Coryphaenidae							
Coryphaena equiselis Linnaeus, 1758					LACM	4, 5, 9, 10	S
Coryphaena hippurus Linnaeus, 1758						3, 9, 10	S
Family Echeneidae							
Phtheirichthys lineatus (Menzies, 1791)						10*	S
Remora australis (Bennett, 1840)						10*	D
Remora brachyptera (Lowe, 1839)						10*	D
Remora osteochir (Cuvier, 1829)					MNHN	10*	D
Remora remora (Linnaeus, 1758)			+		LACM	3, 4, 5, 8, 9, 10	D
Remorina albescens (Temminck and Schlegel, 1850)						10*	D
Family Carangidae							
Carangoides orthogrammus (Jordan and Gilbert, 1882)			+			4, 5, 9, 10	D
Caranx caballus Günther, 1868						4, 5, 9, 10	S
Caranx lugubris Poey, 1860	+	+	+		MNHN, LACM	3, 4, 5, 7, 8, 9, 10	D
Caranx melampygus Cuvier, 1833		+	+	+	SIO, MNHN, LACM	3, 4, 5, 7, 8, 9, 10	D

Table 2, cont'd

Caranx sexfasciatus Quoy and Gaimard, 1825	+	+	SIO, MNHN, LACM	4, 5, 7, 8, 9, 10	S
Decapterus macarellus (Cuvier, 1833)				4, 5, 9, 10	D
Elagatis bipinnulata (Quoy and Gaimard, 1825)		+	MNHN, LACM	3, 4, 5, 8, 9, 10	D
Naucrates ductor (Linnaeus, 1758)			LACM	4, 5, 9, 10	D
Selar crumenophthalmus (Bloch, 1793)			LACM	3, 4, 5, 9, 10	D
Seriola rivoliana Valenciennes, 1833			LACM	4, 5, 9, 10	D
Trachinotus stilbe (Jordan and McGregor, 1898)		+		4, 5, 9, 10	S
Family Bramidae					
Brama dussumieri Cuvier, 1831			SIO	9, 10, 11	D
Family Luvaridae					
Luvarus imperialis Rafinesque, 1810				10*	D
Family Sphyraenidae					
Sphyraena genie Klunzinger, 1870				9, 10	S
Family Gempylidae					
Gempylus serpens Cuvier, 1829				10*	D
Lepidocybium flavobrunneum (Smith, 1843)				10*	D
Ruvettus pretiosus Cocco, 1833				10*	D
Family Scombridae					
Acanthocybium solandri (Cuvier, 1832)		+		3, 4, 5, 9, 10	S
Euthynnus lineatus Kishinouye, 1920				4, 5, 9, 10	S
Katsuwonus pelamis (Linnaeus, 1758)				3, 9, 10	D
Thunnus albacares (Bonnaterre, 1788)		+		4, 5, 8, 9, 10	D
Thunnus obesus (Lowe, 1839)				10*	D
Family Xiphiidae					
Xiphias gladius Linnaeus, 1758				10*	D
Family Istiophoridae					
Istiompax indica (Cuvier, 1832)				10*	S

Table 2, cont'd

Istiophorus platypterus (Shaw, 1792)			9, 10	S
Tetrapturus angustirostris Tanaka, 1915			10*	D
Kajikia audax (Philippi, 1887)			10*	D
Family Nomeidae				
Cubiceps pauciradiatus Günther, 1872			9, 10*	D
Nomeus gronovii (Gmelin, 1789)			10*	S
Psenes arafurensis Günther, 1889			10*	D
Psenes cyanophrys Valenciennes, 1833			10*	D
Psenes sio Haedrich, 1970			10*, 12	D
Order TETRAODONTIFORMES				
Family Balistidae				
Canthidermis maculata (Bloch, 1786)	+	SIO, LACM	3, 4, 5, 8, 10	D
Family Tetraodontidae				
Lagocephalus lagocephalus (Linnaeus, 1758)			9, 10*	S
Family Molidae				
Ranzania laevis (Pennant, 1776)			10*	D

TABLE 3. Results of the statistical analyses to determine completeness of the inventory of reef fishes of Revillagigedo Archipelago (16 families selected if presenting 3 or more species at the site). In bold, tests depicting significant differences between expected and observed values**.**

Family	Observed richness	Expected richness (mean ± SD)	Student t	p	Bootstrap p
Muraenidae	15	15.4 ± 0.9	1.024	0.353	0.362
Acanthuridae	10	10.1 ± 0.6	0.370	0.727	0.579
Serranidae	8	8.7 ± 0.2	7.193	**0.001**	**0.045**
Labridae	8	8.1 ± 0.2	1.003	0.362	0.368
Holocentridae	6	6.1 ± 0.3	1.063	0.336	0.349
Balistidae	5	4.9 ± 0.4	0.402	0.705	0.569
Diodontidae	4	4.8 ± 0.7	2.463	0.057	0.110
Ophichthidae	4	4.7 ± 0.7	2.324	0.068	0.122
Tetraodontidae	4	3.8 ± 0.8	4.763	**0.005**	0.051
Scorpaenidae	3	3.6 ± 0.7	1.836	0.126	0.177
Antennariidae	3	3.2 ± 0.4	1.033	0.349	0.359
Pomacentridae	3	2.9 ± 0.4	--0.363	0.731	0.581
Blenniidae	3	3.1 ± 0.2	1.032	0.349	0.359
Kyphosidae	3	3.1 ± 0.1	1.001	0.363	0.369
Pomacanthidae	3	3.1 ± 0.2	1.146	0.304	0.327
Mullidae	3	3.7 + 0.2	6.884	**0.001**	**0.045**
TOTAL	106	110.0 ± 4.0	2.450	0.058	0.111

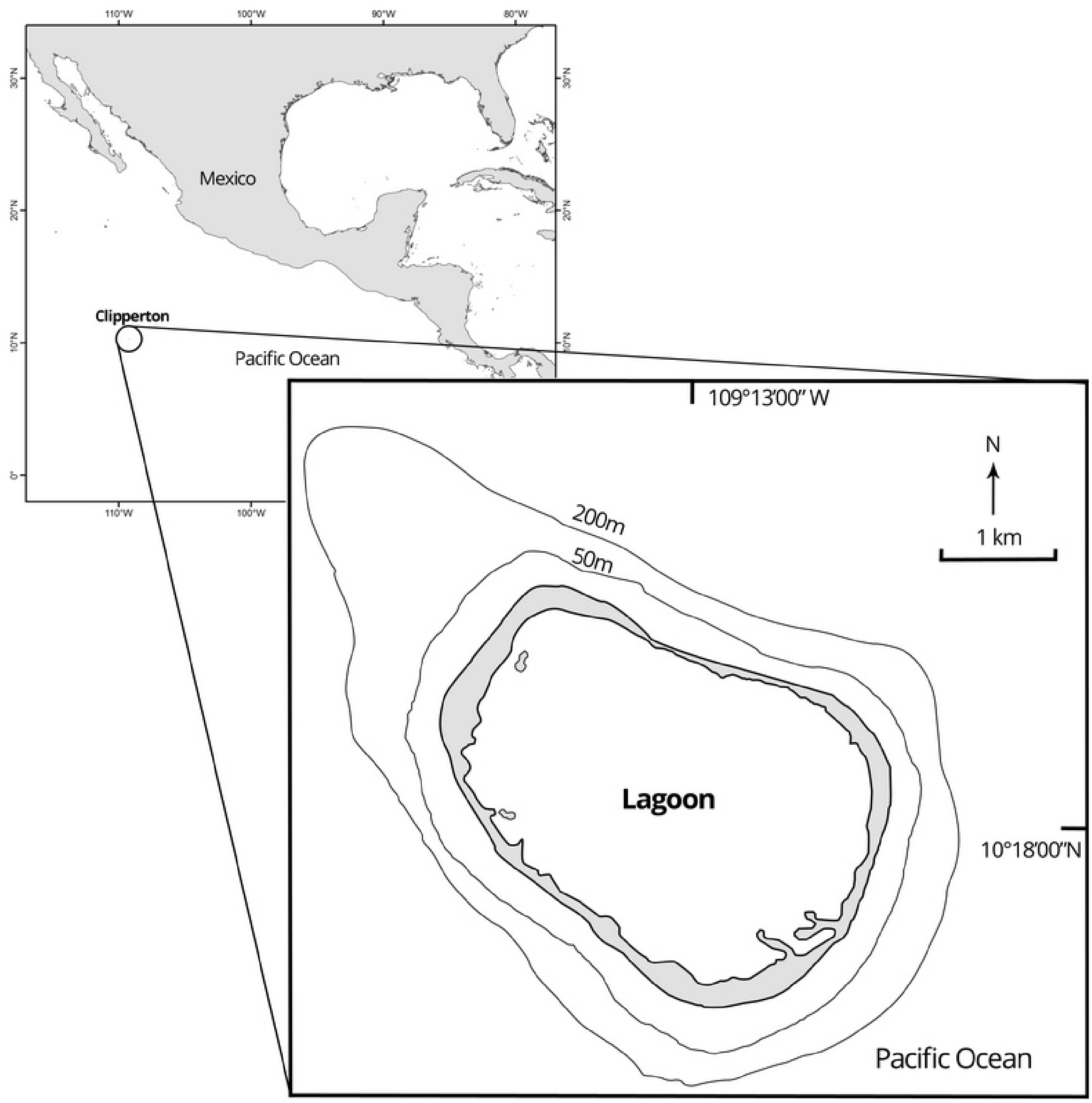

FIGURE 1. Location of Clipperton Atoll, in the tropical eastern Pacific.

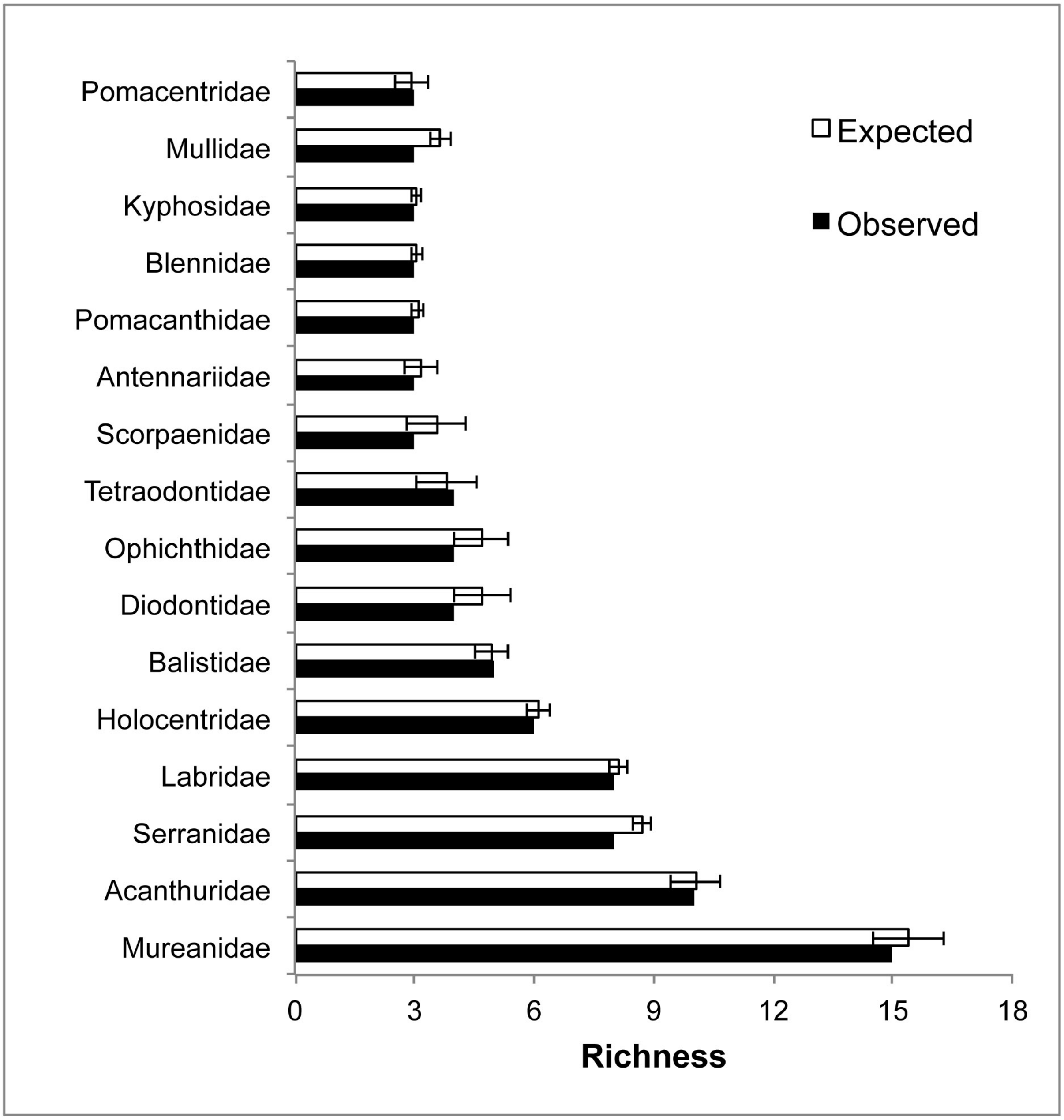

FIGURE 2. Observed species richness of 16 reef fish families at Clipperton Atoll, and expected value of richness (average and standard deviation), according to six non parametric methods applied on data from Table 1.

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