



An Indo-Pacific damselfish well established in the southern Gulf of Mexico: prospects for a wider, adverse invasion

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Abstract

The Indo-west Pacific damselfish *Neopomacentrus cyanomos* was first recorded in the West Atlantic in 2013, when it was found to be common on reefs near Coatzacoalcos, in the extreme southwest corner Gulf of Mexico. During 2014–2015, this species also was found on reefs farther afield in that area, but not in the northwest Gulf, nor the north-eastern tip of the Yucatan peninsula. These data, and information from public databases on invasive reef fishes, indicate that *N. cyanomos* currently is widely distributed in, but restricted to, the southwest Gulf of Mexico. Mitochondrial DNA barcodes of *N. cyanomos* from that area match to those for this species from its natural range, but do not indicate the ultimate origin of the Gulf of Mexico fish. Possible modes of introduction to the Gulf of Mexico and the potential for its further spread with negative effects on the native reef-fish fauna are discussed, and directions for future research suggested.

Key words: Regal Demoiselle, *Neopomacentrus cyanomos*, tropical West Atlantic, invasive species, ichthyology

Introduction

Until 2013, only one exotic species of tropical reef fish, the Indo-Pacific lionfish, *Pterois volitans* (Linnaeus, 1758), was known to have successfully invaded the tropical west Atlantic, establishing a breeding population that spread over a large part of that region. In 2013, however, that situation changed when *Neopomacentrus cyanomos* (Bleeker, 1856), a pomacentrid reef fish from Indo-Pacific reefs, was observed and collected for the first time in the tropical Atlantic by González-Gándara & de la Cruz-Francisco (2014). Those authors found small aggregations of *N. cyanomos* living on shallow, in-shore reefs near Coatzacoalcos, in the extreme southwest corner of the Gulf of Mexico (see Fig 1).

The present report shows that *N. cyanomos* occurs on additional reefs well to the northwest and northeast of the Coatzacoalcos sites, and that its current range spans a large proportion of the southwest Gulf of Mexico, but does not appear to extend beyond that area. The pros and cons are considered of several hypotheses about how *N. cyanomos* may have been introduced to that area: by shipping, relocation of an offshore oil-platform, or aquarium release. DNA barcodes (mtDNA sequences for the COI marker) are provided from fish collected in the Gulf of Mexico, which eventually may help identify the original source(s) of this invader and the mode of its introduction. The prognosis for the wider establishment of *N. cyanomos* in the tropical western Atlantic and the potential for adverse effects of this invasion are discussed. Finally, suggestions are made as to directions of future research on this species in both the Gulf of Mexico and the Indo-Pacific, particularly in relation to hypotheses about determinants of invasion success by exotic organisms.

Study Species and Methods

Biogeography and biology of *N. cyanomos*.

Neopomacentrus cyanomos, commonly known as the Regal Demoiselle, belongs to a tropical Indo-Pacific genus, the Lyretail Damselfishes, with 15 species. Two of those live exclusively in fresh and brackish water, while the remainder occur on inshore and offshore reefs. *N. cyanomos* has a native range that spans most of the Indo-west Pacific, from New Caledonia in the east to the Red Sea and east Africa in the west, between latitudes 25° N and 26° S (OBIS 2015). In its natural range, *N. cyanomos* reaches ~10 cm total length, is diurnally active and forms aggregations that typically include hundreds of fish (G.R. Allen, pers. comm. to DRR; Nov. 8, 2015) while feeding on zooplankton from near-bottom to mid-water, over coral heads at depths between 1–25 m. It occurs on both outer and inshore reefs, including those in protected bays and lagoons, while two congeners, *Neopomacentrus violascens* (Bleeker, 1848) and *Neopomacentrus filamentosus* (Macleay, 1882), are much more commonly seen than *N. cyanomos* in harbors around docks (Allen 1986, 1991, Randall 1995, Randall *et al.* 1997, Allen & Erdmann 2012, Australian Museum 2015). According to G.R. Allen (pers. comm. to DRR; Oct. 1, 2015), who described three members of the genus, including one of the freshwater species, and has extensive experience with the genus over a large part of its range, he has never seen *N. cyanomos* in fresh or low salinity water, and thinks reports of such could refer to the freshwater species *Neopomacentrus taeniurus* (Bleeker, 1856) instead. Among the members of the genus, *N. taeniurus* has the most similar color pattern to that of *N. cyanomos*, and, in some cases, the two can only reliably be distinguished by inspection of the suborbital bone, the edge of which is fused to the cheek and hidden by scales in *N. cyanomos*, but free and not covered by scales in *N. taeniurus*. *Neopomacentrus cyanomos* breeds in a manner typical of the great majority of damselfishes: eggs are spawned on the substrate and guarded by the male until they hatch, in this case four days after spawning (Setu *et al.* 2010). Duration of the pelagic larval stage is 17–19 days (Leis & Carson-Ewart 2003). This species can be spawned in and larvae reared in reduced-salinity conditions (26–28 ppt salinity) in the laboratory (Setu *et al.* 2010). Fish used in that study were collected from a high-salinity reef, and the reduced-salinity breeding experiment was aimed at testing the suitability of this species for aquaculture in brackish mangroves and lagoons (T.T. Ajith Kumar, pers. comm. to DRR; Nov. 20, 2015).

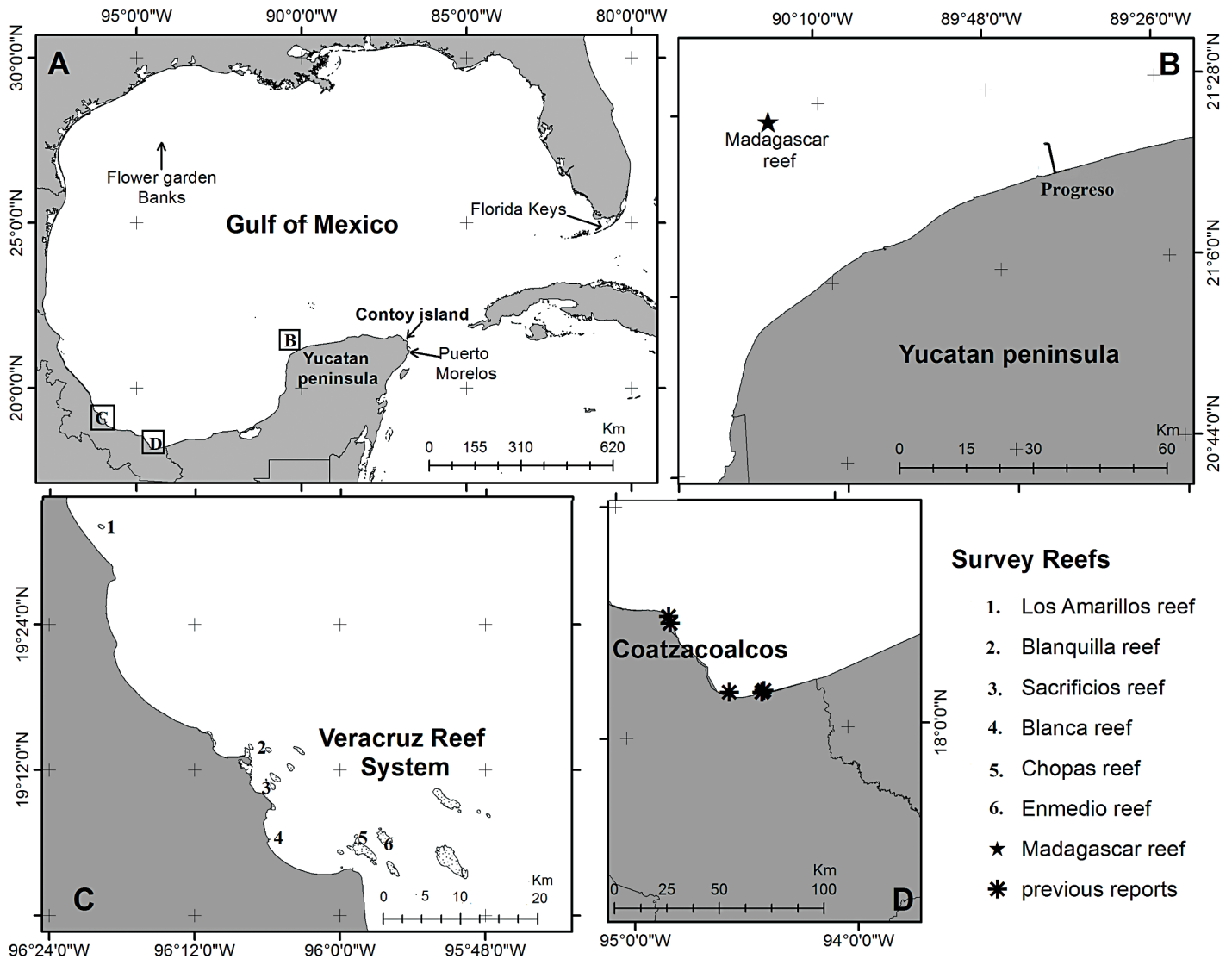


Figure 1. Maps of the Gulf of Mexico and adjacent areas indicating where surveys have been made for *Neopomacentrus cyanomos*. A. General region map; B. Detail of Yucatan Peninsula indicating location of Madagascar Reef; C. Veracruz City reefs; D. Coatzacoalcos reefs surveyed by González-Gándara & de la Cruz-Francisco (2014).

Determining the current range of *N. cyanomos* in and near the Gulf of Mexico.

González-Gándara & de la Cruz-Francisco (2014) censused this species in 143 21-m² transects on four reefs and provided quantitative information on the density of *N. cyanomos*. Our surveys on other reefs in the southwest Gulf of Mexico were more informal. Following the publication of the report by González-Gándara & de la Cruz-Francisco (2014), one of us (HP-E) assessed whether *N. cyanomos* is present on inshore reefs adjacent to Veracruz city, ~160 km northwest along the coast from the reefs surveyed by the former authors (Fig. 1). On April 26, 2015, two of us (DRR & NS) made a familiarization survey of reef fishes at Madagascar Reef, 40 km offshore from Sisal, on the northwest corner of the Yucatan peninsula. Madagascar Reef (Fig. 1), at 21.44° N, 90.28° W, is ~560 km northeast of the nearest reef (Tripie Reef at 18.17° N, 94.38° W) on which *N. cyanomos* was recorded by González-Gándara & de la Cruz-Francisco (2014). Madagascar Reef is a shallow (4–13 m deep), low-relief rock bank about 2.55 km long and less than 0.2 km wide, that resembles a half-buried French baguette. It is thickly covered with small, tree-like gorgonians and supports a few scattered, small colonies of hard corals (Zarco-Perelló *et al.* 2013). During that short survey (two hour-long dives), *N. cyanomos* was serendipitously discovered on that reef, and its relative abundance and habitat associations noted.

To assess the presence or absence of *N. cyanomos* on reefs farther afield in the Gulf of Mexico and in nearby areas, divers were requested (by DRR) to search for this species in three reef areas, one in the northwestern Gulf of Mexico (the Flower Garden Banks; see Fig. 1) and two at the northeastern tip of the Yucatan Peninsula (Isla Contoy

and Puerto Morelos; see Fig. 1). In August/September, 2015, two experienced SCUBA divers and underwater photographers (Carlos & Allison Estape: see Estape 2015) searched for *N. cyanomos* during a diving excursion to the coral reefs of the Flower Garden National Marine Sanctuary (Fig 1), which is located on the outer edge of the Texas continental shelf, 1000 km north from Veracruz. Subsequently one of us (HP-E) also dived and searched for *N. cyanomos* on the Flower Garden Banks in September 2015. In addition, a different diver searched for *N. cyanomos* at depths of 1–8 m on four reefs adjacent to Puerto Morelos, on the Caribbean side of the northeast tip of the Yucatan Peninsula (Fig. 1), during mid-September, 2015. Another diver searched for it at depths of 3–7 m on two shallow reefs at Isla Contoy at the northeast tip of the Yucatan peninsula during September, 2015 (Fig. 1). Prior to these surveys, all divers were provided with various photographs of *N. cyanomos* and information about its cryptic behavior and microhabitat usage in the southwest Gulf of Mexico by DRR. At Santa Marta, Colombia, ~1,700 km south from the tip of the Yucatan Peninsula, DRR surveyed two sites looking for *N. cyanomos* during December 2015.

Citizen science can be useful for determining the ranges of exotic species over large spatial scales (e.g. Delaney *et al.* 2008, Scyphers *et al.* 2014). The organization REEF (see REEF 2015) maintains a sighting-report database on marine-exotic species found on reefs of southeast Florida, deriving information from a large number of member divers who regularly dive in the Florida Keys. That database, which is currently up to date (L. Akins, pers. comm. to DRR; Sep. 23, 2015) was searched on Sep. 23, 2015. A search was also made on that date of the United States Geological Service's Nonindigenous Aquatic Species Database (see USGS 2015a, 2015b) for information relating to the occurrence of *N. cyanomos* in and near U.S. Atlantic waters.

DNA barcoding of *N. cyanomos* from Madagascar Reef.

Two *N. cyanomos* specimens were collected by a diver (NS) at Madagascar Reef in June 2015 (Fig. 2), using clove oil dissolved in ethanol (see Robertson & Smith-Vaniz 2010). These specimens are permanently stored in the Colección Ictiológica Regional de Referencia de la UMDI-Sisal YUC-PEC-239-01-11, with voucher codes CIRR-YUC-PEC-348-A (57 mm SL, 83 mm TL) and CIRR-YUC-PEC-348-B (45 mm SL, 61 mm TL). For genetic assessment, 0.25 cc of tissue was removed from the dorsal fin of each individual, preserved in 97% ethanol, and refrigerated until shipped to the laboratory at the Instituto de Ecología, A.C. Jalapa, Veracruz, México, where these samples were processed by CGR and VJP.

Total genomic DNA was extracted using a salt-extraction protocol (Aljanabi & Martínez 1997). Primers Fish-F1 and Fish-R1 (Ward *et al.* 2010, Vinoth *et al.* 2012) were used to amplify a fragment of the cytochrome oxidase-1 (COI) gene. PCR reactions were carried out in a C1000 Touch™ Thermal Cycler (Bio-Rad) and



Figure 2. *Neopomacentrus cyanomos*, fresh specimen immediately after being collected from Madagascar Reef, image reversed (R. Mendoza).



Figure 3. *Neopomacentrus cyanomos*, seven individuals and a *Chromis multilineata* (upper right) on a turbid reef adjacent to Veracruz City, July 2015 (H. Perez-España).

consisted of a total volume of 20 μL with 2 μL of 50–100 ng DNA template, 4 μL of 5X buffer, 0.4 μL of 5 U/ μL GoTaq® polymerase (Promega), 1 μL of 10 mM dNTPs, 2 μL of 25 mM MgCl_2 , and 0.6 μL of 10 μM of each oligonucleotide. The thermal cycler profile consisted of an initial denaturation step at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 54°C for 30 s and 72°C for 45 s with a final extension at 72°C for 5 min. The resulting amplicons were purified with the QIAquick PCR purification kit (Qiagen, Inc.), sequenced in both directions using the BigDye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems), and read in a 310 Genetic Analyzer (Applied Biosystems) at the Instituto de Ecología, A.C. sequencing facility. Forward and reverse sequences were assembled in Sequencher 5.3 (Gene Codes Corporation) and were manually aligned in Se-Al 2.0a11. Sequences have been deposited in GenBank (accession numbers: KU052527 and KU052528). The obtained sequences were compared to those available in the GenBank database using the program BLAST 2.2.32 (Zhang *et al.* 2000), which calculates the percent similarity and statistical significance of the match between a query sequence and existing sequences in GenBank.

Results

Occurrence of *N. cyanomos* at sites in the southwest Gulf of Mexico and nearby parts of the Greater Caribbean.

Reefs in the southwest Gulf of Mexico: In 2013, González-Gándara & de la Cruz-Francisco (2014) found *N. cyanomos* living in aggregations of 5–30 individuals at depths between 2–21 m on 43 of 134 censuses they made of fish in 2 m x 21 m strip transects on four near-shore reefs distributed along 55 km of the coast near Coatzacoalcos, on the southern coast of Veracruz state. In 2014 and 2015, one of us (HP-E) found smaller aggregations (<10 fish) of *N. cyanomos* on all six reefs near Veracruz City that he searched (Table 1, Figs. 1 & 3). At Madagascar Reef, two divers (DRR and NS) recorded 55 species of native Caribbean area reef fishes at the two sites they visited in

TABLE 1

Number of individuals of *Neopomacentrus cyanomos* observed on six nearshore reefs adjacent to Veracruz City, Veracruz, Mexico

(Note: higher counts in 2015 reflect greater sampling effort)

Reef	Location	Date	# observed
Arrecife Enmedio	19.10° N, 95.94° W	May 9, 2014	7
Arrecife Sacrificios	19.17° N, 96.10° W	May 13, 2014	5
Arrecife Blanquilla	19.22° N, 96.10° W	Dec. 4, 2014	4
Arrecife Blanca	19.09° N, 96.00° W	July 31, 2015	9
Arrecife Chopas	19.10° N, 95.96° W	July 31, 2015	8
Arrecife Los Amarillos	19.54° N, 96.33° W	July 10, 2015	15

April 2015, many of them new records for that reef, as well as *N. cyanomos* (Fig. 1, Table 2). At one site, single individuals of *N. cyanomos* were swimming about inverted, close to the substratum on the under-ceiling of large rock ledges. At the other site, as well as individual adults observed on the underside of rock ledges, a small aggregation of 2 adults and 3 juveniles was located within a ~35 cm wide crevice between two ~1 m diameter brain corals that opened into a small cave formed by heavy erosion of their undersides. Due to this cryptic behavior, these *N. cyanomos* were relatively inconspicuous. *N. cyanomos* on the reefs adjacent to Veracruz City were similarly cryptic in their behavior (HP-E, pers. obs.). When NS returned to Madagascar Reef in June, 2015 and collected two specimens of *N. cyanomos* for genetic analysis, he also encountered a small aggregation of six individuals at a third site on that reef: a vertical rock structure surrounded by sand at 12 m depth.

The largest individual among 15 specimens of *N. cyanomos* collected by González-Gándara & de la Cruz-Francisco (2014) and NS was 83 mm TL. These limited data indicate that *N. cyanomos* from the Gulf of Mexico reach a similar size to that of fish in their native range, while aggregations on those Gulf of Mexico reefs are much smaller than those typically encountered in its natural range.

Flower Garden Banks, Texas: No *N. cyanomos* were observed by two groups of divers on these banks during August and September 2015 (see Table 3).

Northeastern coast of the Yucatan Peninsula: No *N. cyanomos* were observed at either Puerto Morelos or Isla Contoy during mid-September, 2015.

Southeast Florida: In September, 2015, the REEF database contained no records of *N. cyanomos* from Southeast Florida. At that time, the USGS Nonindigenous Aquatic Species database (see USGS 2015b) contained no records of *N. cyanomos*, other than those of González-Gándara & de la Cruz-Francisco (2014). Carlos & Allison Estape (pers. comm. to DRR; Sep. 22, 2015), who are active members of REEF, made 280 dives at depths between 0–35 m at 89 sites covering the entire length of the Florida Keys during 2015, and another 395 similarly widely dispersed dives there in 2014. During those dives, they searched for unfamiliar species to photograph, but did not notice any unusual fish that might have been *N. cyanomos*.

Colombia: DRR surveyed two sites at Santa Marta, Colombia at depths of 1–10 m on Dec. 2 and 4, 2015. One site (at 11.242° N, 74.219° W) comprised the entire seaward side of a shallow, 300 m long rock breakwater that shelters a pleasureboat marina. This marina is <1 km from the docks of the Santa Marta harbor, which handles enough shipping to support 10 large harbor cranes. The Santa Marta port facilities are distinctly smaller than those at Coatzacoalcos, but, while the Santa Marta port is on the seashore, and fully marine, the Coatzacoalcos docks are in a flowing river, 3 km from the sea, and presumably very low salinity. The other site (at 11.33° N, 74.117° W) was a 350 m section of shoreline reef on the western side of the entrance to Gairaca Bay, in Tayrona National Park, 14 km east of the Santa Marta harbor. A variety of common native planktivorous fishes were observed at both sites, but no *N. cyanomos*.

TABLE 2

Reef fishes observed at two sites on Madagascar Reef (Yucatán) on April 26, 2015 that were not recorded there by Zarco-Perelló *et al.* (2014)

Family	Species	Abundance at two sites (see Notes)
Serranidae	<i>Diplectrum bivittatum</i>	common, not uncommon
	<i>Mycteroperca phenax</i>	rare (subadult), absent
	<i>Serranus baldwini</i>	rare, absent
Apogonidae	<i>Apogon pseudomaculatus</i>	rare, absent
Chaetodontidae	<i>Chaetodon capistratus</i>	not uncommon, not uncommon
Pomacanthidae	<i>Pomacanthus paru</i>	uncommon, uncommon
Pomacentridae	<i>Chromis enchrysurus</i>	absent, rare (juvenile only)
	<i>Chromis scotti</i>	absent, rare (juvenile only)
	<i>Neopomacentrus cyanomos</i>	uncommon, not uncommon (adults + juveniles)
	<i>Stegastes adustus</i>	common, common
	<i>Stegastes partitus</i>	not uncommon, not uncommon
	<i>Stegastes planifrons</i>	rare, absent
Labridae	<i>Halichoeres bivittatus</i>	abundant, abundant (see note 2)
	<i>Halichoeres radiatus</i>	absent, rare (juvenile only)
Scaridae	<i>Scarus iseri</i>	not uncommon, uncommon
	<i>Sparisoma radians</i>	common, not uncommon
Acanthuridae	<i>Acanthurus chirurgus</i>	common, common
	<i>Nicholsina usta</i>	not uncommon, rare
Monacanthidae	<i>Cantherhines macroceros</i>	uncommon, rare
Tetraodontidae	<i>Sphoeroides spengleri</i>	rare, absent
Diodontidae	<i>Diodon hystrix</i>	rare, absent

Notes:

1. Abundance level (site 1, site 2): abundant= >50 fish/hr; common= 10–50 fish/hr; not uncommon= 5–10 fish/hr; uncommon= 2–5 fish/hr; rare= <2 fish/hr.

2. Zarco-Perelló *et al.* (2014) recorded an unidentified *Halichoeres* species and the goby *Tigriobius macrodon*. The former is most likely *H. bivittatus*, which was abundant and the only member of the genus common on the reef in 2015. The latter is actually *T. redimiculus*, which is endemic to the southwest Gulf of Mexico (see Robertson & Van Tassell 2015), and occurs between the Veracruz reef system west of Madagascar Reef and at Alacranes Reef, northeast of Madagascar Reef.

TABLE 3

Dive activity during surveys of fishes in the Flower Garden Banks National Marine Sanctuary by Carlos and Allison Estape (Aug. 31–Sep. 2, 2015) and by Horacio Pérez-España (Sep. 12–13, 2015) during which unsuccessful searches were made for *Neopomacentrus cyanomos* in microhabitat similar to that in which this species is encountered in the southwest Gulf of Mexico

Location	Coordinates	Depth	No. Sites	Dive Time
Stetson Bank	28.17° N, 94.29° W	18–24 m	2	3 hrs
West Flower Garden Bank	27.88° N, 93.82° W	21–29 m	6	8 hrs
East Flower Garden Bank	27.91° N, 93.60° W	21–29 m	6	7 hrs

DNA barcoding of *N. cyanomos* from Madagascar Reef.

The two 545-bp COI sequences from the Madagascar Reef specimens are identical, and BLAST analyses show that the average pairwise genetic distance between them and sequences of fish collected by ichthyologists in the field at Madagascar Island (southwest Indian Ocean), the Seychelles Islands (central western Indian Ocean), and the Great Barrier Reef (north-eastern Australia) were 0.013, 0.032, and 0.017, respectively. Other GenBank sequences of this species, listed as from India, apparently came from the aquarium trade and thus their provenance cannot be guaranteed and they were not included in our analysis. These DNA-barcode data confirm González-Gándara & de la Cruz-Francisco's (2014) identification of the Gulf of Mexico fish as *N. cyanomos*, based on the meristics and morphology of specimens they collected. However, because the genetic distance between two populations in the same ocean (genetic distance = 0.026 between Madagascar and the Seychelles islands, both in the Indian Ocean) is greater than that between populations in different oceans (genetic distance between Madagascar Island and the Great Barrier Reef = 0.004), the available data cannot indicate which ocean(s) was the ultimate source of the Gulf of Mexico population, let alone which part(s) of which ocean.

Discussion

The current range of *N. cyanomos* in the tropical northwest Atlantic.

Recent searches showed that *N. cyanomos* is widely distributed and not uncommon on reefs in the southwest Gulf of Mexico, but failed to find this species on reefs in the northwest Gulf of Mexico, southeast Florida, the eastern tip of the Yucatan peninsula, or eastern Colombia. In addition, there are no reports of this species in other nearby areas where there are large numbers of recreational divers attuned to the presence of alien reef fishes (the eastern Gulf of Mexico, SE Florida, and the Mexican Caribbean), or anywhere else in the tropical Atlantic. Hence it appears most likely that *N. cyanomos* was introduced into the southwestern Gulf of Mexico, and currently is restricted to that area. Its abundance on reefs over a wide section of that part of the Gulf (see Fig. 1) indicates that it was introduced well before 2013. The lack of observations of *N. cyanomos* on Madagascar Reef in 2007 (when most observations were done by Zarco-Perelló *et al.* [2014]) does not demonstrate that it arrived there between 2007 and 2015. In 2015, many native Greater Caribbean species were observed on that reef that were not recorded by Zarco-Perelló *et al.* (2014), which indicates that the latter authors either missed some species or that there may be considerable natural turnover in the membership of the native fish assemblage there. In addition the cryptic behavior of *N. cyanomos* would have reduced the chance of it being recorded in 2007, if it were present then.

How was *N. cyanomos* introduced to the Gulf of Mexico?

González-Gándara & de la Cruz-Francisco (2014) proposed that *N. cyanomos* was carried to the reefs of the southwest Gulf of Mexico by ships travelling from its natural range to the port of Coatzacoalcos, near the reefs on which they recorded this species. In support of this “hitch-hiker hypothesis”, those authors noted that at least one species of damselfish (in the genus *Abudefduf*) is known to associate with the hulls of ships. There are several

weaknesses to this hypothesis: first, species of the damselfish genus *Abudefduf* commonly associate with both artificial and natural flotsam (e.g. Luiz *et al.* 2012) and flotsam-dispersal is thought to be the mode of long-distance invasion of the Hawaiian Islands by one such species (Coleman *et al.* 2012). All of the few long distance invasions known for damselfishes involve *Abudefduf* species and are explainable by flotsam-dispersal (Coleman *et al.* 2012, Luiz *et al.* 2012, Azzurro *et al.* 2013, Tsadock *et al.* 2015). While schooling, midwater feeding planktivorous species of the damselfish genera *Abudefduf* and *Chromis* are known to associate with floating objects (Dempster *et al.* 2002, Luiz *et al.* 2012; DRR pers. obs. on *Chromis atrilobata* in Pacific Panama), there are no literature records of species of *Neopomacentrus* doing so. Second, none of the ports in Veracruz state are major endpoints for the global shipping trade (see NCEAS 201, Yoskowitz *et al.* 2013), which has much greater potential to carry organisms to major ports at New Orleans and Miami than to smaller ports in the southwest Gulf of Mexico. Third, any shipping reaching the Gulf of Mexico from the west Pacific would have passed through the Panama Canal, in which a large body of freshwater (Gatun Lake) acts as a barrier to trans-isthmian movements of most marine organisms (McCosker & Dawson 1975). Additionally, there is little direct movements of ships between the west Pacific and the Panama Canal, with most boats moving via west coast U.S. ports, or Hawaii (see NCEAS 2016). Fourth, the distances that would have to be travelled by fish hitchhiking on a ship to the Gulf of Mexico are extremely large: ~20,000 km from the west Pacific, and ~12,000 km from the Red Sea (*Neopomacentrus* are not among the Lessepsian migrants found in the Mediterranean; see Arndt & Schembri 2015). Finally, damselfishes are not among the suite of marine fishes thought to have been transported long distances in ship ballast water (Wonham *et al.* 2000). In sum, long-distance, interoceanic ship-borne dispersal seems unlikely for tropical damselfishes in general, and for the *N. cyanomos* introduction to the Gulf of Mexico in particular.

Another version of the hitch-hiker hypothesis also needs consideration: that *N. cyanomos* was carried to the southwest Gulf of Mexico by an offshore oil-platform, either from the southeast Indian Ocean (via West Africa?) or through the Suez Canal. Oil and gas platforms essentially are large, reef-like structures that can support rich assemblages of tropical and subtropical reef fishes, damselfishes among them (e.g. Hastings *et al.* 1976, Consoli *et al.* 2013, Pradella *et al.* 2013, Friedlander *et al.* 2014). Such platforms are capable of moving substantial numbers of individuals of a variety of species of reef fishes, probably sufficient numbers in some cases to facilitate the rapid establishment of a population of an exotic species in a new area. Translocation of platforms has been implicated in the transport of tropical reef fishes from the West Atlantic to the Adriatic Sea in the central Mediterranean (Dulčić & Dragičević 2013) and to the Canary Islands in the East Atlantic, where there is a major service site for such structures (Falcon *et al.*, in press). Exotic fishes now found at the Canary Islands also include an Indo-Pacific damselfish, *Abudefduf septemfasciatus*, which was misidentified by those authors as the trans-Atlantic species *A. taurus*. As *A. septemfasciatus* is a nondescript species that does not figure in the aquarium trade (see Rhyne *et al.* 2015), its introduction to the Atlantic via a relocated oil platform seems a distinct possibility. In Mexico, offshore oil production occurs in the Bay of Campeche and adjacent to emergent coastal reefs around Tuxpan, ~235 km north of Veracruz (USGS 1997). A search of Google Earth (accessed October 12, 2015) showed two oil platforms 4–20 km from Arcas Reef, an emergent reef on the western edge of the Campeche Bank. The possibility that *N. cyanomos* was introduced to the Gulf of Mexico by this mechanism needs further exploration.

An alternative to the hitch-hiker hypothesis is that *N. cyanomos* was introduced to the Gulf of Mexico through releases from aquaria. Aquarium releases account for the appearance of a range of taxa of Indo-Pacific reef fishes, including lionfish, in southeast Florida (Semmens *et al.* 2004; and see USGS 2015b). *Neopomacentrus cyanomos* has featured in the international aquarium trade that brings Indo-Pacific fishes to the Americas for at least the last eight years (O’Sullivan *et al.* 2008, CORAL Magazine 2015), and is relatively cheaply available in the USA (US\$6–16/fish as of June, 2015; see Aquarium Suppliers [2015]). India and Sri Lanka are major exporters in the aquarium-fish trade (Bruckner 2005), with *N. cyanomos* involved in that trade (see NARA 2009), and apparently aquacultured for that purpose in India (Ajith Kumar *et al.* 2015, ICAR 2003). The Philippines has a huge aquarium-fish industry exporting large numbers of individuals of many species of reef fishes (Bruckner 2005, Rhyne *et al.* 2012), including *N. cyanomos*, which has been captive-bred there (Setu *et al.* 2010). According to Rhyne *et al.* (2015), virtually all *N. cyanomos* entering the U.S. originate in the Philippines.

A release of aquarium-sourced *N. cyanomos* could have been done from any number of population centers along the shore of its present distributional range. Veracruz State has small shoreline and nearshore reef areas

scattered along almost 500 km of coastline. Some of those reefs are very close to large population centers, including Tuxpan, Veracruz City, and Coatzacoalcos. Because *N. cyanomos* in its native range lives on inshore turbid reefs, among other habitats, rock-fill piers that extend up to a kilometer or more (6.75 km in the case of the pier at Progreso, near Madagascar Reef) out from the shore into the shallow waters of the continental shelf of the southwest Gulf of Mexico also may provide suitable habitat for newly released *N. cyanomos*. The aquarium-release hypothesis does, however, have weaknesses. First, *N. cyanomos* is a minor component of the aquarium fish trade (Rhyne *et al.* 2015). Additionally, the aquarium-fish trade, particularly that part involving imports of Indo-Pacific species, is not well developed in Mexico, and few people maintain marine aquaria with non-native species (NS, pers. obs.). Despite these weaknesses the aquarium-release hypothesis seems sufficiently viable to need further investigation.

Prospects for a wider, adverse invasion of the tropical West Atlantic.

The lionfish has been extraordinarily successful in its invasion of the Greater Caribbean, and is now a common demersal fish on reefs across a broad depth range (1–305 m) throughout that area. It occurs on reefs and in adjacent seagrass beds, and in both estuarine and marine conditions (Schofield *et al.* 2015), and has been trawled on soft bottoms at 185 m depth (DRR, pers. obs., off Honduras). This species also reaches a greater body size and population density in the Greater Caribbean than it does in its native range (Darling *et al.* 2011). Habitat plasticity likely has been a significant facilitator of the lionfish invasion (Cure *et al.* 2014). Its success likely is enhanced by its being morphologically and behaviorally an unusual type of predator that native West Atlantic prey fishes have never experienced and against which they have reduced defensive capabilities (Lonnestad & McCormick 2013, Gamazo 2013). Similar naïveté of native predatory fishes may have reduced the impact of predation on lionfish populations in that area (Diller *et al.* 2014), and the abundance of lionfish apparently is unaffected by the abundance of native predators (Hackerott *et al.* 2012). What can the lionfish invasion of the Greater Caribbean tell us about the prospects for the invasion of the same area by *N. cyanomos*?

As González-Gándara & de la Cruz-Francisco (2014) pointed out, a capacity to live in turbid, nearshore conditions may have helped *N. cyanomos* to establish on reefs along the sandy shoreline of the state of Veracruz, which is studded with numerous estuaries and brackish lagoons. However, Madagascar Reef is 40 km offshore, in full-salinity seawater that is particularly clear during summer months. Although the density and group sizes of *N. cyanomos* are low at Madagascar Reef, this may be due to lack of suitable microhabitat on this very low-relief rock bank, which has few large rock shelves and poorly developed coral growth. An ability to live in a range of turbidity conditions, on both inshore and offshore reefs, in both equatorial to subtropical environments, could well allow *N. cyanomos* to colonize shallow waters of reefs throughout much or all of the Caribbean and adjacent tropical and subtropical areas (the Greater Caribbean, see Robertson & Cramer 2014). An extension of its current range by *N. cyanomos* to the eastern tip of the Yucatan would set the stage for its larvae to be dispersed towards southeast Florida and northern Cuba, and to the northern Gulf of Mexico. As well, surface currents in the western Gulf of Mexico could disperse larvae from the southwest corner northwards to the Texas shelf (see RSMAS 2015).

None of the ecological or reproductive characteristics of *N. cyanomos*, except possibly a degree of tolerance for reduced-salinity conditions, demonstrated by the brackish-water breeding experiments of Setu *et al.* (2010), are unusual for tropical reef-dwelling damselfishes. Based on the existing knowledge of its biology and ecology, *N. cyanomos* seems unlikely to have any unusual ecological advantages over native species in the Greater Caribbean analogous to those enjoyed by lionfish. This species is a small planktivorous fish, restricted to shallow water, with a shape, color and behavior similar to that of a common and widespread native West Atlantic planktivorous damselfish, *Chromis multilineata*. *Neopomacentrus cyanomos* will have to compete with numerous native planktivores and likely will represent suitable prey to a broad range of predatory fishes that eat *C. multilineata* and other small planktivorous fishes. Native predatory fishes likely to prey on *N. cyanomos* in the Greater Caribbean belong to the same genera that prey on small damselfishes on Indo-Pacific reefs (e.g. see Rosenblatt 1967, Allen & Erdmann 2012, Robertson & Van Tassell 2015). Hence, unless the native predators have unusual predatory behaviors, *N. cyanomos* seems likely to be subject to levels of predation by native Caribbean predators that are similar to those experienced by similar native prey species.

While invasive exotic species often perform better in their new environment than in their native environment in terms of body size, fecundity, and abundance (cf. lionfish), such high success occurs in only about half the cases (Parker *et al.* 2013). Even though it is distributed over a large area of the southwest Gulf of Mexico, the few data currently available indicate that *N. cyanomos* occurs in smaller aggregations than it does in its natural range, and does not reach a larger body size. This information indicates that *N. cyanomos* may not become unduly successful to the point at which it represents a major competitor of native reef fishes. Invasions by exotic species occur in several stages: establishment, spread, and impact (Vermeij 1996, Carlton 1996, Kolar & Lodge 2002). *Neopomacentrus cyanomos* may still be at the establishment phase of its invasion, and, since there are no obvious reasons why it should not spread much more widely in the tropical western Atlantic, the impact phase of its invasion may only become evident when it spreads more widely and reaches its maximum potential density across a range of reef types and environmental conditions. The highly successful invasion of the tropical west Atlantic by lionfish took 2–3 decades for its full geographic coverage and impact to become evident (Schofield 2010, Scyphers *et al.* 2015, Ferreira *et al.* 2015), and a similar time frame may well apply to the *N. cyanomos* invasion.

Might lionfish facilitate an invasion by *N. cyanomos*?

Neopomacentrus cyanomos shares its entire natural range with, and evolved together with, a variety of species of lionfishes and other morphologically similar Indo-Pacific scorpionfishes in the subfamily Pteroinae, which contains ~20 species in five genera. Hence *N. cyanomos* should be more resistant to lionfish predation than are native West Atlantic prey fishes. Any resultant differential predation rates could reduce competitive pressures on *N. cyanomos* populations from ecologically similar native fishes, and facilitate its invasion (cf. Simberloff & Von Holle 1999). However, lionfish typically hunt in the types of microhabitats (around ledges and caves) used by cryptically behaving *N. cyanomos* in the Gulf of Mexico. Such cryptic behavior could hinder population expansion due to the abnormal abundance of lionfish in the Greater Caribbean.

Some directions for future research on *N. cyanomos* in the Greater Caribbean.

We suggest that future research on this well-established exotic species should include the following aspects of its biology:

Assessing the mode of introduction of *N. cyanomos* to the southwest Gulf of Mexico:

Fish assemblages associated with offshore oil platforms in the southwest Gulf of Mexico should be assessed to determine if they include *N. cyanomos*. Determining patterns of long distance relocation of offshore oil platforms that have been working in the southwest Gulf of Mexico would be useful for testing the hypothesis that such platforms carried *N. cyanomos* there. Given the potential of offshore platforms to enhance the establishment of exotic invasive species by transporting multi-species assemblages of reef fishes that include large numbers of individuals, such a study should be expanded to a global assessment of oil-platform relocations.

Identifying the source population of the invasion:

Currently, DNA barcodes of *N. cyanomos* are available for very few sites within its natural range, and do not resolve the issue of the Indo-Pacific origin of the Gulf of Mexico population. To establish the ultimate source of the Gulf of Mexico population, further sampling of fish should be done at strategically chosen locations scattered across its entire natural range, particularly those that export *N. cyanomos* for the aquarium trade (the Philippines, Indonesia, Taiwan, Malaysia, Sri Lanka, and India). Genetic analyses suggested that lionfish invading the Caribbean comprised a pair of allopatric sibling species (Hamner *et al.* 2007). Hence the possibility of introductions of *N. cyanomos* from multiple sources needs to be evaluated. DNA barcoding of this species from various sites in the southwest Gulf of Mexico would determine how much variability there is within this population, and help clarify whether there was one or more introductions. Finally, fish obtained from U.S. suppliers to that country's aquarium

trade should be DNA sequenced. A finding that the Gulf of Mexico population is most closely related to such aquarium fish would support the notion of an aquarium release. Alternatively, the hitch-hiker hypothesis would be supported if the Gulf of Mexico fish are most closely related to fish from an area of oil-platform activity within its natural range, or from a site within that range that lacks a significant aquarium-fish trade.

Determining and monitoring the extent of the invasion throughout the Greater Caribbean:

Neopomacentrus cyanomos currently appears to be restricted to the southwest Gulf of Mexico. Further surveys should be made of inshore and offshore reefs, both natural and artificial, on the broad Campeche Bank, to establish the limits of its distribution there. To date, *N. cyanomos* is only known from turbid inshore reefs and a mid-shelf reef with clearer water conditions. If it is found in significant numbers on the arc of five emergent reefs scattered along 400 km of the western and northern outer edges of Campeche Bank this would indicate that it can exploit clear-water, offshore reefs, and, hence, potentially could spread throughout most reef areas in the Greater Caribbean. In addition, reefs in areas that could be supplied with fish larvae from the southwest Gulf of Mexico should be monitored for the presence of this species: the northern Gulf of Mexico, east and west Florida, northern Cuba, the Bahamas, and the northwest Caribbean. The similarity of *N. cyanomos* to the common, native planktivorous damselfish *Chromis multilineata* in shape, size, and coloration may let the former pass unnoticed in superficial surveys, particularly when it is behaving cryptically, which needs to be taken into account when assessing its presence or absence.

Neopomacentrus cyanomos was not recorded in the Gulf of Mexico until it had become quite common in an area with reefs that offer sub-optimal diving conditions, and was first noticed as something unusual by reef-fish biologists during diving surveys. This leads us to wonder if this species is not “hiding in plain sight” in similar habitat situations seldom visited by knowledgeable divers elsewhere in the Greater Caribbean, or in other parts of the Atlantic (e.g. offshore oil installations or nearby reefs along the shelf of west Africa?). Its occurrence at ports or near offshore oil installations elsewhere in the Atlantic would support the hitch-hiker hypothesis.

Population monitoring:

At present, *N. cyanomos* in the southwest Gulf of Mexico do not appear to have reached body sizes or densities as high as those that can occur in its natural range. Those populations in the southwest Gulf of Mexico should be monitored to assess whether they are stable, fluctuating, or increasing, and whether maximum body size and group sizes change.

Assessing ecological interactions with the native fish fauna:

González-Gándara & de la Cruz-Francisco (2014) suggested that *N. cyanomos* may compete with and have adverse effects on populations of native planktivorous damselfishes, such as *Chromis multilineata*. Possibilities such as this need to be explored, as not all invasions by exotic fishes lead to strong negative impacts on invaded ecosystems (Kolar & Lodge 2002) and many invasive species are not unduly successful (Parker *et al.* 2013).

The invasive lionfish has the potential to affect populations of most Caribbean reef fishes, both shallow-water species and mesophotic reef species, due to its broad depth range in that area (1–305 m; Nuttall *et al.* 2014, Whitfield *et al.* 2014). In contrast, in its natural range, *N. cyanomos* is limited to water shallower than ~25m (see above). If the depth range of *N. cyanomos* in the Greater Caribbean remains much the same as in the Indo-Pacific, the potential for adverse effects on diurnal planktivorous native fishes would be limited. Most such species (in the genera *Abudefduf*, *Chromis*, *Clepticus*, *Schultzea*, and *Coryphopterus*; see Robertson & Van Tassell [2015]) have much broader depth ranges than *N. cyanomos*, and adults of some (e.g. *Abudefduf saxatilis* and *Chromis multilineata*), range farther above the substrate in relatively deep water when feeding than does *N. cyanomos*. Other diurnal planktivores are restricted entirely to much deeper water than the native depth range of *N. cyanomos* (e.g. species of *Anthias*, *Choranthias*, *Baldwinella*, *Odontanthias*, and *Parasphyraenops*; see Robertson & Van Tassell [2015]). However, juveniles of *Clepticus*, *Chromis*, and *Abudefduf* remain near the bottom in shallow

water, as do adults of some species of native, day-active, reef planktivores that are limited to or concentrated in shallow water and likely occupy similar feeding microhabitats to *N. cyanomos*. These include *Elacatinus jarocho*, which is endemic to the southwest Gulf of Mexico, and *E. atronasmus*, endemic to the Bahamas, juvenile haemulids of multiple species, and various small wrasses (*Halichoeres burekai*, *H. pictus*, *H. socialis*, and *Thalassoma bifasciatum*; see Robertson & Van Tassell [2015]). Other planktivores are more cryptic (e.g. *Gramma* spp.), or feed at night but are found in microhabitats used by *N. cyanomos* during the day (e.g. *Pempheris* spp. and apogonids of various species). A comprehensive evaluation of the ecology of *N. cyanomos* on reefs in the southwest Gulf of Mexico should include assessment of its depth distribution, density, habitat, feeding microhabitat usage, diet, and use of different substrata for breeding. While observing *N. cyanomos* at Madagascar Reef, DRR noticed one individual on the ceiling of a ledge repeatedly attacking cleaner gobies (*Elacatinus oceanops*) moving around on the same ceiling. Close attention should be given to behavioral interactions between *N. cyanomos* and native species in its new range. Those evaluations should involve both adults and juveniles of *N. cyanomos* and of species with which it potentially could interact.

Testing hypotheses about determinants of invasion success— biotic resistance and facilitation in relation to diversity:

The introduction of *N. cyanomos* to the Gulf of Mexico offers opportunities to assess ideas about determinants of invasion success that developed from the seminal work of Elton (1958). These include testing: (i) whether an invasion by *N. cyanomos* will be facilitated by positive interactions with another invasive species (cf. Simberloff & Von Holle 1999), in this case by lower rates of predation by lionfish on *N. cyanomos* than on native planktivorous Greater Caribbean fishes; and (ii) that lower-diversity biotas (here the Greater Caribbean) have low biotic resistance to invasion by competitively superior species from high-diversity biotas (in this case the Indo-Pacific)(cf. Elton 1958). In addition the establishment of *N. cyanomos* in the Greater Caribbean will allow field testing of the idea that naïveté of native prey fishes has contributed to the success of the lionfish invasion of that area. Finally, the invasion of the Greater Caribbean by *N. cyanomos* provides an opportunity to assess whether the rapid and highly successful invasion of that area by lionfish was a unique event related to its unusual biology, or whether similar invasion patterns can be expected when exotic species are ecologically much more similar to native species in that area.

Observations on *N. cyanomos* in its natural range:

To understand what factors affect the abundance, distribution and degree of success of this damselfish in the Greater Caribbean, a comprehensive assessment of its biology, ecology and demography needs to be made on Indo-Pacific reefs, especially at the source(s) from which the Gulf of Mexico fish are derived, with particular attention to similarities and differences in its behavior, habitat usage, age and growth, and competitive interactions with other reef fishes, as well as its relations with lionfish and other predatory reef fishes. Such observations could provide useful insights into the potential for invasion of Greater Caribbean reefs by Indo-Pacific reef fishes belonging to other genera and families that occur in both areas, and for the potential for such invasions to have adverse effects on the native fish fauna.

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