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Research Article

The Indo-Pacific damselfish *Neopomacentrus cyanomos* at Trinidad, southeast Caribbean

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Abstract

The Indo-West Pacific (IWP) damselfish *Neopomacentrus cyanomos* was first found in the Atlantic Ocean in 2013, on reefs in Mexico in the southwest Gulf of Mexico (GoMx). By 2018 it was known throughout most of the GoMx, but nowhere else in the Atlantic. Evidence indicates it was introduced to the GoMx by offshore petroleum infrastructure moved in water from its native range, rather than by aquarium-release or commercial shipping. There are three tropical Atlantic areas with offshore petroleum fields in addition to the GoMx: (i) at Trinidad (southeast Caribbean), (ii) at central Brazil, and (iii) at west Africa. Offshore infrastructure moves between those oilfields, and between them and support facilities in the IWP. If *N. cyanomos* was brought to the Atlantic by such infrastructure relocation, then it could also be at other Atlantic oilfields. To assess that possibility, we surveyed suitable habitat at Trinidad (mid 2019), and nearby Tobago (early 2020). We found *N. cyanomos* at all sites surveyed at Trinidad, but none at Tobago. At Trinidad this species was common on shallow reefs fringing an aquatic "parking lot" for mobile petroleum infrastructure in the estuarine Gulf of Paria. These observations show that this species has well established, isolated populations at offshore oilfields with very different environments at both ends of the Greater Caribbean and provide strong support for the petro-platform relocation hypothesis relating to its introduction. They also show that *N. cyanomos* has considerable ecological plasticity, which may be important for its success. The location of the Trinidad population at the head of the Caribbean Current should aid its spread via larval dispersal throughout the region.

Key words: non-native reef-fish, offshore oil-rig, interocean transport, estuary, coral reef, planktivore, ecological plasticity

Introduction

The study of non-native species (NNS), a research field established by Elton (1958), deals with various major questions relating to such species in their introduced ranges. Those include "where do NNS come from and how do they get to there, what factors determine their success there and what effects do they have on native ecosystems". The global expansion of the offshore petroleum industry in recent decades has led to the realization that oil and gas platforms, which support diverse communities of reef-fishes (Martin and Lowe 2010; Consoli et al. 2013; Friedlander et al. 2014), when relocated between distant regions while floating in the water, can act as vectors for transferring a range of taxa of NNS. While it has long been known that such relocation led to the introduction of benthic NNS attached to platforms (e.g., Foster and Willan 1979), more recently it has been found that it also is involved in transferring associated reef fishes (Ferreira et al. 2006; Falcon et al. 2015; Pajuelo et al. 2016).

The regal demoiselle, *Neopomacentrus cyanomos* (Bleeker, 1856), a planktivorous damselfish (Pomacentridae) native to the Indo-West Pacific (Allen 1991), was first discovered in the western Atlantic in mid-2013, on inshore coral reefs of the southwest corner of the Gulf of Mexico (GoMx) (González-Gándara and de la Cruz-Francisco 2014). During the following two years, it was found on inshore and offshore reefs over most of the southwestern GoMx and on offshore oil platforms there (e.g., see Simoes and Robertson 2016) equivalent to those it has been observed to inhabit off Saba, in its native range (observations by G Bernardi, *pers. comm.* to DRR, October 2018). By 2018 this species was known throughout the western three-quarters of the northern GoMx (Schofield and Neilson 2020). Prior to the present study, there were no indications *N. cyanomos* was anywhere else in the Atlantic other than the GoMx (Robertson et al. 2016, 2018). Various lines of evidence (see review by Robertson et al. 2018) indicate that the most likely mode of introduction of this species to the GoMx was by being carried on the exterior of oilfield infrastructure relocated in-water from the Indo-West Pacific (IWP), rather than by commercial cargo shipping or a release by aquarists. This we refer to as the Petro-platform Relocation Hypothesis (PRH).

There are three other areas of the tropical Atlantic with large offshore oilfields that have connections with the IWP, with the GoMx fields and with each other via in-water movements of oilfield infrastructure that have been implicated in the trans-Atlantic transport of fishes (Pajuelo et al. 2016): (1) Trinidad, in the southeast Caribbean, 3,000 km from the GoMx, (2) off Central Brazil and (3) the West African shelf between Angola and Sierra Leone. Infrastructure movements between the IWP and the tropical Atlantic and between those Atlantic oilfields could carry *N. cyanomos*, leading to the establishment of populations at all those offshore fields.

The offshore oil and gas industry at Trinidad began in the 1950s (Ministry of Energy and Energy Industries 2019). There are three main offshore fields: a large cluster ~ 20–100 km east of southern Trinidad, a small set of Caribbean fields ~ 40 km north of the western islands of Trinidad and a group of fields inside the Gulf of Paria off the southwestern tip of Trinidad (Bush and Fuller 2016; Figures 1, 2 here). Trinidadian waters in the northeast corner of the Gulf also are used as an aquatic "parking lot" for mobile oilfield infrastructure when they are not in use for

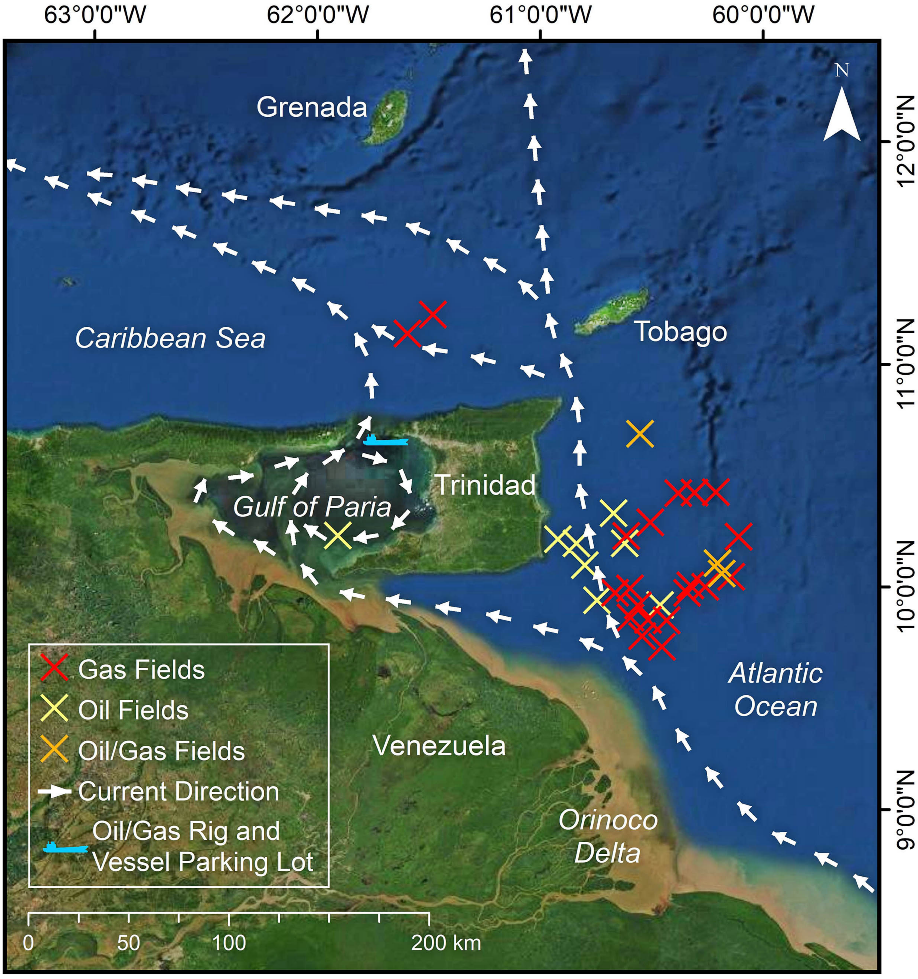

Figure 1. Trinidad and Tobago. The map shows the Gulf of Paria between Trinidad and Venezuela, and the location of the "aquatic parking lot" used by floating offshore infrastructure on the south side of the Chaguaramas Peninsula of northwestern Trinidad. Locations of oil and gas fields are as indicated in Bush and Fuller (2016), with each X representing a separate field. White arrows indicate general current flows inside the Gulf of Paria, the north flowing Guyana current (east side of Trinidad) and the west flowing Caribbean Current (north side of Trinidad) (after Singh et al. 2006, RSMAS 2020, and https://earth.nullschool.net/#current/ocean/surface/currents/overlay=currents/ accessed 9 May 2020). Background imagery/basemap: Esri, DigitalGlobe, GeoEye and Earthstar.

extended periods ("cold stacking"; see Bloomberg 2016) or are awaiting service (Supplementary materials Figure S1). Further, during in-water transits between the IWP and other Atlantic oilfields floating mobile infrastructure sometimes stops at Trinidad for resupply and inspections (e.g., see BPCLC 2011). Finally, there are shoreline facilities and a dry dock in the Gulf adjacent to the "parking lot" that service oil-industry infrastructure and commercial shipping. Ships, drill rigs and other floating infrastructure frequently use that "parking lot". For example, during the July 2019 survey there were five jackup rigs there, and when DRR arrived for the Tobago survey, there were two jackup rigs and a drill ship in that lot.

To test the PRH we surveyed reefs at Trinidad and Tobago, both of which are close to the same set of offshore oilfields, to determine if *N. cyanomos* was there, and how far its population might have spread. Finding the regal demoiselle at either island would provide strong support for the PRH. Here

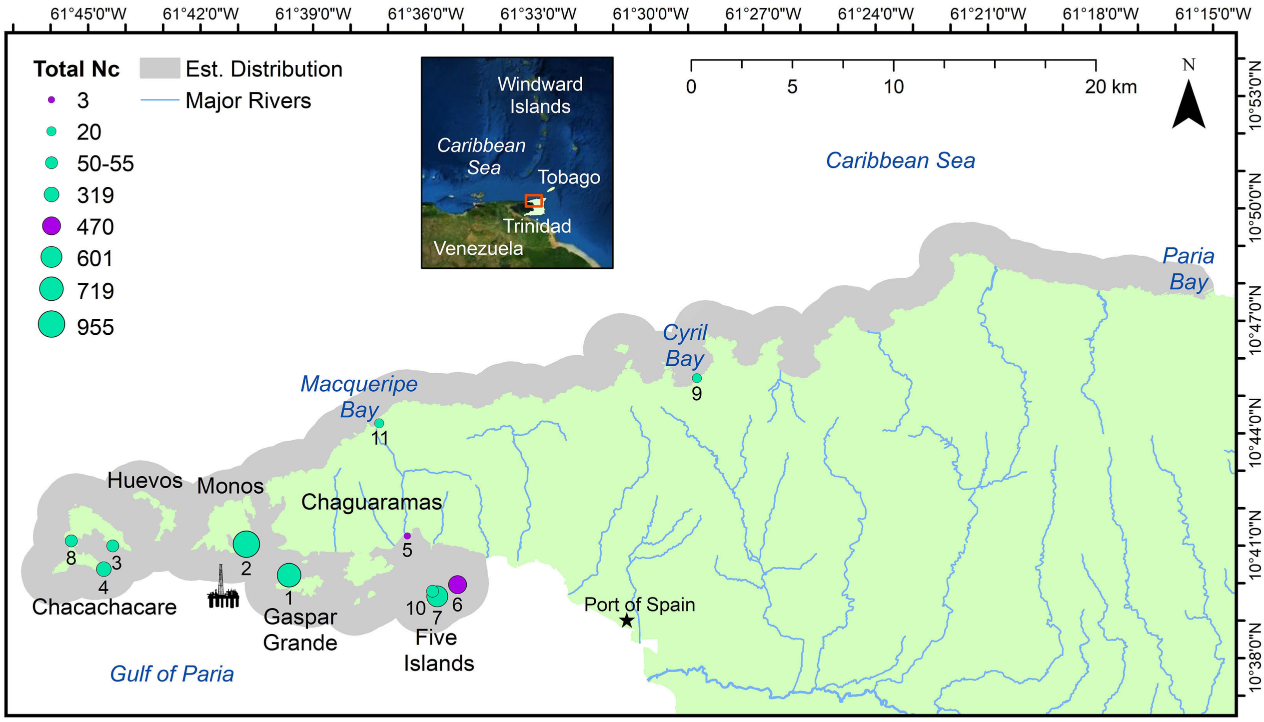

Figure 2. Location of Trinidad survey sites 1–11 at which *Neopomacentrus cyanomos* (Nc) were censused and observed in 2019 and early 2020, including the three named bays on the north coast. The map shows relative numbers of *N. cyanomos* at each site in the Gulf of Paria using incremental circle sizes. Purple circles are shipwreck sites and green sites are rocky reefs. The shaded gray area indicates the estimated distribution range for *N. cyanomos* in Trinidad. Drill-rig silhouette indicates general location of aquatic "parking lot" used by offshore rigs and ships, which extends from the Five Islands area to Chacachacare. Service layer credits for the inset: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS use community.

we describe the results of our surveys in the Gulf of Paria and along the western half of the north coast of that island in 2019. In early 2020 we also made an extensive set of surveys at nearby Tobago Island. This paper expands on an independent video report (Robertson and Kingon 2019) of the results of the Trinidad surveys.

Materials and methods

Study areas

<u>The Gulf of Paria</u>

The Gulf of Paria (Figure 1) is a semi-enclosed, 7,800 km^2 gulf with a narrow southern entrance and a little wider, island-studded northern entrance between the Paria Peninsula of Venezuela and Chaguaramas Peninsula of Trinidad. The western islands of Trinidad extend along the eastern half of the northern entrance between those two peninsulas. The prevailing current flow in the Gulf of Paria is for water to enter from the south and exit via the northern mouths, with a clockwise circulation within that Gulf (Singh et al. 2006). The Gulf receives inputs of freshwater from the main mouth of the Orinoco River, ~ 150 km south of the southern entrance, from subsidiary Orinoco mouths that empty into the Gulf near that entrance and from small rivers on its western and eastern sides. The Gulf is consistently euryhaline, with salinities varying seasonally with rainfall, from 14–34 PSU (Gopaul and Wolf 1995), and sometimes reaching near 0 PSU at the surface (Manickchand-Heileman et al. 2004; IMA 2016). In Trinidad, salinities in the Gulf would be highest during dry season which extends from January through May/June. The great majority of the Gulf is shallower than 25 m deep (Gopaul and Wolf 1995). Visibility is relatively low, the result of high sediment and nutrient loads in the water due to the high riverine input and the Gulf's shallow muddy seafloor (Maharaj and Recksiek 1991). Reefs in the northeastern Gulf of Paria are formed by the mainland and islands' rocky shores, and there is very little coral growth due to the estuarine conditions.

The northern coast of Trinidad is a seasonal mixing zone, with reduced salinity water exiting the Gulf of Paria meeting marine water coming from the Guyana Current in the east (Figure 1). Most of the north coast consists of steep, rocky shorelines interspersed with high energy, sandy beaches in the bays (IMA 2016).

Tobago

Tobago lies ~ 35 km northeast of Trinidad and usually has clearer, marine water conditions. The northward flowing Guyana Current passes between Trinidad and Tobago, and around the eastern end of Tobago. The southwest coast of Tobago has large areas of fringing coral reefs, protected bays and lagoons, low-energy sandy beaches, seagrass beds and mangroves. In contrast, the northeastern end of Tobago has rocky shorelines alternating with high energy sandy bays, with fringing coral-reefs only on the sides of bays (Mohammed et al. 2019).

Trinidad and Tobago Surveys

We made SCUBA surveys to depths up to ~ 20 m at two shipwrecks and five sites along rocky shores in the Gulf of Paria, close to the aquatic "parking lot" used by offshore-infrastructure, at the northwest corner of Trinidad (Figures 1, 2), between July 8–10, 2019. During those surveys, we recorded the numbers of *N. cyanomos* adults (> 5 cm TL), juveniles (> 2 cm to 5 cm) and new recruits (1.5–2 cm; see Leis and Carson-Ewart 2002) for at least 25 mins. per site. Subsequently, four additional sites were surveyed via snorkel between July 17, 2019 and January 16, 2020 by KCK or other local marine biologists familiar with the species, who provided total counts of *N. cyanomos*, and estimated locations and depths. The locations of the 11 survey sites are shown in Figure 2 and site details in Table S2. The extent of the coastline occupied by *N. cyanomos* is indicated by the grey land border in Figure 2, which was generated from our data.

The 31 sites at the southwestern (18) and northeastern (13) ends of Tobago that we surveyed between January 26 and February 6, 2020 are shown in Figure 3. Those were surveyed by 2–5 divers roaming throughout

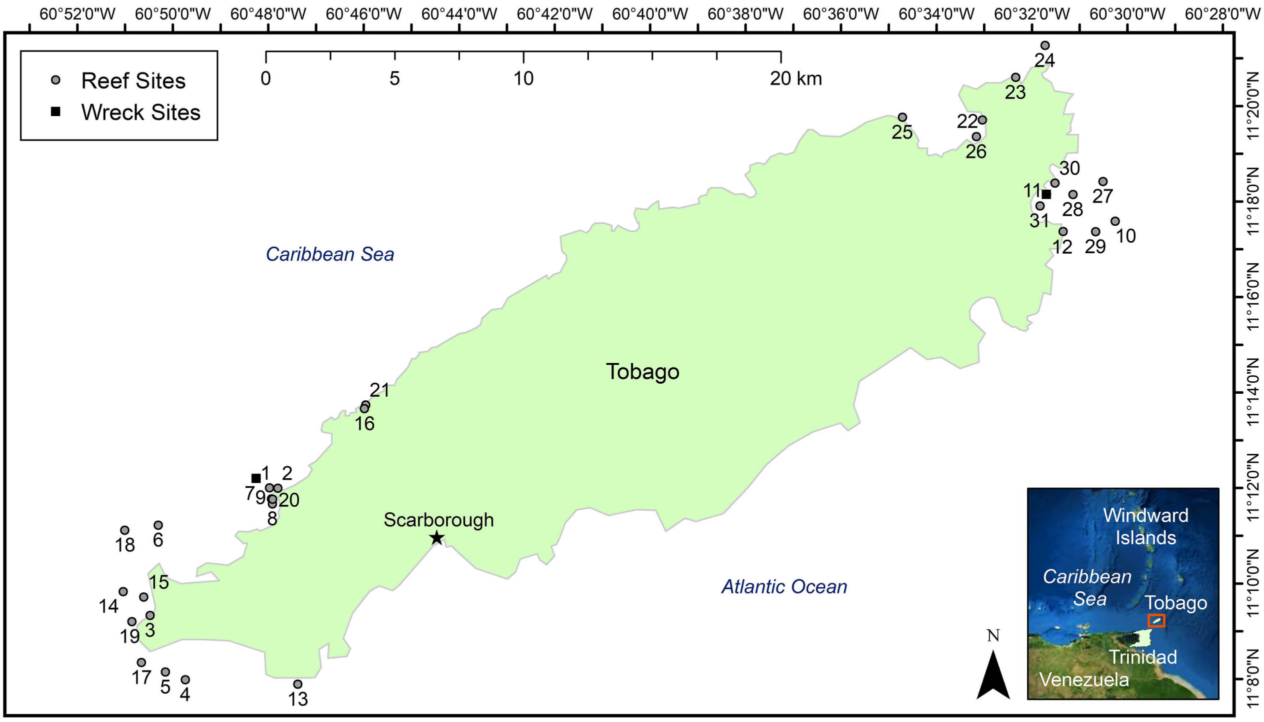

Figure 3. Locations of 31 Tobago sites surveyed for *Neopomacentrus cyanomos*. Sites 7 and 11 were shipwrecks; all the other sites were coral or rocky reef habitats. Service layer credits for the inset: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS use community.

each site for 45–90 minutes, at depths ranging from 5 to 38 m. Those sites included two shipwrecks and several shallow rocky shores, with most comprising coral reefs with varying types and coverages of live coral. The nearest offshore infrastructure to Tobago is the gas and oilfields south of Tobago and east of Trinidad (Figure 1).

Environmental Data Collection

Water quality data were collected immediately prior to each dive at sites 1–7 at Trinidad, and sites 1–20 at Tobago (Figure 3). A YSI Professional Plus meter with a 10 m long cable was used to record temperature (± 0.2 °C), salinity (± 1% of reading, PSU), pH (± 0.2 units) and dissolved oxygen (DO, mg/L or % saturation, ± 2% of reading) data 0.5 m below the surface and at site-bottom-depths up to 10 m deep. GPS coordinates were recorded using a Garmin GPSMAP 78sc as WGS84 latitudes and longitudes. The YSI and GPS equipment were not available for surveys at sites 8–11 in Trinidad and 21–31 in Tobago. Depth data at sites 1–20 at Tobago were measured using an acoustic depth sounder, while divers' depth-gauges were used for all remaining sites.

Identification of Trinidad specimens

Five adults we collected to assess whether their identity fit published descriptions of the morphology, morphometrics and meristics of *Neopomacentrus cyanomos* (Table S1). The Trinidad fish appeared identical

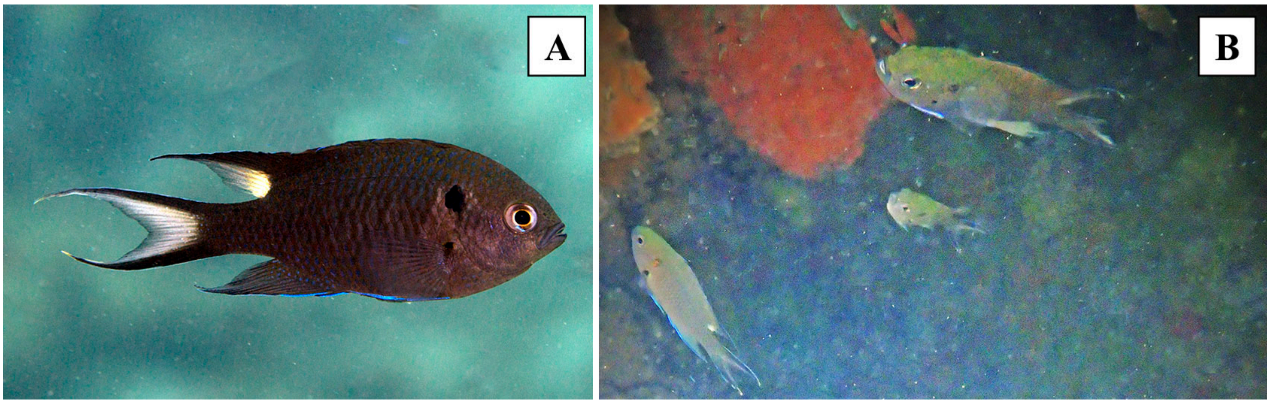

Figure 4. *Neopomacentrus cyanomos* in clear water at Veracruz Mexico (A, photo by CJE) and in highly turbid conditions in the Gulf of Paria, Trinidad (B, photo by KCK).

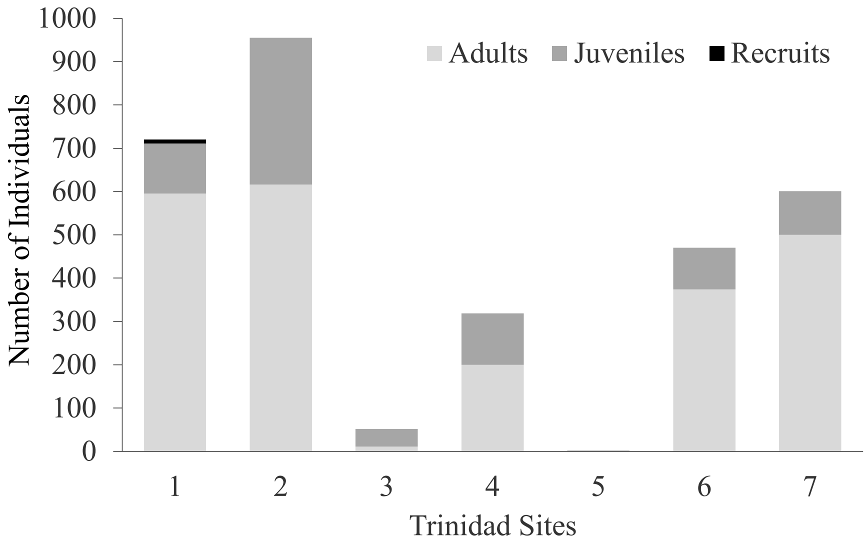

Figure 5. Number of *Neopomacentrus cyanomos* seen at each dive site in Trinidad divided by size class. Adults were defined as individuals > 5 cm, juveniles > 2–5 cm and recruits 1.5–2 cm. Sizes were estimated underwater by DRR.

in form, coloration (Figure 4) and general behavior to those from the GoMx (DRR *personal observations*). Robertson and Kingon (2019) present a video of part of a large aggregation of adults at Trinidad. Males of *N. cyanomos* care for benthic eggs laid in nests after attracting females to them (Setu et al. 2010). Nuptial males of *N. cyanomos* temporarily develop characteristic whitish markings on the upper head and body (see FishBase 2019) that aid in their field identification.

Results

Neopomacentrus cyanomos *surveys*

Trinidad

Neopomacentrus cyanomos were observed at all survey sites in Trinidad. Numbers of adults in large aggregations are approximate due to the continual movements of individuals. Numbers of individuals per site and by size class (adults > 5 cm TL, juveniles > 2–5 cm TL, recruits 1.5–2 cm TL) varied

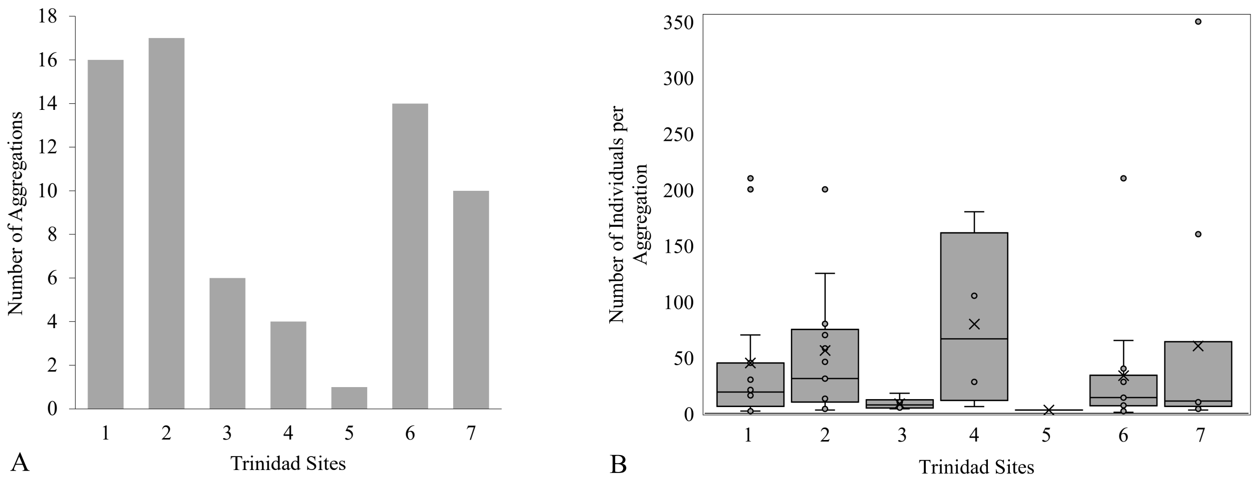

Figure 6. Data on aggregations (groups of individuals in close proximity to each other) of *Neopomacentrus cyanomos*. A: number of aggregations of *Neopomacentrus cyanomos* seen at each dive site in Trinidad. B: box and whisker plots showing statistics for the number of individuals per aggregation by dive site. X represents the mean, the middle line in the box is the median, top and bottom of the box are the first and third quartiles, whiskers are the minimum and maximum and the small circles are the outliers where very large aggregations were seen.

considerably between sites (Figure 5; and see Table S2). The fish we observed were mostly adults, large numbers of which were encountered. Site 2 had the highest numbers of adults, juveniles and in total (955). Site 1, which also had many individuals (719), was the only site where recruits (only 9) were seen. At Site 5, only three individuals were observed: an adult with a juvenile and a single freshly dead juvenile that wafted out of a hole in the hull as we moved past. This site is a relatively new shipwreck (Figure S2) that sank < 1 year prior to our visit, ~ 100 m from shore and the mouth of a small stream, the Cuesa River.

During ~ seven hours diving at the seven sites, we censused ~ 3,119 individuals, 73.7% of them adults, 0.3% recruits, and the remaining 26.1% larger juveniles. As on reefs in the GoMx (DRR *personal observations*), this species forms aggregations of varying sizes on Trinidad reefs (Figure 6). We found an average aggregation size of 46 ± 8.4 (SE) individuals, with the largest aggregation of ~ 350 fish, at Site 1. Sites 1 and 2 also had the highest number of aggregations. Site 6 comprised a pair of derelict ships (Figure S3) that sank in shallow water while anchored together, between 2012–2015. We surveyed only the Mammoth Tide, much of the upper surface of the rear deck of which was covered with scattered growths of sessile *Sargassum* and other macroalgae, where many *N. cyanomos* were found. Site 7 consisted of the entire perimeter of Pelican Island, a ~ 85 m long, shallow (< 3 m deep) rocky island. The entire edge of that islet was heavily undercut with large overhangs and caves. Two large aggregations of *N. cyanomos* at the mouth of such overhangs accounted for 85% of the individuals encountered. The substratum surrounding that island was densely covered in thick, ~ 0.5 m long growths of sessile *Sargassum* and *Caulerpa* growing to within 1m of the island periphery (Figure 7). The *N. cyanomos* remained within that cleared periphery and inside the outer edges of the caves and ledges and did not venture into those macroalgal beds.

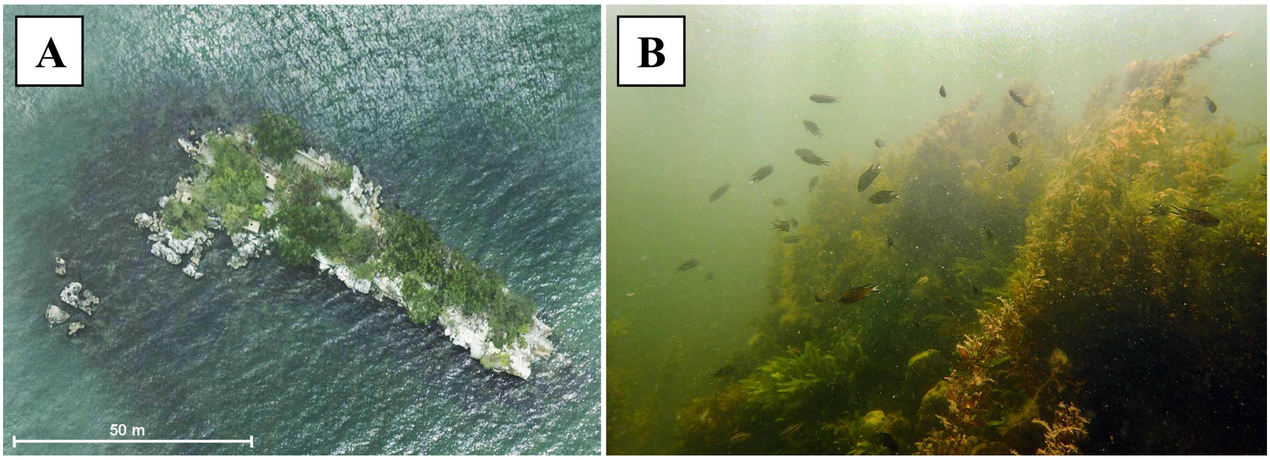

Figure 7. A: Aerial view of Pelican Island, Trinidad, Site 7. B: Part of an aggregation of *Neopomacentrus cyanomos* in front of the shoreline of Pelican Island against a background of sessile *Sargassum* and *Caulerpa* macroalgae. Note turbid conditions. Photographs: A – Institute of Marine Affairs; B – KCK.

At all sites, *N. cyanomos* were seen only in water shallower than ~ 7 m deep, and individual aggregations occupied less than ~ 25 m^2 of habitat. Subsequently, dives and snorkels made between July 17, 2019 and January 16, 2020 by SB and KCK, and two former UTT Marine Sciences graduates led to the discovery of additional *N. cyanomos* at Sites 8–11, in water < 4 m deep, along the north coast of the western islands and the western half of the north coast of Trinidad (Figure 2).

Males displaying nuptial coloration and actively moving between aggregations and benthic nest sites were observed at all sites with large numbers of individuals. Although most nests were hidden inside crevices, two nests containing eggs were found under moveable rocks and another inside a glass jar.

Tobago

No *N. cyanomos* were seen at any of the 31 dive sites we surveyed at either end of Tobago. Scarborough port, on the southern coast, receives ship traffic that moves daily between there and Trinidad. The sites we surveyed included large areas of habitat of types known to be commonly used by this species in the GoMx, and one site was < 8 km from that harbor. If the regal demoiselle was transported to that harbor by such shipping, then a population at Tobago would be at a very early stage of establishment.

Environmental data

Trinidad

In Trinidad, temperatures varied from 28.0 °C to 29.4 °C at the surface and were a little lower at the bottom or 10 m depth (Figure 8; and see Table S2). Although higher at depth than at the surface, salinity was reduced from typical marine conditions (~ 35 PSU) at both the surface (range 22.56–26.06 PSU) and to 10 m depths (range 25.08–29.34 PSU) at all sites. pH was

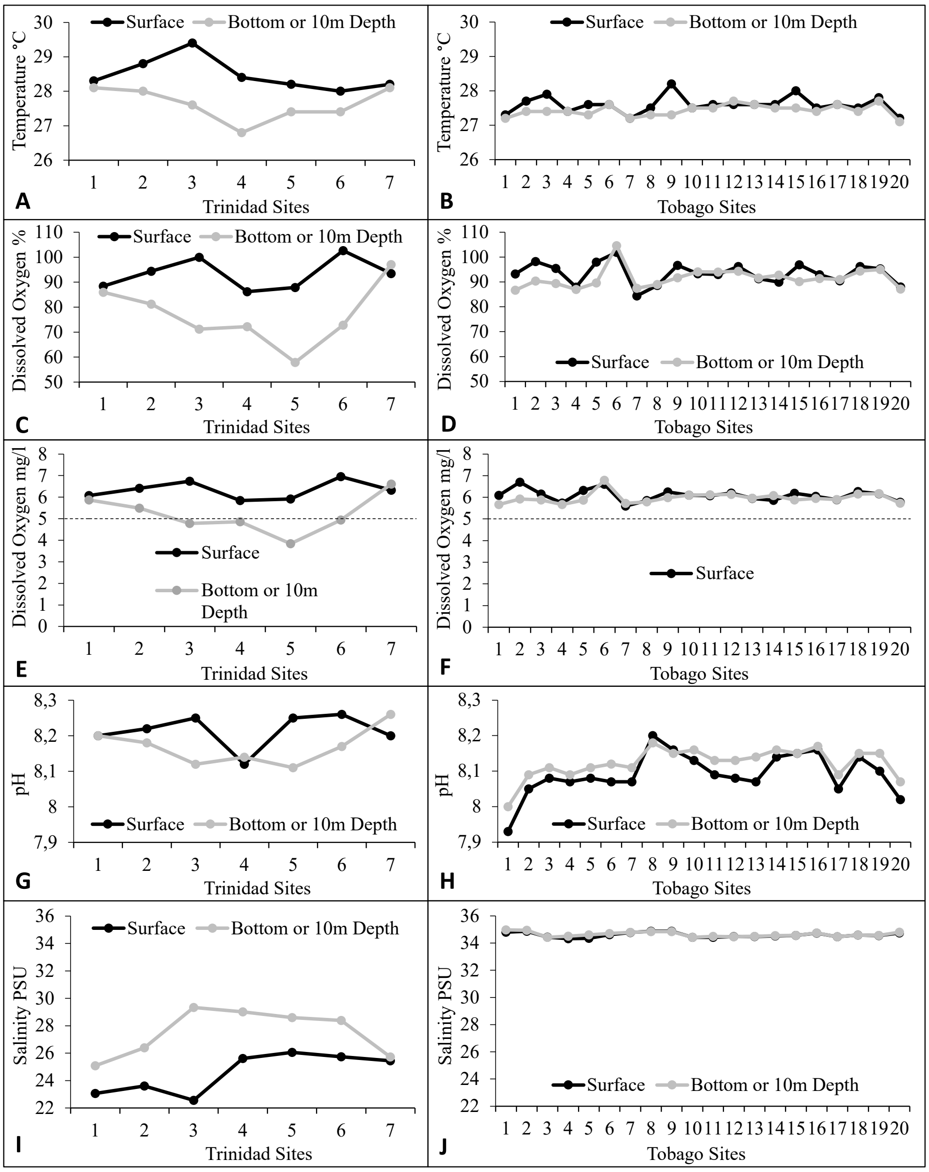

Figure 8. Water quality measurements at 7 dive sites at Trinidad (left, A, C, E, G, I) and 20 sites at Tobago (right, B, D, F, H, J). Site numbers correspond to those in Figures 1 and 2, respectively. From top to bottom, the figures show temperature (A, B), percent saturation of dissolved oxygen (C, D), dissolved oxygen mg/l (E, F), pH (G, H) and salinity (I, J). Measurements were taken at the surface, shown in black, and at the deepest possible depths given the 10 m cable limitation, shown in light gray.

relatively constant, across all sites and depths (ranging from 8.11–8.26), although slightly elevated above levels at Tobago. Dissolved Oxygen (DO) levels (absolute and percent saturation) were high at the surface at all sites. However, those levels were reduced at depth at all sites except site 7, which was only ~ 3 m deep and had a large, dense bed of live, benthic macrophytes growing on the substratum that likely boosted local daytime DO levels through photosynthesis. Four of the seven sites showed bottom DO values below 5 mg/l, with a minimum saturation level of ~ 60%. As those sites are also the sites where we found the fewest *N. cyanomos* this suggests its depth distribution may be limited to some extent by reductions in DO. Visibility was low at all sites, ranging from ~ 5–10 m at sites 1–4, to ~ 3 m at sites 5–7, which are farther into the Gulf away from the northern entrance to the gulf, where clearer marine water mixes with turbid Gulf water (see Figure S3).

Tobago

In Tobago, temperatures were similar at the surface and 10 m depth and a little lower than at Trinidad (Figure 8), likely due to surveys occurring in winter in Tobago versus summer in Trinidad. Salinity varied little with similar values at the surface and at depth and was distinctly higher than the estuarine conditions in Trinidad. pH values were similar at the surface and at depth, and average values were slightly lower than in Trinidad. At Tobago, DO levels were similar to those at the surface at Trinidad, but, unlike Trinidad, there was little difference between surface and depth values. Saturation levels of DO were uniformly high. Visibility was much higher than in Trinidad, with minima of about 15 m, and maxima of 30+ m at some sites.

Discussion

Isolated populations of the regal demoiselle at opposite ends of the Greater Caribbean

Neopomacentrus cyanomos was observed at all sites surveyed at Trinidad and was common at sites with strong current flows, where aggregations of adults reached sizes as large and larger than aggregations seen on coral reefs in the southwest GoMx (DRR *personal observations*). Most of the fish we censused were adults, while there were substantial numbers of juveniles. Many breeding males, as well as nests containing eggs being guarded by males were observed, indicating that this species can complete its life cycle in a large, reduced-salinity estuary. The paucity of recruits seen during our surveys could simply reflect seasonality or irregularity of some aspects of the reproductive cycle. From these observations, it is clear that a substantial, self-sustaining population, which must have taken many years to develop, is present in the Gulf of Paria and the adjacent coastline. The complete distribution of *N. cyanomos* around Trinidad remains unclear, although it does not appear to have spread to nearby Tobago.

To date, neither citizen-science activity nor crowdsourcing has led to the detection of *N. cyanomos* outside the GoMx. Prior to 2019, diving ichthyologists and experienced citizen scientists failed to find *N. cyanomos* anywhere outside the GoMx (southeast Florida, the Bahamas, Bermuda, the Caribbean coast of Mexico, Cayman Is, Roatan, Panama, Colombia or Venezuela; see Robertson et al. 2016, 2018). After our Trinidad finding, information was immediately distributed on two science listserves (campam-l@listserv.gcfi.org; and gcfinet@listserv.gcfi.org) that each reach 900+ scientists and managers in the Caribbean area. Subsequently DRR, CJE and AME spent four days at Dry Tortugas (October 2019), and CJE and AME a month diving at Roatan Island (Honduras) (November 2019).

The Carmabi Marine Biological Station (Curacao) and Venezuelan ichthyologist Oscar Lasso made social media posts about the Trinidad situation in late 2019. KCK dived at the Dominican Republic (November 2019) and Grand Cayman Island (January 2020), and CJE and AME spent March/May, 2020, diving at St. Eustatius island. None of those efforts or queries to local citizen scientists at various islands produced reports of *N. cyanomos*. Thus, all indications are that, as of early 2020, there were only two isolated populations of this species at opposite ends of the Greater Caribbean.

Support for the Petro-platform-Relocation Hypothesis (PRH)

As of early 2020, *N. cyanomos* appears to have substantial populations only at two areas separated by 3,000 km at opposite ends of the Greater Caribbean. Those are in the only two areas in that region with large, long-standing, offshore oilfields. Only one of the two areas (the GoMx) has major ports and large amounts of international commercial shipping, and a large population of marine aquarists cultivating imported Indo-Pacific fishes. These differences provide support for the PRH over the Aquarium-Release and Cargo-Ship-Transport hypotheses, as discussed by Robertson et al. (2018). Mobile oilfield infrastructure could have carried *N. cyanomos* from the Indo-West Pacific to either or both the GoMx and Trinidad, or between either or both of them and other Atlantic oilfields.

The prevailing northward flow of the Guyana Current between the islands may reduce the potential for recruitment of larvae produced in western Trinidad to Tobago and account for the absence of *N. cyanomos* at Tobago if the population originated at Trinidad. The apparent absence of regal demoiselles at Tobago also suggests that it is not present in the offshore fields east of Trinidad and 50–140 km south of Tobago, as those fields lie within the Guyana Current, which likely would have carried larvae to Tobago. This indicates that the Trinidadian population is based inside the Gulf of Paria and could well have originated at the Chaguaramas aquatic "parking lot" for mobile infrastructure.

If the PRH is correct, then two questions arise: (1) Are the GoMx and Trinidadian populations the result of a single introduction from the IWP? (2) Did one of those two populations seed the other via secondary transport of fish between those areas? In 2016, a tube-blenny endemic to northeast Venezuela and the Gulf of Paria was discovered on the west coast of Florida (Schofield and Brown 2019). In 2018, this same species was found on reefs at Veracruz in the southwest GoMx, where it evidently has an established population (Argüelles-Jiménez et al. 2020). This tiny, cryptobenthic reef-fish lives associated with fouling organisms such as are found on oil platforms and likely was transported from the Gulf of Paria to the GoMx by relocating oilfield infrastructure (Argüelles-Jiménez et al. 2020). Thus, it is feasible for the Trinidad population of *N. cyanomos* to have seeded the GoMx population.

The GoMx population of *N. cyanomos* is derived from two of four, well differentiated mitochondrial haplogroups (Robertson et al. 2018). Recent analyses of the haplotype composition of a large sample of Trinidadian fish shows that that population has similar proportions of major haplotypes found in the GoMx (Robertson et al. *in press*). These data indicate that both populations could have been derived from a single introduction but do not indicate whether one population seeded the other.

Ecological Plasticity and Success of the regal demoiselle

Neopomacentrus cyanomos is abundant and breeding on rocky reefs with high water turbidity and strongly varying salinity in the Gulf of Paria. The abundance of adults of this species in shallow water and its apparent avoidance of deeper water there indicate that adults can cope of even lower salinities that occur in shallow water at the height of the rainy season there than those we recorded just after the end of the dry season, before any heavy rains. Levels of pH we measured were similar to those found on coral reefs (Kline et al. 2019), despite this being an estuarine system. Daytime levels of DO in shallow water at Trinidad were somewhat reduced compared to those on coral reefs in other areas (Niggl et al. 2010; Lucey et al. 2020) but similar to those at Tobago. Reduced DO levels below that depth may have contributed to the general restriction of *N. cyanomos* to shallower water as we did not see any below ~ 7 m. Aquaculture experiments (Setu et al. 2010) with this species have shown that spawning, egg development and the larval life cycle can be completed in water with salinity, DO and pH levels similar to those we measured in shallow water where we saw nesting males. Tropical reef fishes in general, including at least one species of *Neopomacentrus* among many species of damselfishes, seem to be relatively resistant to hypoxia (Nilsson and Ostlund-Nilsson 2004), and the daytime snap-shot levels we measured were above the values those authors found to produce stress in those fishes. However, nocturnal reductions in DO in the Gulf of Paria due to lack of photosynthesis could well reach stressful levels.

Ecological plasticity is thought to be an important factor that affects invasion success (Parker et al. 2013). Indications of such are evident for the only other successful NNS of reef fish in the Greater Caribbean, the Indo-West Pacific lionfish, *Pterois volitans* (Linnaeus, 1758) (see NOAA 2019; Cure et al. 2012, 2014). Substantial populations of *N. cyanomos* exist on rocky reefs and shipwrecks in the estuarine Gulf of Paria. Similar populations also occur on both inshore and offshore coral reefs, oil platforms and new and old shipwrecks at depths between 0.5–53 m in the warm southwest GoMx. They are also found on natural- and artificial reefs and oil-platforms in the northern GoMx where there is strong seasonal variation in SST. The evident ecological plasticity of *N. cyanomos* in these situations may be important for the establishment and success of the GoMx and Trinidad populations, and for its future spread in the region.

Potential for spread throughout the Greater Caribbean

Trinidad sits at the southeast corner of the Caribbean, where the Guyana Current flows into the Caribbean (Figure 1). From there the northbound Caribbean Current spreads water throughout the Caribbean Sea (RSMAS 2020). The pelagic larval duration of *N. cyanomos* is several weeks (Johnston and Akins 2016), which should allow larvae produced in Trinidad to be widely dispersed in the Caribbean. Hence, *N. cyanomos* should not be expected to remain restricted to Trinidad for any significant period of time. The apparent current limitation of the Trinidad population to a small area suggests that it is in an early stage of geographic expansion. The dynamics and spatial organization of its inevitable spread beyond the two existing Greater Caribbean populations will provide instructive information about patterns of connectivity among reef fishes throughout the region.

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Ethics and Permits

Specimens of *N. cyanomos* were obtained at Trinidad under an August 5, 2019 permit from the Director of Fisheries of Trinidad and Tobago, using methods approved by the Smithsonian Tropical Research Institute ACUC committee 2017-1107-202-A1.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Taxonomic characteristics of *Neopomacentrus cyanomos*.
Table S2. Names, locations, depths, and dates of surveys, and environmental measurements and numbers of *Neopomacentrus cyanomos* censused at sites at Trinidad and Tobago.
Figure S1. Mobile offshore petroleum infrastructure in the Gulf of Paria "parking lot" south of the Chaguaramas Peninsula of Trinidad in November 2019.
Figure S2. Wreck of the Treasure Queen (Site 5).
Figure S3. A: Mammoth Tide wrecks, Site 6. B: Part of an aggregation of *Neopomacentrus cyanomos* on the upper surface of the rear deck of the Mammoth Tide.

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