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ORIGINAL RESEARCH

Small-scale fishing has affected abundance and size distributions of deepwater snappers and groupers in the MesoAmerican region

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Abstract Deepwater fisheries in the Caribbean Sea are poorly studied and mostly unmanaged, despite their importance to local economies and food security. In the MesoAmerican region, deepwater fisheries are nearshore and easily accessible in many locations by small vessels, but historical and contemporary fishing effort varies by country. We used standardized fishery-independent methods, including vertical longlines and baited remote underwater video (BRUV) to assess the relative abundance and distribution of deepwater (100–550 m) snappers and groupers in Belize and Honduras. Fishery-dependent samples were used to supplement spatial distribution and body length data. Gathered data revealed that Belize, with a smaller fishing population and shorter history of deepwater fishing, had overall higher abundance of groupers and snappers and that fish were significantly larger than those in Honduras, which has a well-established and larger deepwater fishery. Water temperature was found to influence the abundance and occurrence of deepwater snappers more than depth. Deepwater snappers were widely-distributed throughout available habitat in both countries, but groupers were more patchy, and rarely encountered in the more heavily fished areas off Honduras. Our results suggest that a precautionary approach to fisheries management and targeted biological research of these stocks is required, which is particularly relevant for Belize, where climate change and overfishing mitigation measures are focused on an expansion of the deepwater fishery.

Keywords Pristipomoides · Etelis · Lutjanus · Hyporthodus · Belize · Honduras

Introduction

Fishers generally investigate deepwater fisheries after nearshore and coastal resources become limited due to overfishing, habitat loss, or shifts in abundance, and when relevant technology (e.g. depth sounders, GPS) becomes available and affordable (Morato et al. 2006). In many low and middle income countries, fishers' progression to deeper waters is subsidized by governments and international funding agencies to compensate for overfishing of coastal resources (Brownell 1972; Cifuentes Lemus 1979; Giudicelli 1979; Grant 2019). The majority of nearshore deepwater fisheries of the MesoAmerican countries of

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Mexico, Belize, Guatemala, and Honduras are small-scale, with a mean vessel size of 8 m (25 feet) and trip duration of 2.5 days in all four countries (Baremore et al. 2021). While exploitation rates vary by country due to various factors, including fishers' proximity to deep waters, state of existing seasonal coastal fisheries, the cost and availability of equipment, and the strength of the local and export markets (Baremore et al. 2021), only in Honduras are semi-industrial vessels (10–15 m in length, capable of remaining at sea for 5–14 days) used for longer trips to offshore fishing banks. Transboundary deepwater fishing is a top concern for fishers in these countries, who perceived illegal fishing as a direct threat to deepwater fish stocks in their national waters (Baremore et al. 2021).

Despite their proximity, the countries of Belize and Honduras are juxtaposed in terms of exploitation of the deepwater fisheries, with Belize having a young and relatively undeveloped fishery, and Honduras having an established fishery with higher contemporary fishing effort overall (Canty et al. 2019; Grant 2019; Baremore et al. 2021). The majority of deepwater fishing grounds in Belize are accessible only by engine-powered or small liveaboard sailing vessels, equipment is prohibitively expensive and/or unavailable, and export markets have not been stable despite multiple government interventions (Grant 2019; Baremore et al. 2021). In contrast, Honduras has a longer tradition of deepwater fisheries, some fishing grounds are accessible by unpowered vessels (namely in the Bay Islands), equipment such as GPS and hydraulic winches are readily available, semi-industrial 'snapper boats' are able to reach remote fishing grounds, and there are several well-established fish factories that process deepwater snappers for domestic fish sellers and for export (Gobert et al. 2005a; Canty et al. 2019; Baremore et al. 2021). Furthermore, while deepwater fishers interviewed in Belize did not perceive reduction in fish size or abundance, fishers in Honduras indicated that the fishery had declined over the last 30 years (Baremore et al. 2021).

In Belize, the development of the nearshore deepwater fishery is being promoted by fisheries managers and the World Bank as a climate change adaptation measure (Grant 2019; see MCCAP), despite a lack of biological and ecological information on the species that are targeted and landed (Tewfik et al. 2022). To manage and equalize fishing effort throughout Belize, The Government of Belize created a territorial user rights for fisheries (TURFs) based 'Managed Access' program in 2011 (Belize Fisheries Department 2015; Alves et al. 2022) that limits fishers to two fishing 'Zones' out of eight managed zones throughout the country's coastal fishing habitats. The deep slope falls under Zone 9, which is provided by the authorities as an additional 'bonus' Zone and declared open access (https://fisheries.gov.bz/managed-access/). The deepwater fishery is perceived as an untapped resource in Belize, and managers promote its potential for offsetting fishing effort in the overfished coastal regions; however, the available habitat for target deepwater species is a narrow band of waters between 90 and 450 m depth, which contributes to less than 20% of the total available fishing surface area in the country (~2600 km^2 deepwater vs. ~ 11,000 km^2 shallow inshore and atolls) (Baremore et al. 2021). Considering the likelihood that benthic fishes in these depths have conservative life history strategies such as long lifespans, slow growth, late reproduction, and low genetic diversity (Cook et al. 2009; Newman et al. 2016; Manel et al. 2020; Andrews and Scofield 2021; Scherrer et al. 2021), any unmanaged increase in fishing effort may lead to rapid declines in those fish populations.

Coastal fisheries in Belize and Honduras are overfished (Graham et al. 2008, 2009; Paddack et al. 2009; Dunn et al. 2010; Tewfik et al. 2020), though demand for high quality seafood products from domestic and international sources continues to increase. Deepwater snappers and groupers are highly sought by restaurants and individuals in the region, and fishers reported that the higher quality and larger size of the fish were primary reasons for entering the fishery. Profits from the sale of this product can be undermined by the higher effort and costs needed to obtain the fish (Baremore et al. 2021). Despite the difficulties of the fishery, most practicing deepwater fishers in both countries indicated that they intended to continue to fish in deep waters, with the fishery in Belize primed to rapidly expand in the coming years (Grant 2019), especially among the recreational sector (Baremore et al. 2021).

Exploitation by fisheries affects life history characteristics of fish species, and can result in faster growth, earlier maturity, truncated age and size classes, and distributional shifts (Beverton and Holt 1957; Rochet 1998; Levin et al. 2006; Beamish et al.

2006; Liang et al. 2014). These effects are greater for slower growing, larger species, with late maturity, such as many deepwater teleosts (Jennings et al. 1999). Age- and size-truncation have considerable implications for reproductive potential, as larger, older fish tend to produce more and higher quality eggs (Hixon et al. 2014). A study comparing size, age, and growth rates for deepwater snappers between areas with contrasting fishing exploitation histories in the Indo-Pacific found that the fished population had a truncated age composition, which was not apparent from examination of length data alone (O'Malley et al. 2019). Though many deepwater fisheries in the world can be classified as small-scale, localized depletions of stocks can occur within a few years (Koslow 2000). In Bermuda, the expansion of fishers into the 'red snapper' fishery using vertical longlines in 1980 likely contributed to the collapse of the fishery less than two years (Luckhurst and Ward 1996). As the majority of deepwater tropical fish populations lack basic biological, fisheries, and distribution data (Newman et al. 2016), and tend to be intrinsically vulnerable to overexploitation, species- and region-specific data are needed to inform management and conservation plans.

In addition to other challenges these fish populations face, climate change can affect distribution and behavior of fishes and fisheries (Sainsbury et al. 2018, 2021). Fishing practices in the MesoAmerican region have been affected as seasonal weather patterns and currents become less predictable and extreme weather conditions increase (Stephenson and Jones 2017). While changes in surface temperatures and currents, increased perturbation from higher winds and storms, and increasingly regular sargassum influxes affect the distribution of coastal species (Biasutti et al. 2012; Stephenson and Jones 2017; Oviatt et al. 2019), the deeper waters across the globe are becoming warmer, more acidic, and less oxygenated (Levin 2019). Commercially important deepwater species like the snappers and groupers inhabit different depth strata by life history stage, and therefore may be affected by these changes differently across their life spans (Newman et al. 2016; Barbeaux and Hollowed 2018). Spawning coral reef-associated groupers have narrower thermal tolerance than non-spawners, and warmer waters led to a contraction of spawning season and reduction of spawning probability (Asch and Erisman 2018; Gokturk et al. 2022). Depth-constrained spawning deepwater species may be subjected to similarly narrowed thermal niches (Magnuson and DeStasio 1997). There is currently very little information on the benthic environment or biodiversity below 50 m along the MesoAmerican Barrier Reef, and therefore a baseline of data is needed to gauge potential shifts in these features as the climate continues to change and fishing effort increases.

To improve underpinning knowledge, subsequent management, and consequences of deepwater fisheries in the MesoAmerican region we set out to: (1) provide a baseline of species distribution and abundance data for commercially important deepwater snappers and groupers; (2) describe the depth and temperature preferences of these species as well as the factors influencing them; (3) determine if higher exploitation rates in Honduras in relation to Belize have affected the abundance and size structure of deepwater snappers and groupers targeted by the deepwater fishery.

Materials and methods

Study sites

In Belize, surveys were conducted along the Belize Barrier Reef and all three offshore atolls (Fig. 1). The topography of the seafloor to the east of the barrier reef and atolls is extremely steep in many places (maximum slope of 48 degrees), hence limiting available habitat. Benthic habitats are a mix of complex structure, sand, and hard bottom at the atolls, and is mostly sand and hard sand along the barrier reef with patches of complex structure. Slopes between the barrier reef and Turneffe and Glover's Reef Atolls are gentler and the benthic habitats are largely mud (Fig. 1; Baremore et al. 2021). There are no restrictions on deepwater fishing in Belize, with the exception of four 'no take' zones with small areas that extend into deeper waters (< 40 km^2 of surface waters). The approximate available deepwater fishing habitat (100–550 m) is approximately 2600 km^2 of the surface waters.

Surveys in Honduras were conducted in western Honduras from Puerto Cortés to Punta Sal, at the Bay Islands of Guanaja, Roatán, and Utila, and along a bank that stretches from the southeastern point of Utila to the east between the Bay Islands and the Cayos Cochinos (Fig. 1). The bottom habitat of

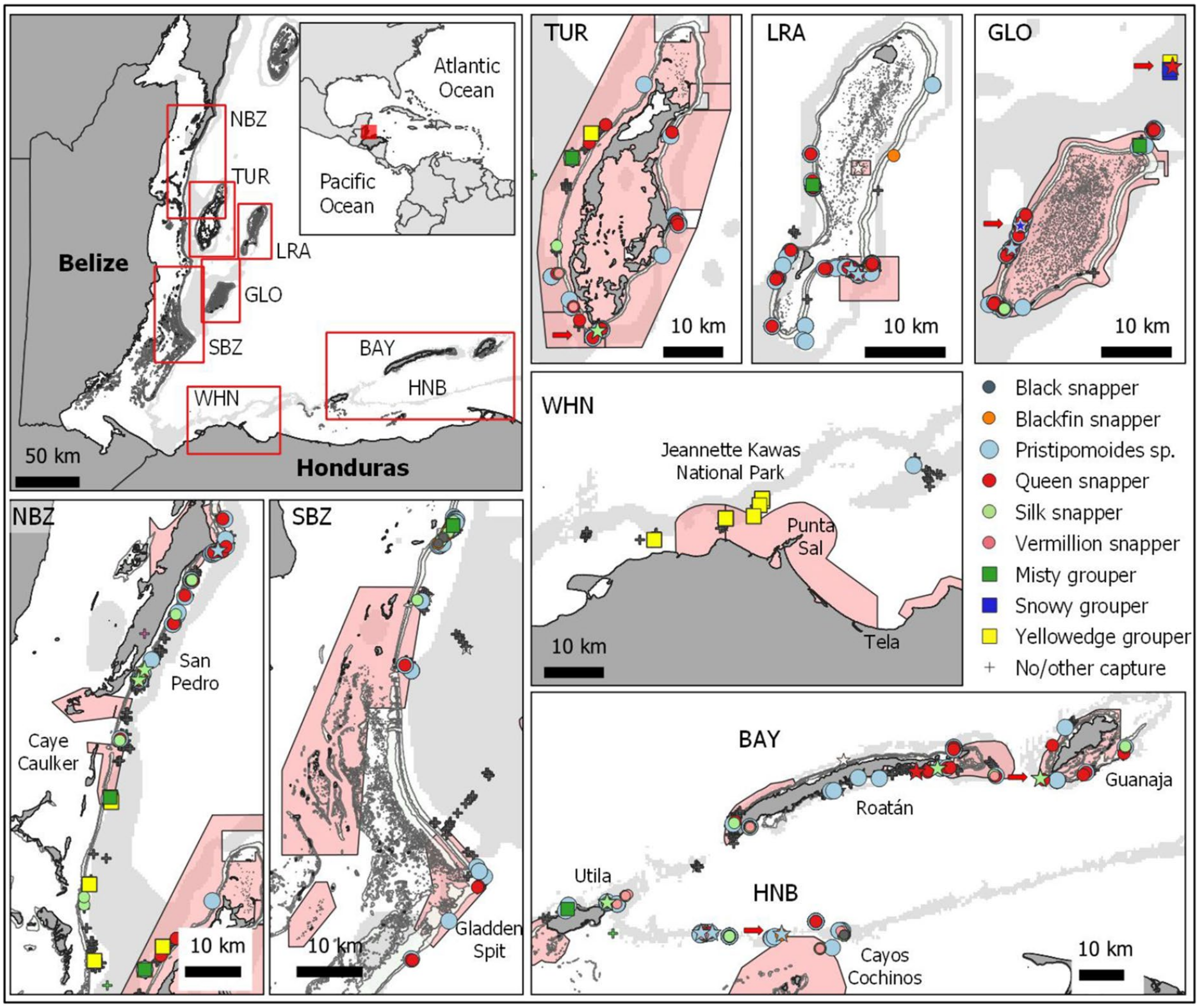

Fig. 1 Captures and sightings of deepwater snapper and grouper species from fisheries independent, fisheries dependent (filled circles) and BRUV deployments (filled stars) in Belize (TUR = Turneffe Atoll; LRA = Lighthouse Reef Atoll; GLO = Glover's Reef Atoll; NBZ = Northern Belize; SBZ = Southern Belize) and Honduras (WHN = Western Honduras; BAY = Bay Islands; HNB = Honduras Banks) 2015–2022. Arrows denote locations where BRUV sightings revealed different species than captures from concurrent vertical longlines. Total available sampling area was from 100 to 550 m, indicated by the light grey filled area

western Honduras is mostly mud, and the water is often turbid due to the influence of several rivers during the rainy season. The waters of the Bay Islands are clear, and the benthic habitats are comprised of a mix of structure and hard sand bottoms. The deep bank between the Bay Islands and the mainland is a mixture of mud and complex structure, with clear water year-round. MPAs in the Bay Islands include closed areas and restrictions on commercial gear, but closed areas do not extend to the sea floor, while seasonal closures for spawning fishes in western Honduras do not include deepwater species. The approximate available deepwater fishing habitat in the study area (western Honduras to the eastern extent of the Bay Islands) is 2600 km^2 of the surface waters.

Data collection

Fishery-independent methods

Scientific vertical longline surveys were used to capture deepwater snappers and groupers in Belize and Honduras from 2015 to 2022 across all months (Table 1). Survey locations were haphazardly chosen based on *a priori*, randomly selected sampling sites, and an attempt was made to sample at three depth strata: 150, 250, and 350 m using a portable depth sounder. Surveys were typically 1–5 days in duration per location and were conducted from small vessels (8 m) by a crew of five persons. Due to the small scale of the survey, sampling effort was opportunistic and therefore not evenly distributed across locations by year or site. Vertical longlines consisted of monofilament line terminating in a gangion with five evenly spaced offset circle hooks, held vertically with a surface float. Hook sizes were 9/0, 10/0 or 13/0 for each gangion and hooks were baited with either Atlantic bonito (*Sarda sarda*), blackfin tuna (*Thunnus atlanticus*), barracuda (*Sphyraena barracuda*), or mackerel (*Scomberomorus sp.*) based on local availability. Due to species similarities, bait types were aggregated into scombrids (bloody baits) and non-scombrids (non-bloody baits) for further analysis. Different hook sizes were used for analysis of fish size selectivity. Lines were set between approximately 100 and 550 m depth, soaked for a minimum of 30 min, and were deployed to the seabed and retrieved by hand. Temperature depth recorders (TDRs, LOTEK LAT1400) were attached to lines to record depth and temperature data for each set wherever possible (887 of 1182 surveys).

Captured teleost fishes were identified to species and stored on ice with a small identification tag to mark the set and hook number. Upon landing, fish were measured for straight-line standard (SL, cm), fork (FL, cm), and total lengths (TL, cm), and weighed (precision 0.1 kg). When possible, otoliths were removed, cleaned, and stored dry, and a sample of muscle tissue (1–5 g) was kept on ice and then stored frozen for future analyses. Fish were sexed and staged by macroscopic examination of the gonads based on a modification of Gobert et al. (2005b). Identification of *Pristipomoides* species in the region is problematic, as both wenchman (*P. aquilonaris*) and cardinal (*P. macrophthalmus*) are similar in appearance and may partially overlap in both horizontal and vertical distributions (Robertson and Van Tassell 2019). Several attempts were made to ensure species identification was correct over the course of this study. Lateral line scale counts were made opportunistically, which suggested those captured were *P. macrophthalmus*; however, this was not carried out for every fish. One individual was identified as a likely *P. aquilonaris* during sampling, as it was found to be mature at a very small size (17.8 cm TL) in relation to all other sampled fish: a lateral line scale count reinforced this identification. Additionally, relationships between FL, TL, and body weight were examined for outliers, with no obvious patterns observed to suggest multiple species were captured. Although it is likely that the *Pristipomoides* sp. captured in this study were cardinal snappers, for the purposes of the manuscript, the species will be referred to as *Pristipomoides* sp. due to ongoing identification uncertainties.

A deep water Baited Remote Underwater Video (BRUV) system was used to record species and seabed habitat type when sea conditions were favorable. BRUVs were set and deployed by hand using a monofilament line attached to a surface float. BRUVs were either set simultaneously within visual range of vertical longlines or set opportunistically to increase sample sizes. BRUV deployments ranged from 30 to 120 min and a TDR was fixed to the BRUV frame when possible. In several cases (13 of 39 deployments; 66%) the cameras did not record for the anticipated minimum 60 min, mostly due to currents or surface winds dragging the frame off station. The bottom habitat type was determined visually from gathered video data, and occasionally verified physically by sediments that were trapped in the frame. After all BRUVs were reviewed, habitat types were classified into four types: sand (mostly uniform, small grain), hard sand (mostly sand with rocky features), mud, and structure (Fig. 2). Benthic and pelagic invertebrate species were identified to the lowest taxonomic level possible and enumerated. Bottom habitats noted from cameras were used to inform the habitat types of nearby vertical longline sets. A species accumulation curve was used to determine the effectiveness of BRUV surveys to characterize species occurrence for grouper and snapper species. The number of new species sighted in each subsequent BRUV was calculated and plotted, and the order in which the surveys were analyzed was randomized to determine how many BRUV sets were needed to accurately assess species diversity. The number of surveys needed to describe 90% of the total species sighted was calculated using the R package vegan (Oksanen et al. 2017).

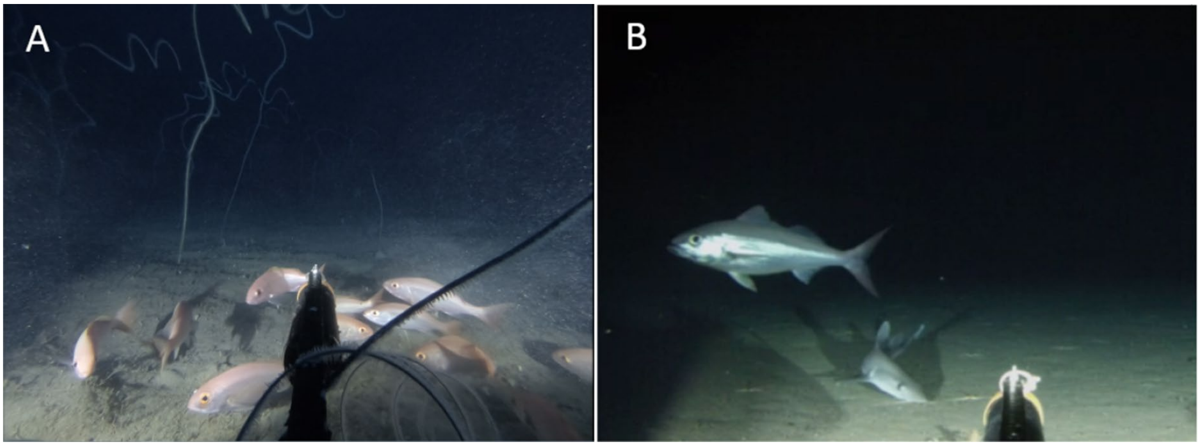

Fig. 2 Baited remote underwater video (BRUV) showing candidate species and habitat types: **A** vermilion snappers over soft sand (classification-sand) with whip corals off Utila, Bay Islands, Honduras; and **B** a queen snapper and smoothhound shark (*Mustelus* sp.) over hard structure (classification-structure) at an offshore bank between atolls in Belize

Table 1 Effort by month for fishery-independent vertical longline sets, sampled fishery-dependent trips, and baited remote underwater video (BRUV) by country from 2015 to 2022

Fishery-independent sets	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total sets	Fish sampled
Belize		81	65	49	112	41	36	52	107	122	62	46	773	438
Honduras				96	48			83	31	127	11		396	114
Fishery- dependent trips													Total trips	Fish sampled
Belize		1							2	1		2	6	64
Honduras	1	2	4	1	5		2	6	1		3	1	26	252
BRUVs deployed													Total BRUVs	Species observed
Belize			1	2	4	1		2	4	5	2	2	23	6
Honduras				8	1			1		6			16	5

Fishery-dependent sampling

Due to regional COVID restrictions, fishery-independent surveys could not be conducted in 2020. To supplement sample sizes for spatial and size distribution and life history analyses, deepwater snappers were obtained whole from fishers during this time. All landed fish from five fishing trips were purchased. Fishers provided coordinates (latitude and longitude) and approximate depth of capture. Fish were collected whole and processed as described above.

Fish abundance and distribution

Scientific vertical longline captures and BRUV sightings were mapped using QGIS (QGIS Development Team 2020), and depth and temperature of capture/sighting were examined to assess horizontal and vertical distribution of snappers and groupers in Belize and Honduras. The seabed depth region between the 90 and 550 m contour was extracted from the General Bathymetric Chart of the Oceans (GEBCO) and mapped to represent the approximate habitat available to deepwater fishes and therefore represented the available sampling area. Bottom temperatures at depth were plotted, and smoothed trend lines were plotted by region using LOESS smoothers for visualization of mean temperatures at depth. Species-specific captures were plotted by depth and temperature to determine the vertical distribution of deepwater snapper and grouper species.

Catch per unit effort (CPUE) was calculated for each species by vertical longline set:

$$CPUE = \frac{\#\ individuals\ captured}{\#\ hooks * soak\ time\ (hrs)}$$

To minimize sampling bias, sets with the longest and shortest soak times were removed from further analyses by restricting the data to the central 90% of the soak distribution. Sets with ineffective hooks (bite offs) were also removed from CPUE analyses. No differences were found in CPUE among bait types for aggregated species. For general comparisons among countries, differences in mean CPUE between countries were tested using Wilcoxon rank sum tests for species where sample sizes were sufficient (Zar 1999).

Generalized additive models (GAMs) were used to explore the relationships between species abundance and spatial, habitat, and environmental variables. GAMs are useful regression tools for investigating relationships that are nonlinear, such as those between the presence of a species and its depth distribution (Wood 2006). Additive models fit a smoothing curve through the data and are valuable tools for standardizing abundance estimates due to their flexibility. CPUE and occurrence were modeled for the snapper species with sufficient capture information using the R package mgcv (Wood 2011) in R (R Core Team 2021). A Tweedie distribution with a log-link was used for the CPUE model because of the high number of sets with zero captures (Shono 2008), and a binomial GAM with a logit-link function was used to model occurrence (Zuur et al. 2009). The restricted maximum likelihood (REML) score was used to select the degree of smoothing. Collinearity of predictor variables was examined using variance inflation factors (VIF), where variables with VIF > 5 were excluded from the models (Zuur et al. 2009). Final model selection was based on minimization of the akaike information criteria (AIC) (Akaike 1974) and improvement of the percent deviance explained (% dev): a step-wise approach was guided by the approximate significance ($p < 0.1$), with non-significant variables removed only if the % dev improved by more than 1% (Bentley et al. 2012). Percent deviance was calculated for individual terms by running a series of models using each term as a single variable and adding one term at a time. Candidate explanatory variables included in the full models were:

$$\begin{aligned} \mathrm{CPUE/Occ} &\sim \mathrm{f(country) + f(hook\ size) + f(habitat)} \\ &+ \mathrm{f(bait\ type) + s(month,\ radial) + s(depth)} \\ &+ \mathrm{s(temperature) + s(Latitude),\ + s(Longitude);} \end{aligned}$$

where f indicates a factor, and s is a smoothing term. Latitude and longitude were modeled separately and as interaction terms using the te function to account for spatial autocorrelation (Wood 2011) that models interactions between smooth terms (Pedersen et al. 2019), as were depth and temperature.

For BRUVs, the maximum number of individuals sighted in one frame at the same time (termed 'MaxN') was calculated per BRUV deployment and a mean average calculated by country. Frequency of occurrence (%FO) of a species was calculated as the number of BRUV deployments in which each species was observed divided by the total number of BRUV deployments. Species occurrence was compared to results from concurrent vertical longlines to gauge potential bias in sampling methods.

Fish body length

Mean TL was calculated for snapper and grouper species overall and by country for fish collected by scientific vertical longline and fishery-dependent samples combined. Data were combined for this analysis only to increase sample sizes across multiple species that were under sampled by fishery-independent surveys. To reduce bias among methods, fishery-independent data only included fish captured on size 10/0 hooks, mirroring fishery-dependent methods. Violin plots were used to assess differences in mean size between Belize and Honduras, and Wilcoxon rank sum tests were performed to determine whether differences were significant for the most common species (Zar 1999).

Linear and additive models were used to assess relationships between the sizes (TL) of snapper species and depth of capture by scientific vertical longline where sample sizes were sufficient. Both generalized linear models (GLMs) and GAMs were investigated for species with sufficient capture data. Goodness-of-fit diagnostic plots and AIC values were used to determine whether the linear or additive model was more appropriate for each species. Candidate explanatory factors in the full model included depth, hook size, and country, and final model selection was based on AIC criteria and/or percent deviance as described previously. Density plots were used to visually assess the distribution of the depth and size for captured fish. All statistical analyses were accomplished using Program R (R Core Team 2021) and the tidyverse group of packages (Wickham et al. 2019) were used for data visualization.

Results

Fishery-independent and dependent sampling

Vertical longlines (n = 1182) were deployed in Belize and Honduras from 2015 to 2022 (Table 1), resulting in the capture of 552 individuals from six species of snappers and three species of groupers (Fig. 1; Tables 1 and 2). A further 316 individuals were sampled from fishery-dependent sources (Table 1). Fishery-independent effort was higher and more evenly distributed across months in Belize in comparison to Honduras (Table 1). *Pristipomoides* snappers (*Pristipomoides sp.*) were the most commonly captured by vertical longlines (n = 336), followed by queen snappers (*Etelis oculatus*) (n = 119), and silk snappers (*Lutjanus vivanus*) (n = 40) (Table 2).

Vertical longlines were set from 90 to 696 m depth (Fig. 3), and proportions of sets by 50 m depth strata were even across countries (Table 3). Depth of capture for snappers and groupers ranged from 140 to 437 m (Fig. 3a; Table 2). Temperature at depth was similar across sampling sites, apart from western Honduras near the outflow of Ulúa River, which was markedly colder at shallower depths, especially below 200 m (Fig. 2a). Black (*Apsilus dentatus*) and blackfin (*Lutjanus buccanella*) snappers preferred shallower and warmer waters, ranging from 140 to 224 m and 24.0–16.3 °C, while silk, *Pristipomoides*, and queen snappers had broader distributions at 140–437 m and 24.0–10.0 °C (Fig. 3b; Table 2).

Table 2 Numbers of snappers and groupers captured by fishery-independent vertical longline surveys, sampled from fishery-dependent sources, and sighted on BRUVs in Belize (BZ) and Honduras (HN)

Common name	Species	Vertical longline		BRUV		Fishery-dependent		Min depth (m)	Max depth (m)	Max temp (°C)	Min temp (°C)
		BZ	HN	BZ	HN	BZ	HN				
Black snapper	*Apsilus dentatus*	9					10	140	174	23.6	18.3
Blackfin snapper	*Lutjanus buccanella*	9	1	1			30	140	275*	24.0	16.3*
Pristipomoides sp.	*Pristipomoides sp.*	276	60	5	6	36	34	150	403	19.7	10.3
Queen snapper	*Etelis oculatus*	102	17	3	4	26	24	193	437	18.7	10
Silk snapper	*Lutjanus vivanus*	25	15	4	3		148	140	325	23.6	12.7
Vermilion snapper	*Rhomboplites aurorubens*	4	13	1	1		6	152	325	19.7	12.7
Misty grouper	*Hyporthodus mystacinus*	5	1			1		197	269	16.6	15.3
Snowy grouper	*Hyporthodus niveatus*	3		2				255*	322*	15.5*	13.9*
Yellowedge grouper	*Hyporthodus flavolimbatus*	5	7			1		200	285	17	13.8

Minimum and maximum capture/sighting depth and temperatures are given

*Denoting a value from a BRUV deployment and all others being from fishery-independent vertical longlines

Table 3 Distribution of fishery-independent vertical longline sets (% of total sets) by 50 m depth strata for Belize and Honduras across the sampling period

Depth	Belize	Honduras
150–200	10.6	17.1
200–250	26.3	32.0
250–300	38.0	27.1
300–350	16.5	10.6
350–400	5.7	3.9
400–450	1.9	4.9
450–500	0.4	3.1
500–550	0.3	0.5
600–650	0.1	0.5
650–700	0.3	0.3

Table 4 Observations from deepwater BRUVs, describing species MaxN, the sum of MaxN, occurrence (Occ) across all BRUVs, and percent frequency of occurrence (%FO) for all species

Species	MaxN	Sum MaxN	Occ	%FO
Blackfin snapper	1	1	1	2.7
Pristipomoides sp.	6	18	11	29.7
Queen snapper	2	8	7	18.9
Silk snapper	8	18	7	18.9
Vermilion snapper	18	20	2	5.4
Snowy grouper	1	2	2	5.4

BRUVs were deployed in Belize (n = 23) and Honduras (n = 16) (Table 1), between 120 and 500 m depth. Species accumulation curves indicated that 90% of species were sighted after 26 BRUV deployments, indicating that a sufficient number of BRUVs were deployed to describe candidate species occurrence. Five species of snappers and one grouper species were observed, with *Pristipomoides* snappers having the highest occurrence (%FO = 29.7), then queen and silk snappers (%FO = 18.9, each) (Table 3). Vermilion snappers (*Rhomboplites aurorubens*) were only observed on two BRUV deployments, but were in high abundance (MaxN = 18) at one location off of Utila, Honduras (Fig. 1; Table 4). Sightings from BRUVs mostly aligned with vertical longline captures; however, in 16% (n = 6) BRUVs, species were observed that were not captured by concurrently fishing lines. In some BRUV sightings, the fish may have been too small for capture, but in other notable BRUV sightings, large queen snappers and snowy groupers were captured by the camera but not the lines.

Fish abundance and distribution

Following data cleansing (i.e. eliminating soak data outside the 5th–95th percentiles and sets with ineffective hooks), 979 vertical longline sets (83%) were available for CPUE analysis. Snapper and grouper abundance from fishery-independent vertical longlines was more than two times higher in Belize than Honduras for all species combined (CPUE = 0.037 vs. 0.013 fish per hook hour; Table 5). Species-specific CPUE by country was investigated for *Pristipomoides* sp., queen, and silk snappers, as there were sufficient fishery-independent data for comparison (Fig. 4) and median CPUE was higher in Belize for all three species. CPUE was significantly higher in Belize for *Pristipomoides* sp. (Wilcoxon rank sum, W = 110,888; $p < 0.001$) and queen snappers (W = 102,421; $p < 0.001$), but not for silk snappers (W = 97,296; $p > 0.10$); (Fig. 4; Table 5). Misty (*Hyporthodus mystacinus*), snowy (*H. niveatus*), and yellowedge groupers (*H. flavolimbatus*) were captured in Belize, while only the yellowedge and misty groupers were found in Honduras during fishery-independent sampling (Table 2).

Results from GAM standardization of CPUE data indicated that country and temperature were the unifying factors influencing abundance and occurrence for *Pristipomoides*, queen, and silk snappers (Fig. 5; Table 6), with CPUE being higher in Belize than Honduras. Latitude explained 23.1% and 13.2% of the total model deviance for *Pristipomoides* and queen snappers, respectively (Table 6), with generally decreasing CPUE from north to south and from west to east (Fig. 5). Temperature and depth were highly correlated (VIF > 5), and temperature was found to be more suitable in the models than depth for all three species. Although depth was a significant factor in the models, its inclusion both lowered the percent deviance explained by the models and raised the AIC substantially in comparison to temperature. Temperature accounted for 8.6, 7.04, and 14.7% of deviance for *Pristipomoides*, queen, and silk snappers, respectively. The factors hook size and habitat type were only found to be influential for *Pristipomoides* sp. abundance (Fig. 5; Table 6), and explained only 1.5 and 1.7% of model deviance. Hook sizes smaller

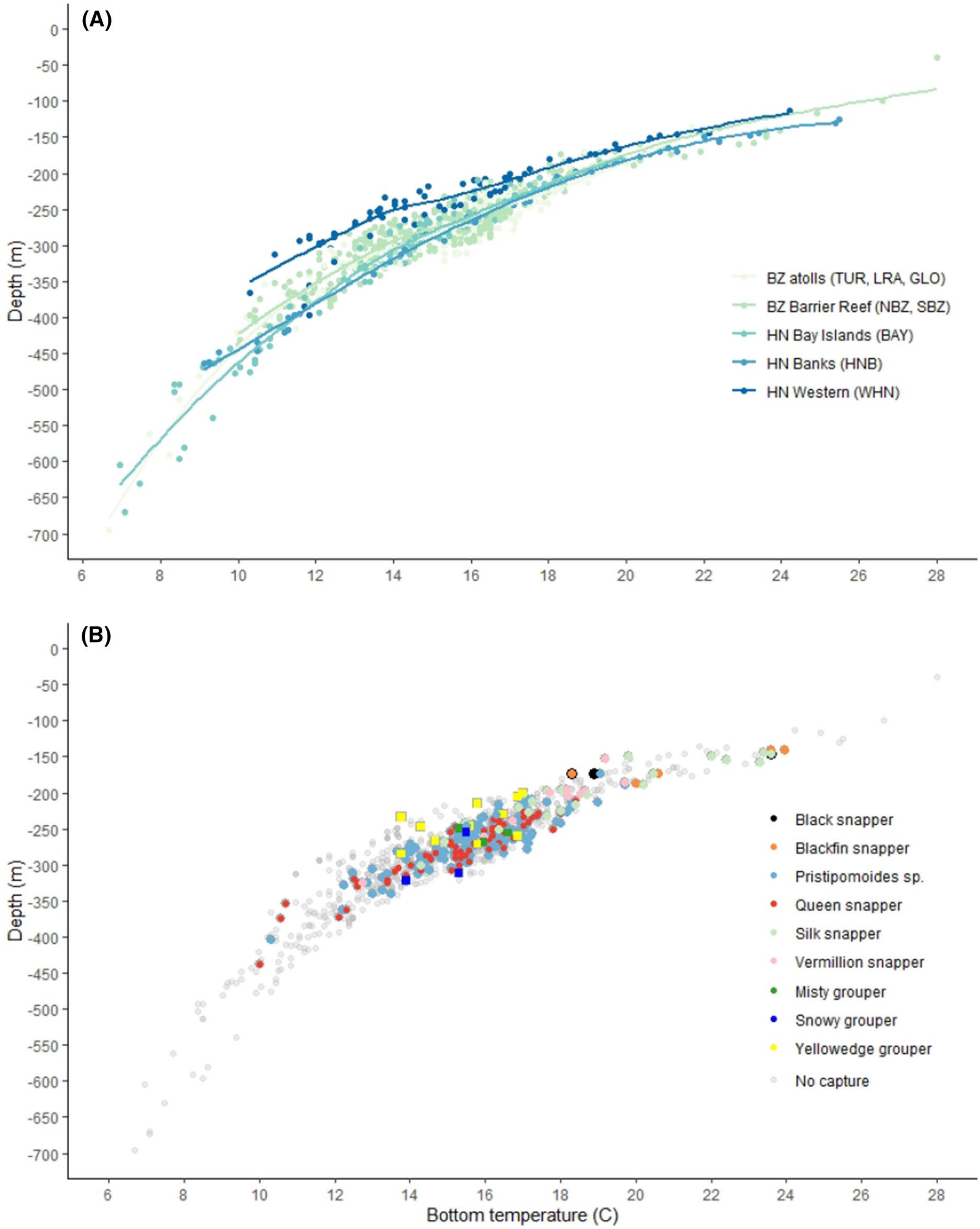

Fig. 3 Seabed temperature **A** for all vertical longline and BRUV deployments color coded by area (LOESS); and **B** with snapper (filled circles) and grouper (filled squares) captures and sightings

Table 5 Mean CPUE (number of fish per hook hour) for the five most abundant snapper and two grouper species captured by scientific vertical longline

Species	Belize	Honduras	Ratio: Belize to Honduras
Pristipomoides sp.	0.134*	0.039	3.39
Queen snapper	0.038*	0.012	3.22
Silk snapper	0.012	0.008	1.43
Misty grouper	0.001	0.002	0.76
Yellowedge grouper	0.001	0.004	0.30
All groupers and snappers	0.037*	0.013	2.85

*Indicates that the difference in CPUE was significantly different ($\alpha < 0.05$, Wilcoxon Rank Sum) between countries

than 13/0 were associated with higher abundance for *Pristipomoides* sp. Bait type was significant for silk snappers, explaining 5.1% of model deviance.

Binomial occurrence models revealed similar results to the abundance models (Table 6), though for *Pristipomoides* sp. hook size was not included in the final model, while country, habitat, longitude, latitude, and temperature were all highly significant. Occurrence of *Pristipomoides* sp. was influenced most by latitude, longitude, and temperature with deviance estimates of 12.5, 6.9, and 7.4% (Table 6). *Pristipomoides* sp. were not captured over hard substrate, but occurrence was fairly evenly distributed among the other habitats of sand, hard sand, mud, and structure (Table 5). Silk snapper occurrence was highly influenced by bottom temperature. GAMs explained between 20.2% and 54.2% of the deviance for CPUE and between 14.7 and 30.2% for occurrence (Table 6).

Fish body length

Combined fishery-independent and –dependent length data (n = 475 records) for fish captured by size 10/0 hooks revealed that mean and median sizes of snappers were larger in Belize than Honduras (Fig. 6; Table 7). Mean *Pristipomoides* snapper TL for fish captured in Belize was 7 cm larger than those captured in Honduras, while queen snappers were 11 cm larger, and silk snappers were 7 cm larger (Table 7). Only mean TL for blackfin snappers was larger for Honduras; however, this was mostly driven by one very large individual (86 cm TL), and the median size was larger in Belize (Fig. 6). Differences in TL were significant between countries for black (Wilcoxon rank sum, W = 73; $p < 0.050$), *Pristipomoides* (W = 6169; $p < 0.001$), queen (W = 895; $p < 0.001$), and silk snappers (W = 2650, $p < 0.001$), but not blackfin snapper (W = 148; $p > 0.100$) (Table 7). Low sample sizes precluded statistical tests among grouper sizes.

Sufficient fishery-independent data to describe the relationship between length and depth were only available for *Pristipomoides* sp., queen, and silk snappers. A linear modeling approach was used based on examination of data (Fig. 7) and model residuals. For *Pristipomoides* snappers, country and depth were significant (Table 8; $p < 0.0001$), while hook size was not influential, and there was a significant increase in size with increasing depth (Table 8; Fig. 7a; $p < 0.0001$). The final model for queen snappers included country and depth: although depth was not significant (Table 8; $p = 0.0853$), body size (TL) generally increased with increasing depth for snappers captured in Belize but not Honduras (Fig. 7b). For silk snappers, there was no significant trend in size with depth (Fig. 7c; $p = 0.1410$). Density plots of capture depth and size distributions indicated that sampling depth distribution was similar between countries for *Pristipomoides* and queen snappers, with clear differences in the distribution of capture length (Fig. 7), indicating that differences in size at depth were not due to sampling bias.

Discussion

Depth is generally considered a robust estimator of the distribution of fish species (Koslow 2000; Zintzen et al. 2017; Wellington et al. 2021), and variables such as temperature and dissolved oxygen are often excluded from deepwater species distribution modeling because they are highly correlated with depth (Parra et al. 2017). Temperature and depth in this study were highly correlated, and therefore included separately and as interaction terms during the model selection process for GAMs describing the abundance and occurrence of three deepwater snapper species. Model outputs for all three species indicated that temperature was a stronger predictor of abundance and occurrence than depth, and that including both

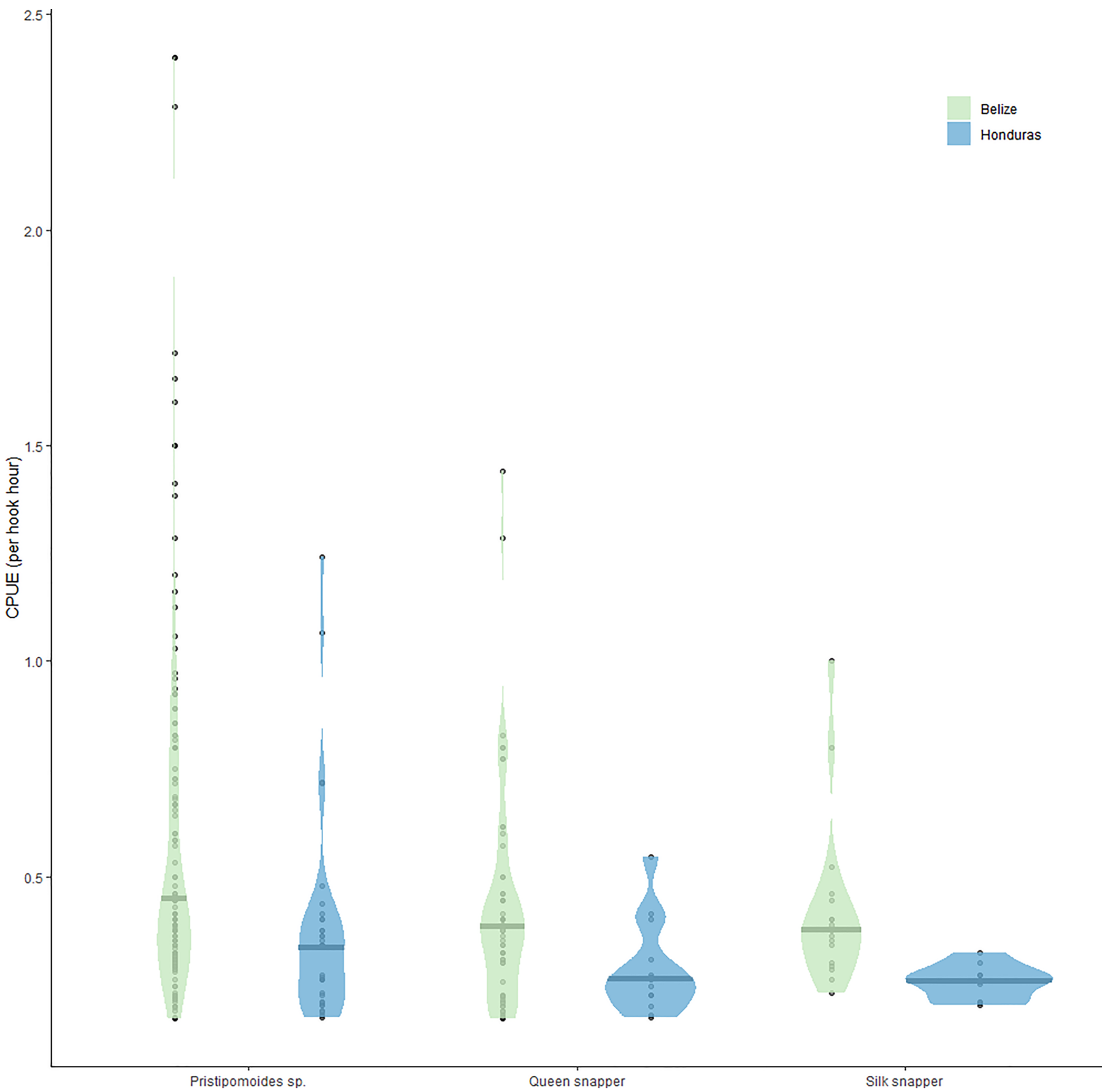

Fig. 4 Distributions of CPUE as violin plots for the three most commonly captured snapper species in Belize (green, left) and Honduras (blue, right), excluding sets with 0 captures. Dark horizontal lines represent median CPUE

variables as interaction terms did not improve model fit. Though a seemingly obvious predictor of poikilotherm fish distribution, studies have largely failed to unravel changes in fish distribution due to temperature shifts from the effects of fishing, growth rates, and ontogeny (Campana et al. 2020). Temperature and depth were less predictive of abundance and size for queen snappers than for *Pristipomoides* sp., which may be a function of morphology and behavior. Queen snappers are streamlined, have small, delicate otoliths, and smaller swim bladders, while *Pristipomoides* sp. are more robust, have large otoliths, and suffer from barotrauma more than the queen snappers. It may be that queen snappers are more migratory, both vertically along the seafloor and horizontally, than the *Pristipomoides* sp. (Paxton 2000; Lombarte and Cruz 2007; Pelster 2015), though these

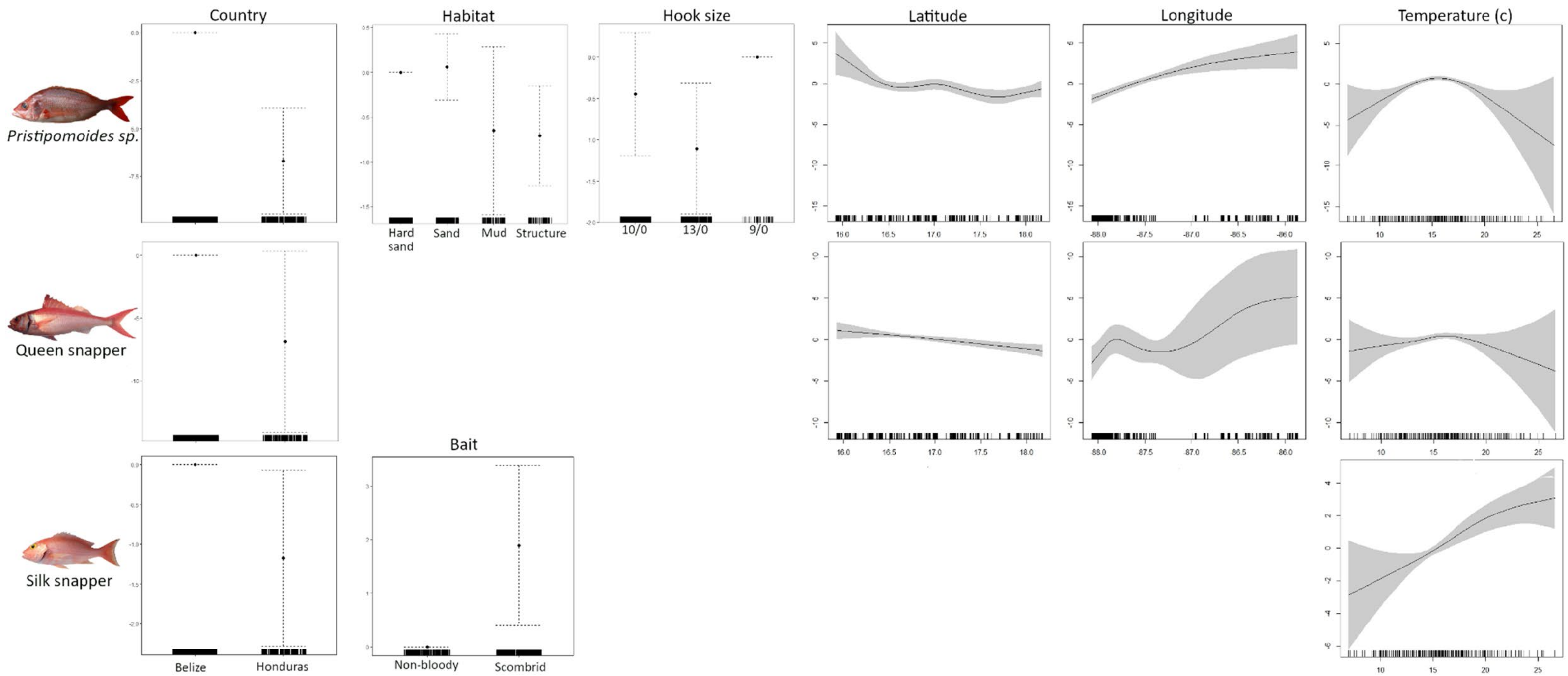

Fig. 5 Statistical modeling of CPUE for three species of deepwater fish. Variables (factor and continuous) selected in Generalized Additive Models (GAMs) for CPUE of *Pristipomoides* sp. (top row), queen (middle row), and silk snappers (bottom row) captured by scientific vertical longline in Belize and Honduras. Point plots with 95% confidence intervals (factor variables: country, habitat, bait, and hook size); Line plots with 95% confidence intervals (grey shaded areas—continuous factors: latitude, longitude and temperature). Data intensity revealed by rug marks on x-axis

Table 6 Summary statistics from generalized additive models (GAMs) for catch per unit effort (CPUE) and occurrence of the three most frequently captured deepwater snapper species by scientific vertical longline

	CPUE				Occurrence				
	Estimate	DF/edf	*p* Value	% dev		Estimate	DF/edf	*p* Value	% dev
Pristipomoides sp.									
Intercept	0.01845		0.9747		Intercept	0.6254		0.2739	
Country (HN)	– 7.66535		0.0000	6.08	Country	– 7.7359		0.0000	2.59
Hook size (10)	– 0.32011		0.3631	1.47					
Hook size (13)	– 0.86703		0.0217						
Habitat (Sand)	0.05934		0.7534	1.67	Habitat (Sand)	2.2721		0.0021	0.81
Habitat (mud)	– 0.65098		0.1749		Habitat (Mud)	2.5597		< 0.0001	
Habitat (structure)	– 0.70956		0.0122		Habitat (Structure)	2.3580		0.0038	
Latitude		4.99	< 0.0001	23.10	Latitude		4.11	0.0008	12.50
Longitude		2.394	< 0.0001	13.30	Longitude		2.68	< 0.0001	6.99
Temperature		3.565	< 0.0001	8.62	Temperature		3.52	0.0001	7.37
				54.24					**30.26**
Queen snapper									
Intercept	– 2.3655		0.0045		Intercept	– 1.2273		0.1510	
Country (HN)	– 6.464		0.0710	4.09	Country	– 6.0002		0.1040	1.57
Latitude		1.249	0.0003	13.20	Latitude		1.05	0.0097	6.10
Longitude		4.577	0.0000	10.80	Longitude		4.49	0.0001	5.01
Temperature		2.461	0.2271	7.04	Temperature		1.87	0.0574	4.34
				35.13					**17.02**
Silk snapper									
Intercept	– 6.0478		< 0.0001		Intercept	-4.08		< 0.0001	
Country (HN)	– 1.174		0.0374	0.38					
Bait (Scombrid)	1.888		0.0133	5.13					
Temperature		1.6650	< 0.0001	14.70	Temperature		1.687	< 0.0001	14.70
				20.21					**14.70**

DF degrees of freedom, *edf* effective degrees of freedom

*Indicates significant *p* values ($\alpha < 0.05$), % dev is the percent of deviance explained by each factor, and bold values represent the total % dev of each model

are suppositions that need to be tested using genetic analyses and telemetry where possible.

Deepwater snappers were widely distributed throughout the available habitat in Belize and Honduras; however, fish were more abundant and larger in Belize than in Honduras. Groupers were more widely-distributed in Belize, but rarely encountered in most of the sampled areas of Honduras. Differences in mean sizes were especially striking for the queen snappers, which were 11.0 cm larger in Belize and for the *Pristipomoides* sp. snappers, which were 6.7 cm larger in Belize than Honduras. Higher exploitation in Honduras (Canty et al. 2019; Baremore et al. 2021) appears to have affected the depth distribution of some snappers as well, with *Pristipomoides* sp. and queen snappers being smaller at depth in Honduras, and more rarely encountered at depths deeper than 300 m. Much of the nearshore deepwater fishing grounds of the Bay Islands in Honduras (Fig. 1) have undergone a long history of fishing effort, but stretches of the bank that forms between the Bay Islands and the mainland may still host healthier stocks due to the remoteness and lack of shelter from wind and currents. In 2021, a fisher captured an 86 cm TL blackfin snapper just north of the Cayos Cochinos, which is larger than the reported maximum size of 75 cm (Lieske and Meyers 1994). Additionally, the river-influenced and colder waters in western

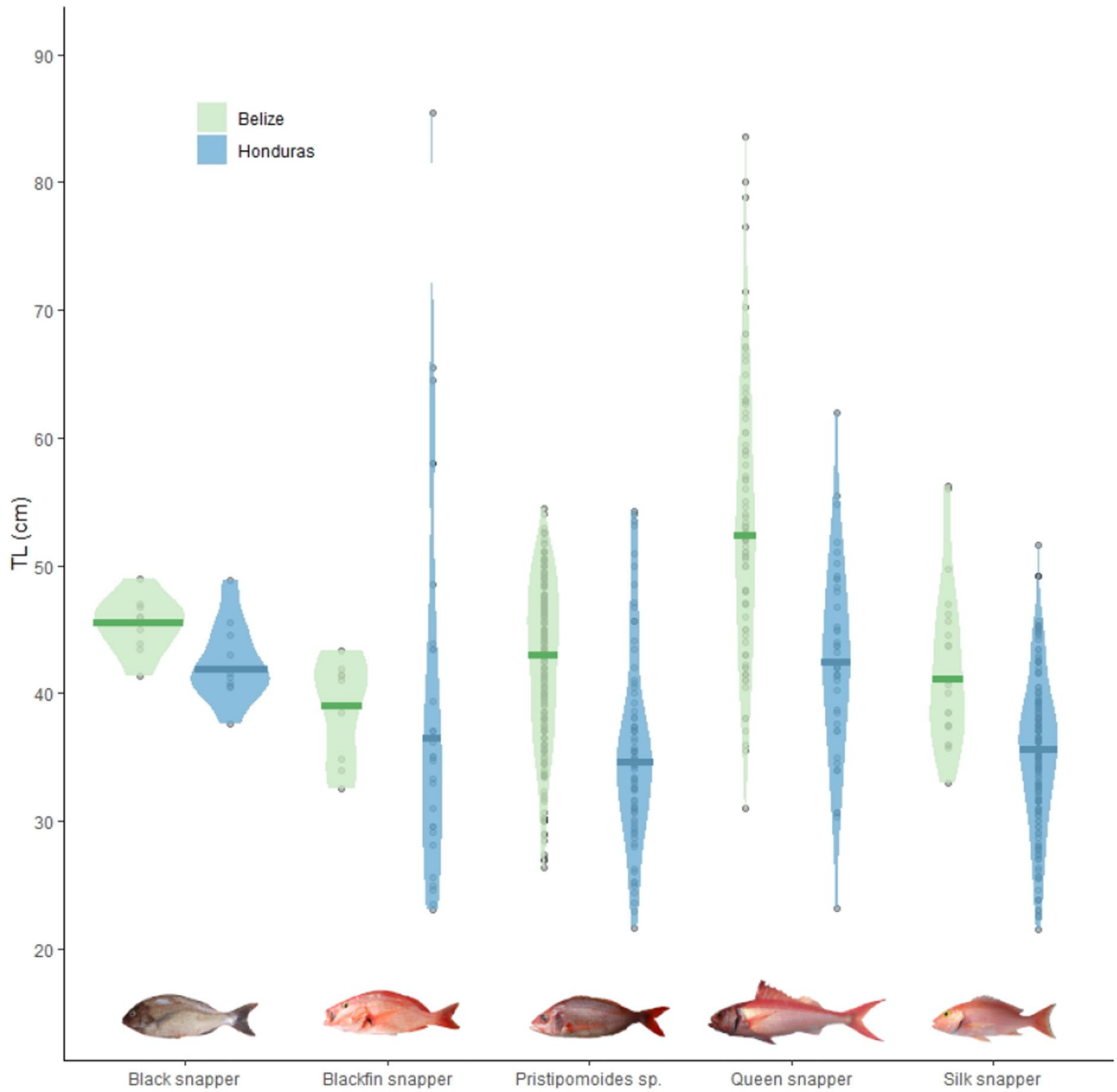

Fig. 6 Distribution of total lengths (TL) as violin plots of five snapper species from fishery-independent and -dependent samples for hook size 10/0, combined from Belize (green, left) and Honduras (blue, right). Dark horizontal bars represent the median TL.

Honduras supported a seemingly high number of yellowedge groupers. Strong currents and river debris make the area difficult to fish year-round, which may offer some natural protections to the groupers. Some of the habitat is within the Blanca Jeannette Kawas National Park, with seasonal closures for spawning finfish and shellfish. Areas closed to fishing, whether by natural features such as inaccessible seas, or through active conservation measures, are important to protect against the loss of spawning biomass potential of the largest individuals.

Deepwater BRUV systems provided complementary data to the vertical longline surveys, and in some cases additional species records that were not revealed by nearby sampling lines. BRUV data also allowed for examination of the seabed habitat and observations of unusual behaviors, such as interactions between grouper and snapper species.

Table 7 Mean size (TL) of deepwater snapper and grouper species from combined fishery-independent and -dependent sources in Belize and Honduras, and the difference in mean size

Species	Belize	SD	N	Honduras	SD	N	Difference
Black snapper	45.4	2.3	8	42.4	3.2	10	3.0*
Blackfin snapper	38.8	4.0	9	39.3	15.0	25	− 0.5
Pristipomoides sp.	42.4	6.3	123	35.7	7.6	67	6.7*
Queen snapper	53.5	10.8	65	42.5	7.8	33	11.0*
Silk snapper	42.1	6.4	18	35.3	6.0	103	6.8*
Misty grouper	99.8	27.5	4	86.5		1	13.3
Snowy grouper	96.5		1				
Yellowedge grouper	101.7	16.6	3	93.3	13.0	5	8.3

*Indicates significant differences between countries

Unfortunately, the strengths of the BRUV, including its lightweight frame and ease of deployment were also its weaknesses. BRUVs could not be deployed during all sampling days due to unfavorable conditions at the sea surface, and only 20 (66%) deployments met the desired minimum hour soak due to the frame being dragged or upturned by surface currents. As such, this design may not be ideal for estimates of abundance; however, for deployments where snappers and groupers were recorded, all species were sighted within 10 min of making contact with the seabed, and species accumulation curves revealed that 90% of species were recorded after 26 deployments. As such, estimates of occurrence, even for short deployments, were likely robust for the snapper and grouper species. Use of a lighter surface float or floating braided line could help to reduce drag on the frame and should be investigated. Future work with BRUVs will include more deployments, the addition of a hydrophone to detect spawning activity which could have an acoustic signature, as well as improving the spread and homogeneity of the lighting.

The shallower-dwelling, but widely-distributed species such as blackfin and silk snappers were somewhat under-sampled by the fishery-independent vertical longline survey, as the gear did not sample particularly well in the shallowest depths due to depredation and entangling with bottom structure. To address this possible bias, estimates of abundance were limited to fishery-independent sets with no depredation/loss of hooks, and the shortest and longest sets were removed from analyses. We found that overall, estimates of CPUE were higher for all species, but sample sizes were only sufficient for standardization of CPUE indices for three deeper-dwelling species. Commercial fishers generally use shorter soak times at shallower depths, often only setting the line until the fish take the hook and then hauling immediately. As we used a minimum 30 min soak time, one or more hooks set at depths less than 150 m were occasionally lost to sharks or barracuda, or the gear became hooked on the seabed. A more robust estimate of abundance for these species would likely mimic the commercial fishers' methods more closely, though CPUE would not be directly comparable to this study. Other species that were undersampled included black and vermilion snappers, but this was more likely due to patchy distribution rather than sampling bias. Black snappers prefer rocky seabed habitats, while vermilion snappers are often found in schools (Allen 1985). Continued work with BRUVs in the area will delineate these habitat and species distributions.

Three species in the genus *Pristipomoides* co-occur in the western north Atlantic Ocean, and are all found in deeper waters, but wenchman and cardinal snappers are the most similar in appearance. Current distributional maps for cardinal snappers do not include Belize or Honduras, and the maximum size is reported to be only 50 cm (Allen 1985; Robertson and Van Tassell 2019). The most robust method of identification appears to be enumeration of lateral line scales: wenchman possess between 48 and 52, while cardinal snappers have 54–57 lateral line scales (Robertson and Van Tassell 2019). All *Pristipomoides* species in this study were presumed to be cardinal snappers, and all examined fresh or via high resolution photos had lateral line scale counts ≥ 54. Wenchman are likely smaller in maximum size and have a shallower depth distribution than cardinal snappers, but confusion in species identification is a persistent problem facing fisheries managers.

While entry into the deepwater fishery remains prohibitively expensive and time-consuming for commercial fishers in Belize ($1000 USD for gear, $150

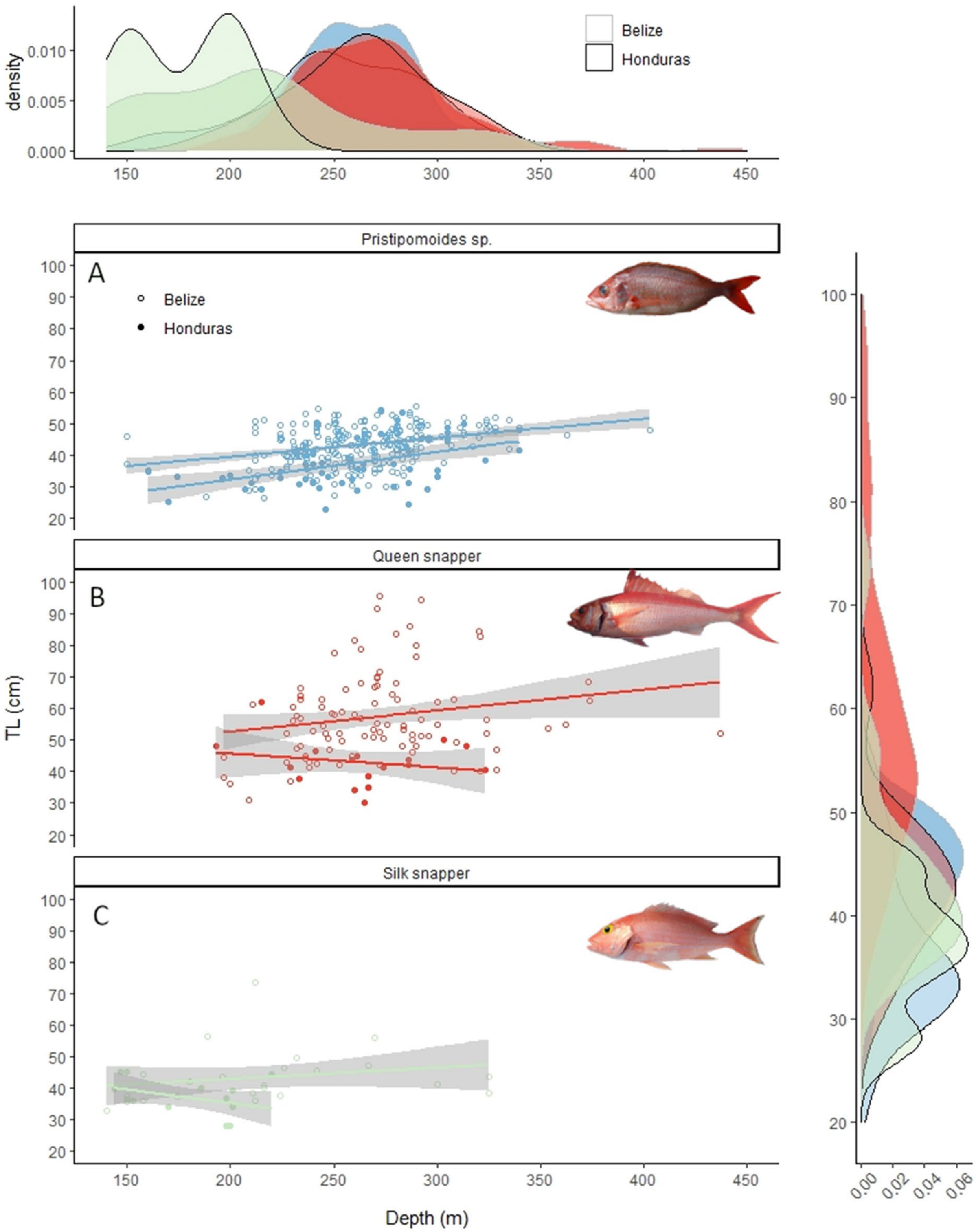

Fig. 7 Length-at-capture depth for **A** *Pristipomoides* sp.; **B** queen; and **C** silk snappers captured by fishery-independent methods with lines representing trends of GLMs by country and standard error shaded. Density plots describe the distribution of depths at capture (top) and sizes (right) by species and country

Table 8 Summary statistics from generalized linear models (GLM) for *Pristipomoides* sp. and queen snappers fitted to length (TL) data. *Indicates significant p values ($\alpha < 0.05$)

	Estimate	Std. Error	p Value
Pristipomoides sp.			
Intercept	25.8646	2.6152	< 2e–16*
Country (HN)	− 5.7956	0.8575	< 0.0001*
Depth	0.0661	0.0098	< 0.0001*
Queen snapper			
Intercept	42.8808	8.46649	< 0.0001*
Country (HN)	− 14.2058	3.32814	< 0.0001*
Depth	0.05385	0.03101	0.0853

in fuel per trip), many fishers in the recreational sector have more disposable income and relatively easier access to the offshore fishing grounds with higher powered engines (Baremore et al. 2021). Armed with electric reels and cell phone apps that mark offshore banks that can only be reliably found with higher end depth sounders, recreational fishers and tour guides are increasingly landing large groupers and deepwater snappers where they were previously unattainable (R. Edwards per comm). Recreational fishers and tour guides can also take advantage of the unrestricted entry to the deeper waters (Zone 9) of the Managed Access program, and many have commercialized their catches by selling directly to restaurants or markets. Commercial deepwater fishers in Belize generally participate in the fishery during the closed season for lobster in the first half of the year (Baremore et al. 2021), while recreational fishers can take advantage of smoother seas in the latter half of the year. The Government of Belize remains committed to developing the commercial deepwater fishery, and funded ice boxes and gear for fishers in 2018 (Grant 2019); however, high and rising fuel costs and lack of robust supply chains have hampered efforts.

Stakeholder meetings with commercial and recreational fishers as well as managers in Belize and Honduras were held in 2021 and 2022, where preliminary results from this study were presented. Attendees at these meetings expressed surprise at the longevity of the grouper species, but fishers thought that the main conclusions—the fish are bigger and more abundant in Belize—were reasonable. Many commercial deepwater fishers primarily target silk snappers due to their wide-spread and relatively shallow distribution, while recreational fishers were more likely to seek out larger trophy fish such as large groupers and queen snappers. Some fishers in Belize noted that the deepwater snappers at Turneffe Atoll, which is the closest to the population center of Belize City, were becoming less plentiful over the last five years, while fishers in Honduras said that they had to go further to find good fishing grounds than in the past 20–30 years. Fishers seemed amenable to ideas such as time area closures, though the recreational sector was more receptive to measures to protect the large groupers. Transboundary fishing remained a top concern for fishers from both countries.

Deepwater snappers and groupers are commercially important species in several fisheries around the world (Pollack and Ingram 2008; Sadovy de Mitcheson et al. 2013; Newman et al. 2016; Sanchez et al. 2019). Eteline snappers (including the *Etelis* and *Pristipomoides* genera) are especially economically valuable in Pacific and Indo-Pacific fisheries (Misa et al. 2013; DeMartini 2016; Oyafuso et al. 2017; Uehara et al. 2020). Many of the deepwater fisheries are small-scale and most are data limited with few species-specific studies (Newman et al. 2016). Where studies have been conducted, underestimation of longevity and maximum size of exploited stocks of deepwater fishes is common, which has led to incorrect stock assessment estimates (Cook et al. 2009; Andrews et al. 2013; Newman et al. 2016; Andrews and Scofield 2021).

Very little is known about the life history of the snapper species captured by the deepwater fisheries of the MAR, but the grouper species are especially long-lived. Yellowedge groupers can reach more than 80 years of age (Cook et al. 2009), snowy groupers have a minimum longevity of 56 years (Sanchez et al. 2019), and misty groupers may live for more than 100 years (Luckhurst and Dean 2009). Of the snapper species, only the blackfin snapper has been reliably aged, with the oldest individual at 27 years of age (SEDAR 2011; Burton et al. 2016). Congeners of the Eteline and Pristipomoides snappers in the Pacific have life spans of 40 or more years (Andrews and Scofield 2021; Scherrer et al. 2021). Research on the life history and ecology of the Caribbean deepwater species, notably spawning seasonality and spawning aggregations, is needed to assess their vulnerability to overexploitation at current and projected fishing mortality. Combined with data on the fishery characteristics, these data will be used to develop an ecological risk assessment of the fishery.

This study provided baseline information on the spatial distribution of commercially important deepwater snapper and grouper species in the MesoAmerican countries of Belize and Honduras. Results indicated that higher fishing effort in Honduras (Canty et al. 2019; Grant 2019; Baremore et al. 2021) has led to lower abundance and smaller mean sizes of fish, and grouper species were especially rare in the Bay Islands. This manuscript offers a potential vision of the future of the deepwater fisheries in Belize if fishing effort continues to increase on its current unregulated trajectory. While Honduras has extensive deepwater fishing grounds in the remote eastern EEZ that are accessible by semi-industrial fishing boats, Belize's deepwater fishing grounds are narrow and unlikely to support large-scale fishing effort, similar to the collapsed deepwater fishery in Bermuda (Luckhurst and Ward 1996). Measures such as time area closures or gear restrictions should be considered by managers in both countries to conserve this increasingly important fishery.

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Author contributions The project was conceived by RG and all authors contributed to the study design. Data collection was primarily conducted by IB, and data analysis was undertaken by MW and IB. SO designed and built the deepwater BRUV, and video footage was analyzed by IB and SO. The first draft of the manuscript was written by IB and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare they have no conflicts of interest.

Consent for publication All the authors agree with the contents of the manuscript and give their consent to submit. This work represents original research, and all authors consent to publication of this paper.

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