Characterization of Prey Diversity of the Commercially-Important Queen Snapper (Cartucho), *Etelis oculatus*

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Executive Summary

The queen snapper (Cartucho-*Etelis oculatus*) fishery is becoming an increasingly important fishery in Puerto Rico and wider Caribbean region. In Puerto Rico queen snappers' commercial landings reached 135 tons in 2007, valuing around $770,000 (Matos Carabello 2012). Even though the queen snapper is a vital component essential to Puerto Rico's commercial fishing industry (CMFC 2016), not much is unknown about this species' general biology and ecology (life history, habitat preferences, prey, etc.). The lack of available information has made it challenging to manage this species. This project's main goal was to summarize the population of queen snapper off the west coast of Puerto Rico, and characterize the diversity in preys between sexes, size and locations.

A total of 157 queen snappers were collected from November 2019 to July 2020 at seven different locations, ranging in depths from 256 m at Bajo Medio to 402 m at Site 3. The size and weight of queen snappers collected during this study significantly varied between sampling time and location (PERMANOVA, $p<0.0001$). However, from the estimates of the components of variation, sampling time had a more of an influence on the size and weight of fish than the location.

The mean (±SE) standard, fork and the total length of queen snappers during the sampling period was 442.73 ± 11.53 mm, 472.06 ± 11.90 mm, 595.34 ± 15.24 mm, respectively. Smaller fish were caught at Site 4 and Site 3, while larger fish were caught at Site 6 and South of Pichincho. On average, fishers caught the largest fish in July and the smallest fish in November. The mean (±SE) weight of the queen snapper during this project was 1,948.39 ± 144.22 g, ranging from 195 g to 10,568 g. The mean fish weight was the lowest during January, followed by November. The highest weights were observed during July. There was a strong positive relationship between the

fork length and weight (Regression, R=0.99, p<0.0001). The power parameter calculated for this study was 2.80, confirming that the queen snapper exhibits isometric growth.

There was significant spatial and temporal variability in Gonadosomatic Index (GSI) values during the study (PERMANOVA, p<0.0001). Queen snappers are known to spawn during between October and November. However, in this study, July collections exhibited the highest GSI values between the west coast sites. Therefore, queen snappers might spawn during late summer. However, more samples should be collected during July and August to confirm this observation.

Our study of the prey composition suggests that *E. oculatus* is a large carnivore that mainly feeds on squids, shrimps, and deep-water fishes. Our approach identified *Diaphus brachycephalus, Diaphus dumerilii, Myctophum selenops, Coccorella atlantica, Sigmops elongatus* and *Bonapartia pedaliota* as the most common fish preys and *Abralia veranyi*, *Doryteuthis pealeii, Abalia redfieldi* (all three squids) and *Oplophorus gracilirostris* and *Systellaspis debilis* (both shrimps) as the main invertebrate preys. Given the unbalanced design of the sampling, our data was inconclusive of whether the variation in diet composition varies across locations. However, we did observe higher prey diversity at Pichincho seamount, which could be related to high structural complexity of the karst terrain of the seafloor. We did observe variation in species composition of preys across size classes. *B. pedaliota*, *S. elongatus* and *H. benoiti* were more common in the stomach contents of larger queen snappers, while *D. brachycephalus*, *Myctophum nitidulum*, *D. dumerilii*, *Elagatis bipinnulata*, and *Lepidophanes guentheri* more common in smaller queen snappers.

A major aspect of this study is our approach. Unlike previous cases with analysis of fish gut contents, most of the fish prey we found were identified to the species level and even some of the most common invertebrate species were also identified to the species level. This high resolution

in the identification of prey items in deep-water snappers is atypical and represents a viable alternative to continue learning about the biology of these species of commercial value. This study provides baseline information and is part of a larger project funded by the Caribbean Fisheries Management Council to examine the food web of the queen snapper. More samples are needed to determine the size structure of queen snapper not only along the west coast but in other areas like the north and east coast.

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Introduction

Commercial fisheries support many US Caribbean people's livelihoods, as they are a vital source of employment and sustenance. Like many other Caribbean countries, the commercial fishing in Puerto Rico and the US Virgin Islands are artisanal, and occurs mostly on the insular shelf with the use of small boats. The catch consists primarily of shellfish (lobster), conch and finfish, with snappers and groupers being the most important finfish landed by weight. From 2007 to 2011, queen and silk snapper were the most landed species (Matos-Caraballo 2012). Many snappers are caught by recreational and commercial fishers on the west and east coast in deep waters (>200m). The two main fish species found within these depth ranges are the silk (*Lutjanus vivanus*) and queen snapper (*Etelis oculatus*).

Over the years, silk snappers were the primary targets for deep-water fisheries. However, in Puerto Rico queen snapper landings and revenues have increased through time. The decrease in silk snapper revenues could be due to changes in the way fisherman fish these species, from traps to vertical longlines, and management initiatives, with seasonal closures (October to December) and annual catch limits. The queen snapper fishery is becoming an increasingly important fishery. Matos-Carabello (2012) reported queen snappers' commercial landings to reach 135 tons in 2007, valuing around $770,000. Queen snapper represents about 10% of the entire finfish annual catch (CFMC 2010). Even though the queen snapper is a vital component essential to Puerto Rico's commercial fishing industry (CMFC 2016), not much is unknown about this species' biology and ecology (life history, habitat preferences, prey, etc.). The lack of available information has made it challenging to manage this species.

Queen snappers are members of the family, Lutjanidae, one of the largest fish family in the Caribbean. The distribution of the queen snapper is extensive in the western Atlantic Ocean, from

North Carolina to eastern Brazil, and is also found in the Gulf of Mexico. The queen snapper is the deepest dwelling snapper species, contributing to the lack of information collected about this species. The depth range of queen snapper was previously reported to range from 130 to 450 m (Allen 1985). In the most recent NOAA Okeanos Expedition in 2018, scientists observed the queen snapper as deep as 539m, possibly breaking a new record depth for this species. However, in Gobert et al. (2005), a fisherman in Guadeloupe reported catching queen snappers in depths from 100 to 550 m.

Like the silk snappers (Boardman and Weiler 1980, SAFE report 2005), it has been assumed that queen snappers also display a depth and ontogenetic relationship, where recruits and juveniles are found at shallower depths and adults move to the deeper habitats. Individuals smaller than 45- 50 cm were caught by fishermen close to the shore or at the shelf edge in Roatán, Honduras (Gobert et al. 2005). Juveniles have been sighted close to the shelf in less than 30 m (Appledoorn et al. 1987), and observed at mesophotic depths (59m) of the southeastern United States (Cuellar et al. 1996).

Observing recruits and juveniles of the queen snapper in the wild has been a problematic task. Thus, estimations of the queen snapper's life cycle have occurred by calculating the gonadosomal index (GSI). In Puerto Rico, queen snappers spawn throughout the year. However, Rosario et al. (2006) estimated the peak spawning times during October and November. At Vieux Fort in St. Lucia, Lesser Antilles, two recruitment peaks per year were observed for the queen snapper, one in March and one in August (Murray et al. 1989). However, Gobert et al. (2005) reported queen snappers spawning at the end of the year in the Lesser Antilles. In the same study, Gobert et al. observed the maturation size varied between sexes. Age maturity was 23 cm in females and 31 cm in males (Rosario et al. 2006). While Gobert et al. (2005) found that the smallest

fish with developing gonads was 39 cm and 29 cm for females and males, respectively. The size structure of a population of queen snapper is dependent on the sex. Female snappers, in general, tend to grow bigger and faster (Claro and Garcia-Arteaga 2001). Females have been recorded to reach 90 cm in fork length in Guadeloupe, and for the total length between 94 cm in St. Lucia (Murrary 1989) and 100 cm in Venezuela (Cervigon 1991).

In Puerto Rico, the fishers catch queen snappers with weighted vertical longlines. Many times, this fishing gear is lost in crevices or entangled in deep-sea corals and sponges. Lost fishing gear was observed frequently during the Okeanos Expedition (Wagner et al. 2018), specifically at areas of high structural relief (SM Williams pers comm). High relief submerged reefs, like the Mona Passage and Desecheo Ridge, are targeted by fishers because they are the main habitats of the queen snappers (Tonioli and Agar 2011). Garcia Sais et al. (2018) AUV study, which characterized the habitat and benthic composition of targeted queen snapper sites, found the density and relative composition of sessile-benthic organisms to be highly varied along the west coast of Puerto Rico. Submerged areas with substrate discontinuities and high topographic relief were hotspots of biological diversity and locations of increased abundance of queen snappers (Garcia Sais et al. 2018, Wagner et al. 2018). The percent of cover by hard, soft and black corals in the Mona Passage was high, close to 43% on hard substrate. This value is greater than the percent live coral on shallow-water coral reefs around Puerto Rico. Like the shallow-water counterparts, high topographic relief areas correlated to enhanced benthic productivity, microhabitat availability, and ecosystem biodiversity. Additional factors such as availability of hard bottom, depth, slope, and distance from shore may also be regulating sessile-benthic community structure and possibly the distribution of queen snappers.

Most of the research on queen snapper has occurred along the west coast of Puerto Rico and has focused on describing the benthic habitat at targeted snapper fishing sites (Garcia Sais et al. 2015, 2018). However, the queen snapper distribution around Puerto Rico is extensive (Wagner et al. 2018) (Fig. 1). Queen snappers were observed at six of the 19 sites during the Okeanos Expedition –which covered the entire island of Puerto Rico. Most of the sites with queen snapper observations were along the west coast. However, queen snappers were also observed in Ponce and south of St. Croix, US Virgin Islands. Also, as observed from landing data (Carballo-Matos 2012), queen snapper was landed all around Puerto Rico, with the east having the second-highest landings in 2010 (9,942 lbs.), followed by the north (5,215 lbs.) and south (4,589 lbs.).

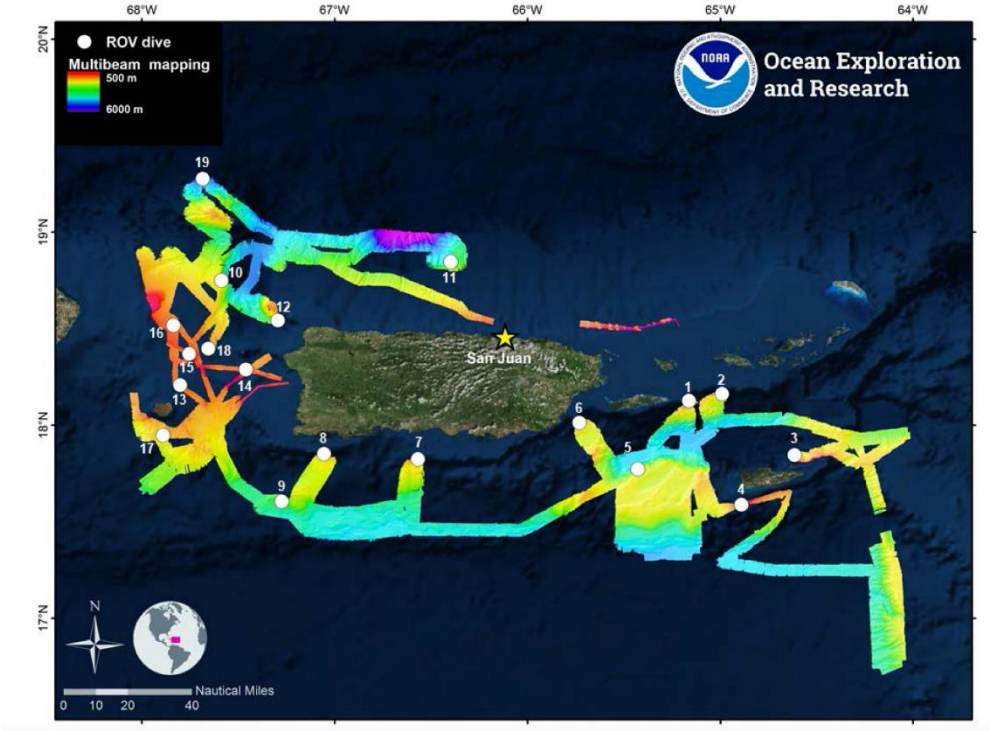

Figure 1 Map showing the ROV dives from the Okeanos Expedition in 2018 (Wagner et al. 2018). Queen snappers were observed at Sites 4, 7, 13, 14, 15 and 16.

This study provides the first attempt to characterize the diet of the queen snappers, *Etelis oculatus*. We characterized and quantified the diversity in preys between sexes, size and locations of the queen snappers. In addition, we summarized the demographic information of the queen snappers collected and analyzed. Given the commercial importance of queen snapper and the lack of available information on this species, this study is essential. It provides baseline information and is part of a larger project funded by the Caribbean Fisheries Management Council to examine the food web of the queen snapper. We have provided some preliminary recommendations on the management of this species.

Methods

Processing fish samples

Commercial fishers of the west coast including, Nelson Crespo and Luis Roman, were contracted to collect queen snappers at known fishing grounds during November 2019, January-February, April and July 2020. The name, geographical location and depth of the site or area were recorded most of the time by the fishers. Given that this species is in high demand, the exact geographical location was not given for some sites because of the sensitivity of the fishing area. Therefore, the name of the coral reef system was reported. Figure 2 gives a general area of where the fish were collected. Once landed, queen snapper samples were stored in coolers full of ice until processed.

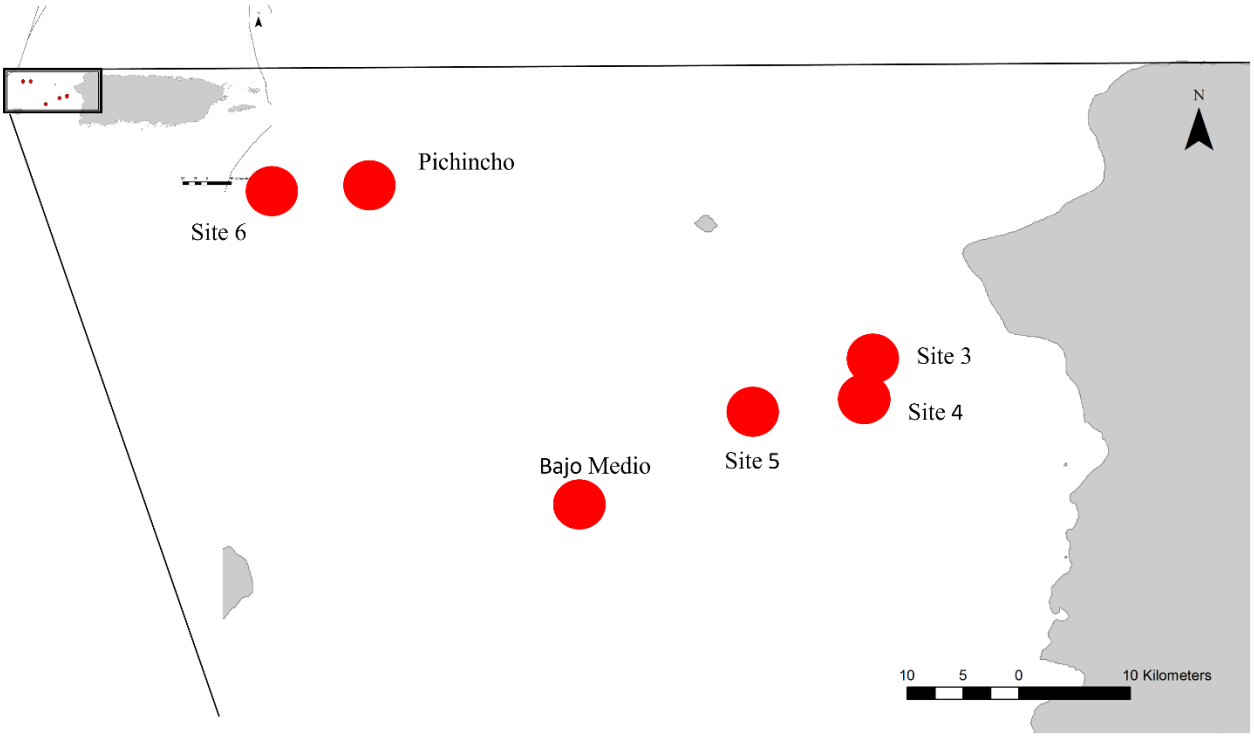

Figure 2 Map of the locations where queen snapper samples were collected during the study along the west coast of Puerto Rico. Coordinates were not available for South of Pichincho site.

Queen snapper samples (Fig. 3a) were identified by a code and were photographed next to a ruler (Fig. 3b). Fish were weighed to the nearest gram, except for fish caught at South of Pichinchos. Total, fork, and standard length were recorded for each fish with a ruler. A small piece (3 cm) of tissue sample was collected and preserved in DMSO to preserve the DNA. Stomachs and any remaining prey items in the mouth were removed and placed in a sterile Whirl-pack bag. Gonads were removed, weighed with a digital scale, photographed (Fig. 3c) and placed in a zip lock bag. Graciela Garcia-Moliner and Noemi Peña Alvarado identified the sex of most of the gonad samples via the photographs. Otoliths were removed, rinsed and dried. Once dried, the otoliths were placed in a plastic vial. Eyes were removed with a knife, and the left eye was wrapped in tin foil. Eyes were placed in a zip-lock bag. Knives, tweezers and processing tables were cleaned with a 10% bleach solution before and after the collection of stomach and tissue samples. Gloves

were replaced after each sample to avoid cross contamination of the samples. All samples were labeled and stored in a freezer with a temperature of -20°C, except the otoliths. Gonads, eyes and otoliths were sent to Dr. Virginia Shervette at the University of South Carolina Aiken. Stomachs and tissue samples were sent to Dr. Carlos Prada and Dr. Diana Beltran at the University of Rhode Island.

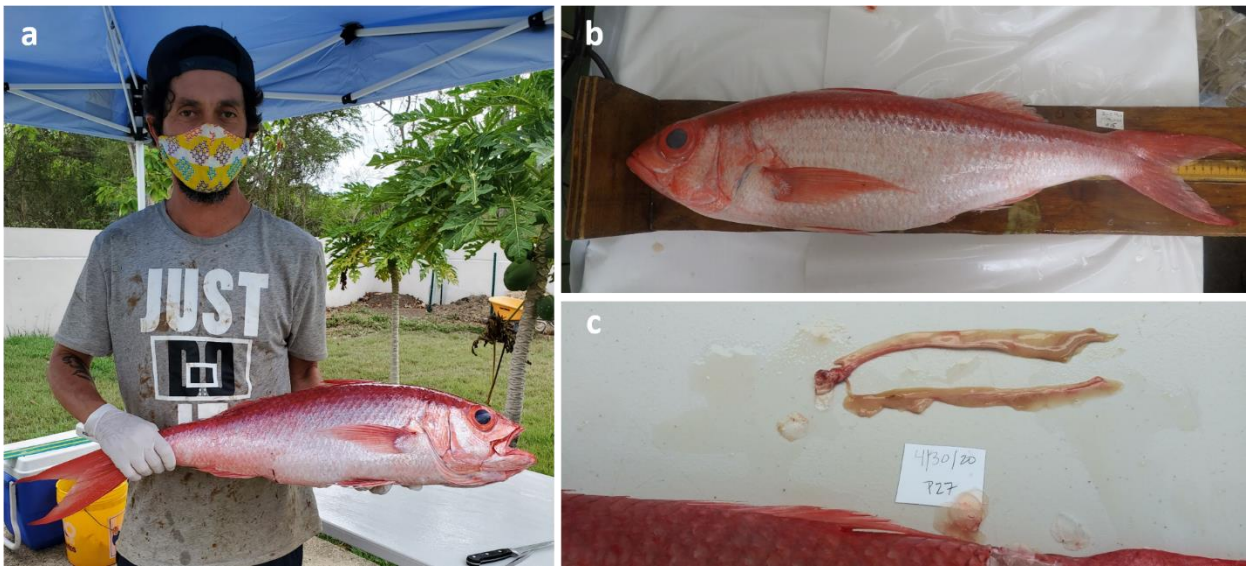

Figure 3 Photographs of (a) a queen snapper sample, (b) queen snapper length measurement and (c) gonads collected during the study.

Stomach analysis

To initially identify the prey items present in *E. oculatus*, the undigested items of individuals were collected from each of the stomachs (Fig. 4). Items were placed in individual labelled tubes, and stored at -80 °C. To genotype each prey, we extracted genomic DNA from the muscle tissue of each prey following the QIAGEN DNeasy Kit protocol. We used a Bio-Rad 4000 thermal cycler for PCR amplifications with varying cycling conditions depending on the marker. A detailed description of primers sequence is provided in Table 1. We followed standard PCR

conditions with 35 amplification cycles and annealing temperature of 54°C and 52°C for TELEO2 and COI, respectively. Preys were genotyped for the mitochondrial protein coding gene cytochrome oxidase I (COI), using two primers sets one for fish (Baldwin *et al.* 2009) and one for invertebrates (Folmer et al. 1994). A cycle-sequencing reactions were produced in both directions to add fluorescent labels and analyzed them on an ABI 3130xl using the amplification primers. Sequences for each gene were assembled, edited, and aligned using Geneious R8 8.1.4 (Kearse *et al.* 2012). To identify species, we manually blast each COI sequence on the NCBI website using the blastx algorithm.

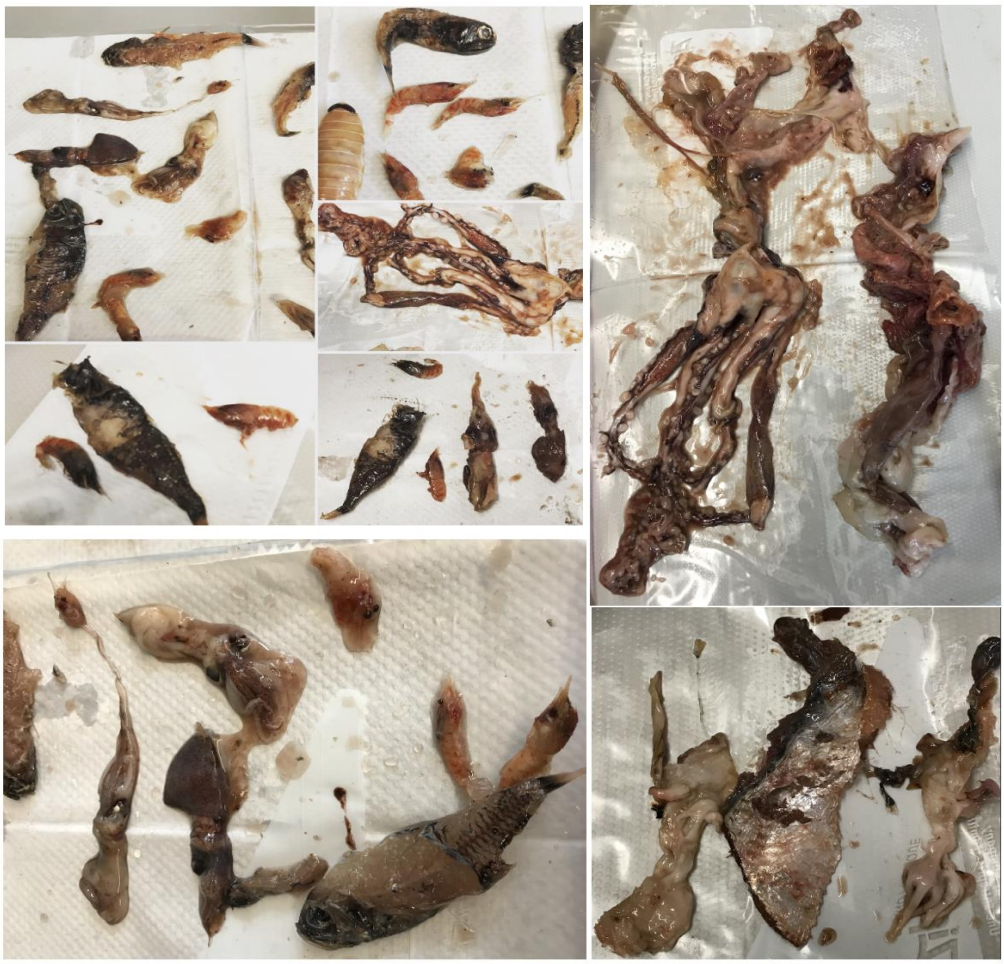

Figure 4. Prey items collected from stomachs of Etelis oculatus samples.

To better characterize the prey diversity in *E. oculatus*, we used a second approach with the metabarcoding protocol, largely following the latest standardized protocols and reducing confounding variables. For each collected fish, we recovered the digested content in the stomach and intestines, likely containing undigested preys. For each liquid sample, we extracted the DNA using a Macherely Nagil eDNA extraction kit. We then generated amplicons (three per sample) using specific primers, combined each replicate, sequence the amplicons in an Illumina MiSeq and then computationally identified species (Deiner et al. 2017; Fig. 4). Since only markers for vertebrates reliably allow species level resolution, we used the mitochondrial 12S gene with the TELEO2 primers (Tarbelet et al., 2018). Along with the samples, we run PCR negative controls to test for the presence of contamination or PCR artifacts.

Table 1 Cytochrome oxidase I and Tele02 primer sequences.

Marker	Primer Name	Primer Sequence	Reference
COI	FISHCOILBC	5'-TCAACYAATCAYAAAGATATYGGCAC-3'	Baldwin et al. 2008
	FISHCOIHBC	5'-ACTTCYGGGTGRCCRAARAATCA-3'	Baldwin et al. 2008
	LCO1490	5'-GGTCAACAAATCATAAAGATATTGG-3'	Folmer et al. 1994
	HC02198	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	Folmer et al. 1994
12S	tele02-F	5'-AAACTCGTGCCAGCCACC-3'	Taberlet et al, 2018
	tele02-R	5'-GGGTATCTAATCCCAGTTTG-3'	Taberlet et al, 2018

Statistics

Demographic analyses

Given the unbalanced nature of the data, four one-way distance Permutational Multivariate Analyses of Variance (PERMANOVA) tests (Anderson 2001) were performed to examine the

difference of the fork length between sample sites and time. We ran the same analyses to test for variation in weight across locations and sexes. Since the fork length is a univariate measure, the similarity matrix was based on Euclidean distances. Euclidean distance measures for univariate PERMANOVA analyses produce sums-of-squares estimates equivalent to parametric ANOVA (Anderson, 2001) and allow the same methodological framework to be used for all community attributes.

We calculated the gonadosomatic index (GSI) for each sample. The GSI was calculated using this algorithm GSI= (GW/FW)*100, where GW= gonad weight (g) and FW= fish weight (g). Two one-way PERMANOVA tests were run to assess the patterns in GSI between sampling sites and time. We followed the same PERMANOVA procedure above. PERMANOVAs were performed in PRIMER-E software.

A regression analysis was performed to examine the relationship between the fork length and weight of the fish. Fork length and weight were log transformed before the analysis. Regression analysis was run in Statistica 7.1 software.

Genetic analyses

To identify species from each sample, we initially trimmed Primers using Cutadapt (v. 1.9.1) (Martin 2011) and imported sequences into DADA2 for a quality filter, trim, check for chimeras, and finally, we merged them into a table of amplicon sequence variants (ASVs), the atomic unit of analysis (i.e., the taxonomic unit). ASVs were assigned taxonomy using a naive Bayesian classifier method that takes in the ASVs and a trained set of reference sequences from the ANACAPA database. We used blast (BLASTn) searches on ASVs represented in GenBank and BOLD (Barcode of Life Data Systems) (Ratnasingham and Hebert 2007). To assess the

accuracy of IDs, we used different sequence identity cut-offs and different taxonomic assignment methods such as RDP Classifier, SPINGO, and SINTAX (Leray et al. 2018). The end result was an ASV presence-absence matrix and a taxonomy file with the unique ASV ID and associated taxonomy. These files, along with sample metadata information, was imported into the R package *Anacapa* for downstream analyses and visualization (R Core Team, 2017).

One-way PERMANOVAs were performed to examine the distribution of prey items between the different locations, sex of the fish, and size. Species composition (presence/absence) was calculated with the Jaccard similarity index, which considers only the presence and absence of each species in each sample and allows comparisons of the proportion of species between locations. Similarity percentage tests (SIMPER) were also performed to identify which prey species contributed the difference in the factors (locations, sex, and size). SIMPERs were also performed in PRIMER-E software.

Results

Demographic results

A total of 157 queen snappers were collected from November 2019 to July 2020 at seven different locations (Fig. 3), ranging in depths from 256 m at Bajo Medio to 402 m at Site 3. The number of samples collected at each site/area varied (Table 2). Most fishers targeted Bajo Medio (55 samples) and Pichincho (29 samples). The size and weight of queen snappers collected during this study varied between sampling time and location. However, from the estimates of the components of variation, sampling time had a more significant influence on the size and weight of fish than location. The patterns of queen snapper size and weight are detailed below.

Table 2 The number of queen snapper samples collected at each site and sampling time along the west coast of Puerto Rico.

Site	Sampling time	Number of samples
Bajo Medio	11/13/2020	10
Bajo Medio	1/16/2020	10
South of Pichincho	1/29/2020	8
Bajo Medio	2/2/2020	15
Bajo Medio	2/4/2020	20
Site 3	2/21/2020	15
Site 4	2/29/2020	15
Pichincho	4/30/2020	29
Site 5	4/30/2020	15
Site 6	7/6/2020	20

Size

The mean (±SE) standard, fork and the total length of queen snappers during the sampling period was 442.73 ± 11.53 mm, 472.06 ± 11.90 mm, 595.34 ± 15.24 mm, respectively. The standard size of queen snapper samples ranged from 190 mm to 756 mm, fork length ranged from 220 mm to 808 mm, and total length ranged from 260 mm to 970 mm.

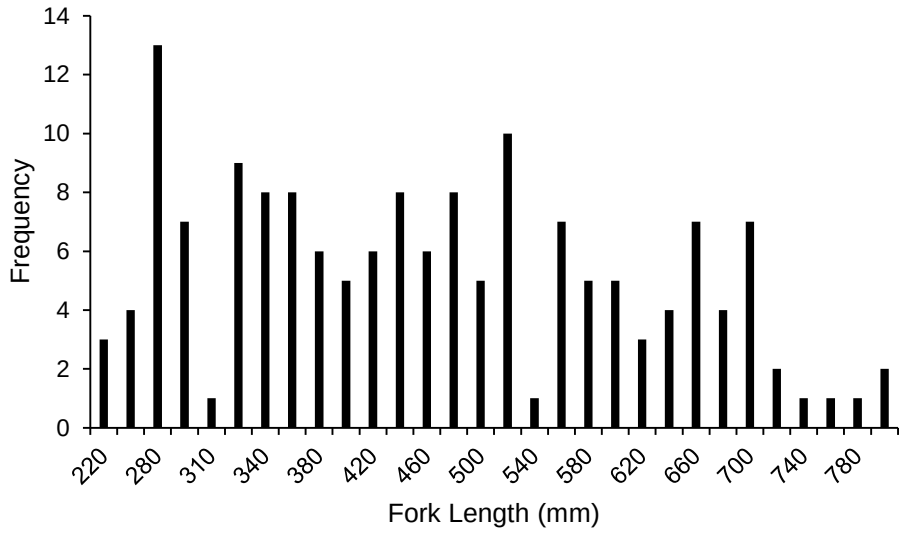

Figure 5 Fork length distribution of queen snapper samples collected at seven sites along the west coast of Puerto Rico.

As seen in Figure 5, the size distribution was skewed slightly to the left towards smaller fish. More fish were sampled with a fork length between 280 -300 mm and 520-540 mm in fork length.

Table 3 Permutational Multivariate ANOVA results of the difference of fork length (mm) of the queen snapper samples between sites and sampling times for the west coast of Puerto Rico.

Dependent variable: Fork Length (mm)					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**p value**
Site	6	1.01E+06	1.68E+05	10.22	0.001
Time	4	793650	198410	11.27	0.001

The fork length size significantly varied between sampling time and locations (Table 3). Smaller fish were caught at Site 4 and Site 3, while larger fish were caught at Site 6 and South of Pichincho. On average, fishers caught the largest fish in July and the smallest fish in November (Fig. 6).

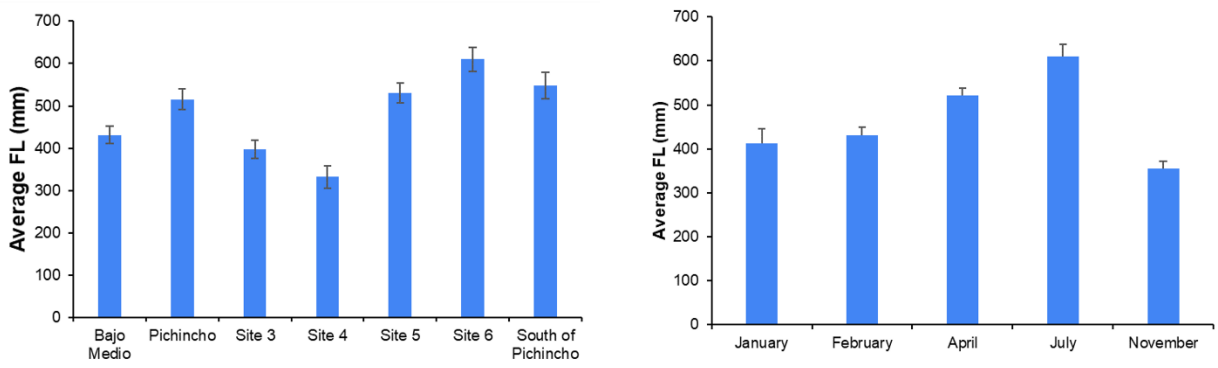

Figure 6 Mean fork length of queen snappers between sites (left) and sampling times (right) on the west coast of Puerto Rico. Bars denote standard errors.

Weight

The mean (±SE) weight of the queen snapper during this project was 1,948.39 ± 144.22 g, ranging from 195 g to 10,568 g. Given the size differences between sites, it was not surprising that fish's weight also significantly varied between locations (Table 4).

Table 4 Permutational Multivariate ANOVA results of the difference of weight (g) of the queen snapper samples between sites and sampling times for the west coast of Puerto Rico.

Dependent variable: weight (g)					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**p value**
Site	5	1.09E+08	2.18E+07	8.49	0.001
Time	4	1.03E+08	2.59E+07	9.96	0.001

The weight variation within site was more extreme for fish weight than length, especially at Site 5. For sampling time, mean fish weight was the lowest during January, followed by November. The highest weights were observed during July (Fig. 7).

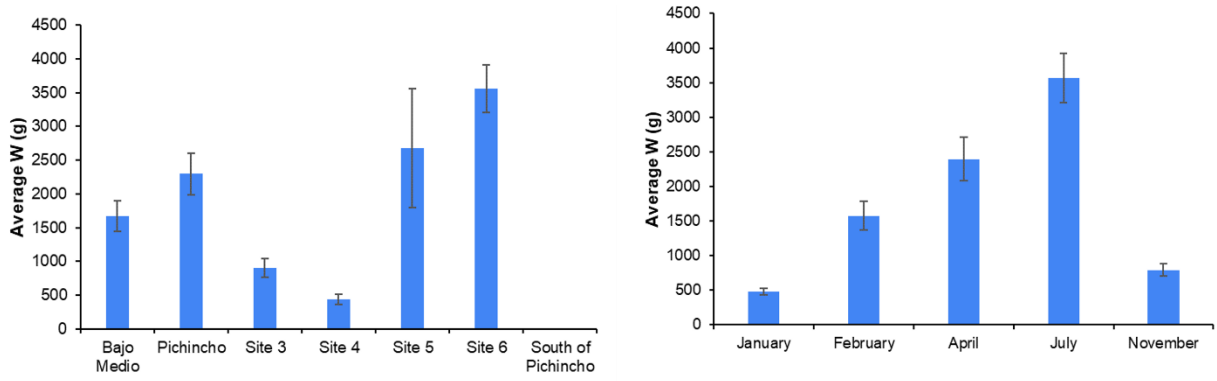

Figure 7 Mean weight of queen snappers between sites (left) and sampling times (right) on the west coast of Puerto Rico. Bars denote standard errors. Fish weights were not collected for South of Pichincho site.

As seen in Figure 8, there was a strong positive relationship between the fork length (mm) and weight (g) (Regression, $R=0.99$, $p<0.0001$).

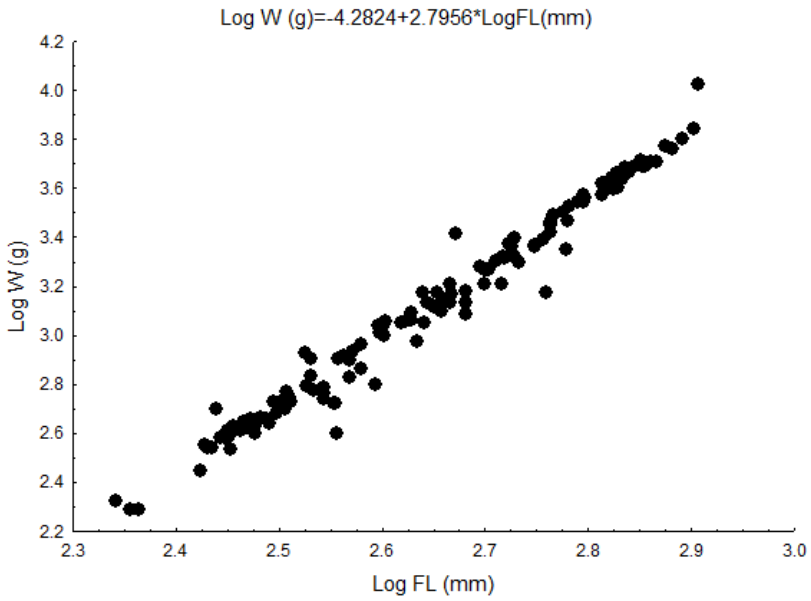

Figure 8 Strong linear relationship between the log weight (g) and log fork length (mm) of queen snappers sampled during this study performed along the west coast of Puerto Rico.

Gonads

We were able to identify the sexes from 110 queen snappers. The majority of the fish sampled were males (69%). Females had slightly greater average (± SE) fork length size (548. 61± 25.12 mm) than males (432.8 ± 14.82 mm). The average (± SE) gonad weight during this study was 11.82 ± 21.31 g. As seen by the standard error, there was a high variability of gonad weight, ranging from 0.1 g to 121.6 g (Site 6). Females had a higher average GSI (0.59 ± 0.10) compared to males (0.23 ± 0.03).

Table 5 Permutational Multivariate ANOVA results of the difference of the gonadosomatic index (GSI) value weight of the queen snapper samples between sites and sampling times for the west coast of Puerto Rico.

Dependent variable: Gonadosomatic index (GSI)					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**p value**
Site	5	11.99	2.40	15.14	0.001
Time	4	10.87	2.72	16.37	0.001

There was significant spatial and temporal variability in GSI during the study (Table 5). The GSI ranged from 0.02 at Pichincho to 2.78 at Site 5. GSI greatly varied at Site 5 and Site 6 (Fig. 9).

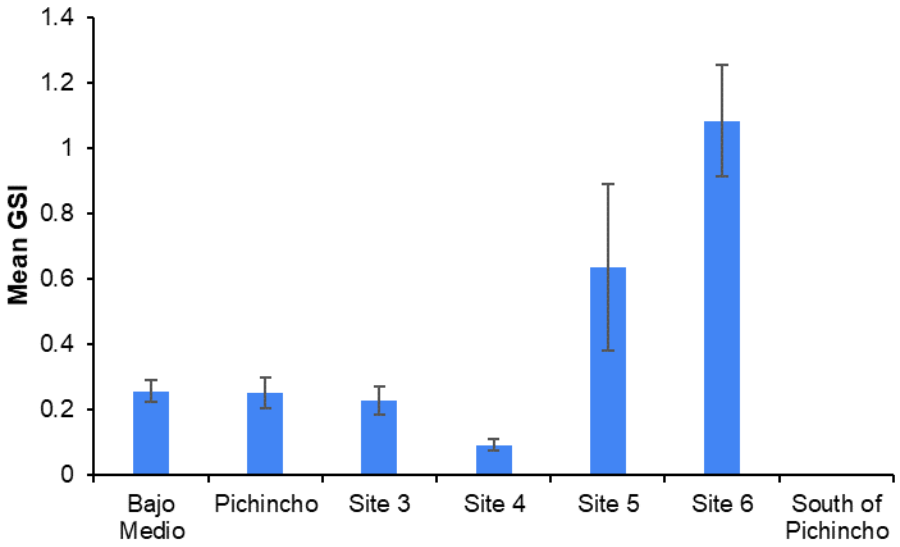

Figure 9 Mean gonadosomatic index value of queen snapper samples collected at seven sites along the west coast of Puerto Rico. Bars denote standard errors.

GSI significantly varied between sampling times, which was due to the high values calculated during July (Fig. 10).

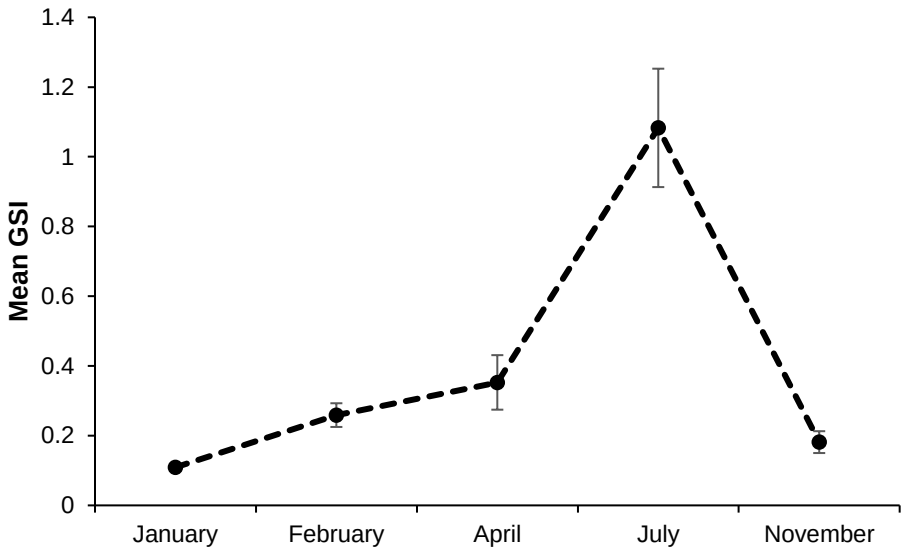

Figure 10 Mean gonadosomatic index value of queen snappers collected during sampling times along the west coast of Puerto Rico. Bars denote standard errors.

Prey detection

Individually separated items

Preys from individually separated undigested items in stomach contents were identified using the Cytochrome oxidase I (COI) marker. Out of the 146 of collected stomachs, 35 had undigested items (24% of the captures). The 75% of the fish collected exhibit signs of traumatic decompression, including regurgitation of the gut content.

Seven species of invertebrates (2 arthropods, 4 mollusks, and 1 isopod) and 16 fish species were found within those undigested items. Detection of some fish species was difficult in some samples because of competing co-amplification of the COI marker with the queen snapper's DNA. The issue persisted even after we washed the sample multiple times and used blocking primers. We often got unreadable chromatograms. Table 6 describes all the different species identified using the COI marker along with the common name and the number of times found in the different samples. We reported all species found in stomach including those commonly use as baits such as skipjacks (*Katsuwonus pelamis*), little tunny (*Euthynnus*

alletteratus), blackfin tunas (*Thunnus atlanticus*), herring (*Opisthonema oglinum*,), ladyfish (*Albula vulpes*), and squids (N. Crespo pers comm). Bait species were identified in Table 6 and 7 with a red asterisk. We identified the genetic information of eight species used as bait corresponding to the 38% of the separated undigested items found in all the stomach contents.

Table 6 Species identified using Cytochrome oxidase I (COI) marker in undigested items found in the Etelis oculatus stomach contents. See Index 5 for pictures and web link to species details on FishBase.

	Scientific name	***Common name***	***Prey number***
1	*Abralia veranyi* *	midwater squid	9
2	*Oplophorus gracilirostris*	shrimp	7
3	*Myctophum selenops*	Wisner's lantern fish	4
4	*Coccorella atlantica*	Atlantic sabretooth	4
5	*Diaphus dumerilii*		3
6	*Systellaspis debilis*	shrimp	3
7	*Gonostoma elongatum*		2
8	*Opisthonema oglinum* *	Atlantic thread herring	2
9	*Doryteuthis (possible pealeii)* *	longfin inshore squid	2
10	*Euthynnus alletteratus* *	little tunny	2
11	*Lampadioteuthis megaleia* *	wonderful firefly squid	2
12	*Electrona paucirastra*	belted lanternfish	1
13	*Abralia redfieldi* *	Redfield's enope squid	1
14	*Argyropelecus aculeatus*	lovely hatchetfish	1
15	*Lepidophanes guentheri*	Günther's lanternfish	1
16	*Astronesthes similus*		1
17	*Scomberomorus regalis**	cero	1
18	*Katsuwonus pelamis* *	skipjack tuna	1
19	*Myctophum obtusirostre*	bluntsnout lanternfish	1
20	*Diaphus perspicillatus*	transparent lantern fish	1
21	*Sphyraenops bairdianus*	triplespine deepwater cardinalfish	1

Metabarcoding approach

We obtain metabarcoding sequence from 89 corresponding to 83%, out of 107 stomachs samples. Using the 12S marker, we found a total of 43 prey species present in the queen snapper stomach content samples (Table 7, Index 1 and 6), representing 37 genera (Index 2), and 24 prey families (Index 3). *Diaphus dumerilii, Euthynnus alletteratus, Lepidophanes guentheri*, were the only fish species detected with both molecular approaches. A picture of each species, including a link to their full description on FishBase is detailed in Index 6.

Table 7 Prey species of Etelis oculatus using two molecular approaches, Cytochrome oxidase I (COI) and Tele02.

Order	Family	Specie	Cytochrome oxidase I (COI)	Tele02 (12S)
Acanthuriformes	Pomacanthidae	*Centropyge aurantonotus*		x
Acropomatiformes	Epigonidae	*Sphyraenops bairdianus*	x	
Pempheriformes	Howellidae	*Howella brodiei*		x
Anguilliformes	Anguillidae	*Anguilla rostrata*		x
	Derichthyidae	*Derichthys serpentinus*		x
	Muraenidae	*Gymnothorax saxicola*		x
Argentiniformes	Opisthoproctidae	*Monacoa grimaldii*		x
Aulopiformes	Evermannellidae	*Coccorella atlantica*	x	
	Alepisauridae	*Omosudis lowii*		x
	Synodontidae	*Saurida caribbaea*		x
	Scopelarchidae	*Scopelarchoides danae*		x
	Scopelarchidae	*Scopelarchus analis*		x
Beryciformes	Trachichthyidae	*Gephyroberyx darwinii*		x
Carangiformes	Carangidae	*Coryphaena equiselis* *		x
	Carangidae	*Elagatis bipinnulata* *		x
Caproiformes	Caproidae	*Antigonia combatia*		x
Clupeiformes	Clupeidae	*Opisthonema oglinum* *	x	
Decapoda	Oplophoridae	*Oplophorus gracilirostris*	x	
	Oplophoridae	*Systellaspis debilis*	x	
Gadiformes	Phycidae	*Urophycis floridana*		x
	Macrouridae	*Ventrifossa macropogon*		x
Myctophiformes	Myctophidae	***Diaphus dumerilii***	**x**	**x**
	Myctophidae	*Diaphus perspicillatus*	x	
	Myctophidae	***Lepidophanes guentheri***	**x**	**x**
	Myctophidae	*Electrona paucirastra*	x	
	Myctophidae	*Myctophum obtusirostre*	x	
	Myctophidae	*Myctophum selenops*	x	
	Myctophidae	*Diaphus mollis*		x
	Myctophidae	*Diaphus brachycephalus*		x
	Myctophidae	*Notolychnus valdiviae*		x
	Myctophidae	*Myctophum nitidulum*		x
	Myctophidae	*Diaphus splendidus*		x
	Myctophidae	*Centrobranchus nigroocellatus*		x
	Myctophidae	*Hygophum benoiti*		x
	Myctophidae	*Hygophum reinhardtii*		x
	Myctophidae	*Bolinichthys photothorax*		x
	Myctophidae	*Diaphus* sp.		x
Myopsida	Loliginidae	*Doryteuthis* (possible pealeii)	x	

Table 7. cont.

Order	Family	Specie	Cytochrome oxidase I (COI)	Tele02 (12S)
Oegopsida	Lampadioteuthidae	*Lampadioteuthis megaleia* *	x	
	Enoploteuthidae	*Abralia redfieldi* *	x	
	Enoploteuthidae	*Abralia veranyi* *	x	
Scombriformes	Scombridae	***Euthynnus alletteratus*** *	**x**	**x**
	Scombridae	*Katsuwonus pelamis* *	x	
	Scombridae	*Scomberomorus regalis* *	x	
	Scombridae	*Thunnus obesus* *		x
	Trichiuridae	*Benthodesmus tenuis*		x
	Chiasmodontidae	*Kali macrodon*		x
	Scombridae	*Scomberomorus cavalla* *		x
	Scombrolabracidae	*Scombrolabrax heterolepis*		x
	Pomatomidae	*Pomatomus saltatrix* *		x
Stomiiformes	Gonostomatidae	*Gonostoma elongatum*	x	
	Stomiidae	*Astronesthes similus*	x	
	Sternoptychidae	*Argyropelecus aculeatus*	x	
	Phosichthyidae	*Ichthyococcus ovatus*		x
	Phosichthyidae	*Ichthyococcus polli*		x
	Stomiidae	*Idiacanthus fasciola*		x
	Stomiidae	*Stomias affinis*		x
	Gonostomatidae	*Sigmops elongatus*		x
	Stomiidae	*Chauliodus sloani*		x
	Stomiidae	*Astronesthes atlanticus*		x
	Gonostomatidae	*Bonapartia pedaliota*		x

A total of 61 species belonging to eighteen orders, 38 genera and 31 families were observed in the stomach contents of queen snappers using the two molecular approaches (Table 7, Index 1, 2, and 3). The total number of prey species identified in stomach samples includes both the natural preys and the ones used as bait (see Table 6). We also identified the presence of other pelagic fishes in the stomach samples such as *Scomberomorus regalis*, *S. cavalla*, *Elagatis bipinnulata, T. obesus*, *Pomatomus saltatrix*, *Coryphaena equiselis* and *Opisthonema oglinum.* Therefore, it is unclear if queen snappers naturally are able to eat the juveniles of these species.

The most common prey item was the *Diaphus brachycephalus*, the short-headed lantern fish, which was found in 25 stomach samples, followed by *Sigmops elongatus* in 23 and *Bonapartia pedaliota* in 19 (Fig. 11 and Index 1). *D. brachycephlus* is a bathypelagic fish dwelling in deep waters a depth between 200 to 600 m (FishBase 2002). The two other common species, *S. elongatus*, elongated bristlemouth fish, and *B. pedaliota*, longgray fangjaw, are also bathypelagic fish inhabiting deeper waters, ranging usually between 100 to 1500m (FishBase 2002).

Myctophiformes was the most common order among the identified preys, with 16 species recognized within the family Myctophidae. We found 59 samples with Myctophidae preys. Stomiiformes fishes were the second most common order observed in this study, represented by eleven families in our sampling. Preys from the families Gonostomatidae and Stomiidae were identified in 34 and 17 stomach samples, respectively. The third most common order of prey observed in the stomach samples was the Aulopiformes. Four families represented by five prey's species were observed in the queen snapper stomach content (Table 7, Index 1 and 3).

We identified five squid species including the midwater squid (*Abralia veranyi*), longfin inshore squid (*Doryteuthis sp*. (possible *pealeii*)), wonderful firefly squid (*Lampadioteuthis megaleia*), and Redfield's enope squid (*Abralia redfieldi*), and also two types of shrimps *Oplophorus gracilirostris, Systellaspis debilis* (Table 6).

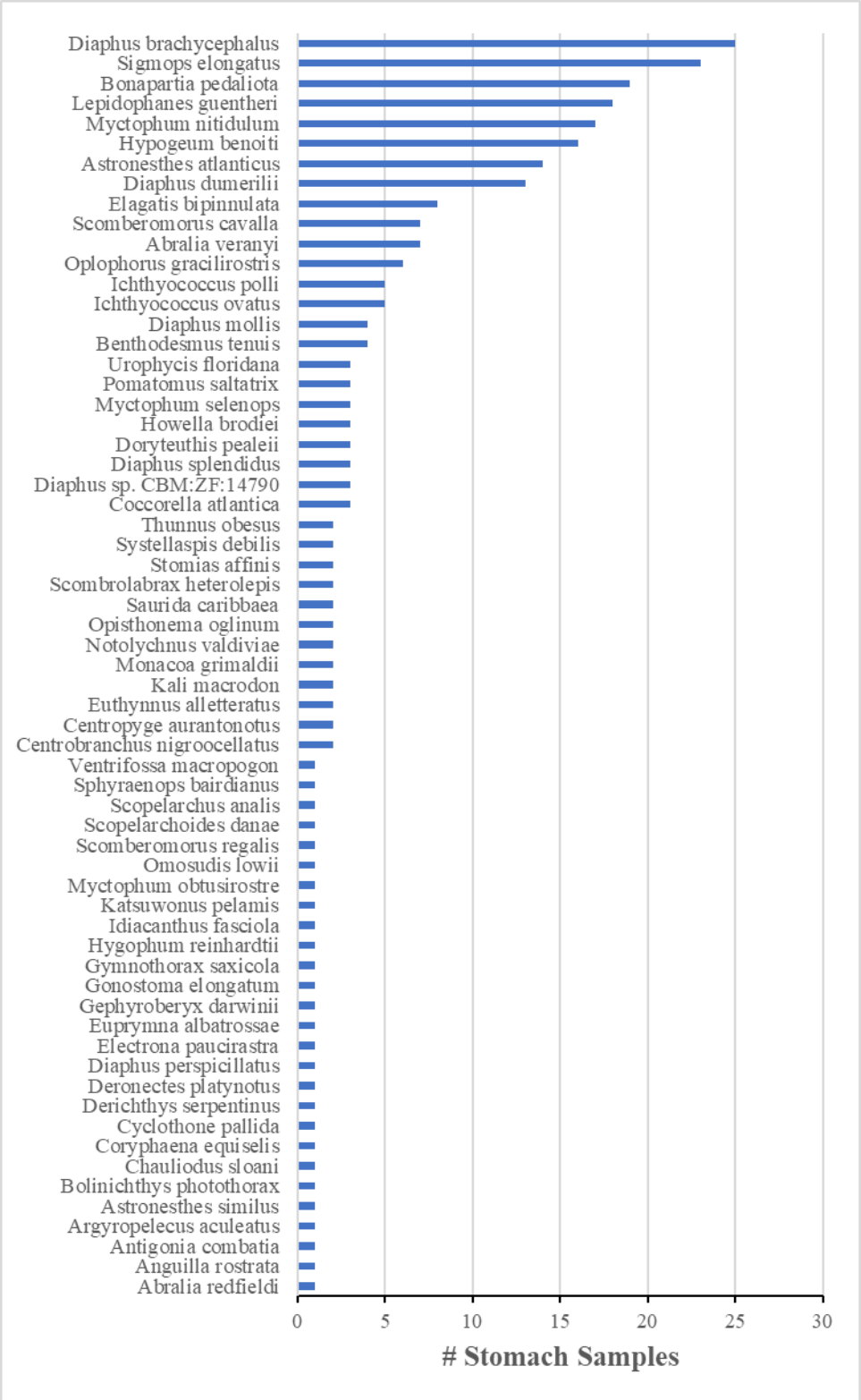

Figure 11 Species composition of stomach contents of Etelis oculatus.

Prey composition differed among locations (Table 8); however, these results should be taken with caution as the sample numbers greatly varied per site. As seen in Figure 12, Pichincho displayed the highest prey diversity with 33 different prey species. We also observed high prey diversity at Bajo Medio, another seamount and popular fishing ground for many species of fish especially queen snapper.

Table 8 The one-way Permutational Analysis of Variance tests examining the difference of prey composition between the locations along the west coast of Puerto Rico and sex of Etelis oculatus.

Source	df	SS	MS	Pseudo-F	p value
Location	6	43020	7170	1.6712	0.001
Size	1	7268.2	7268.2	1.6367	0.034

The most common prey species identified at Bajo Medio were two species of *Diaphus*, *D. brachycephalus* (11 samples) and *D. dumerilii* (8 samples). At Pichincho, *Sigmops elongatus* (11 samples) was the most common prey item sampled, followed by *Bonapartia pedaliota* (8 samples). *Hypogeum benoiti* and *Lepidophanes guentheri* (8 samples), were the most common prey species sampled at Site 6.

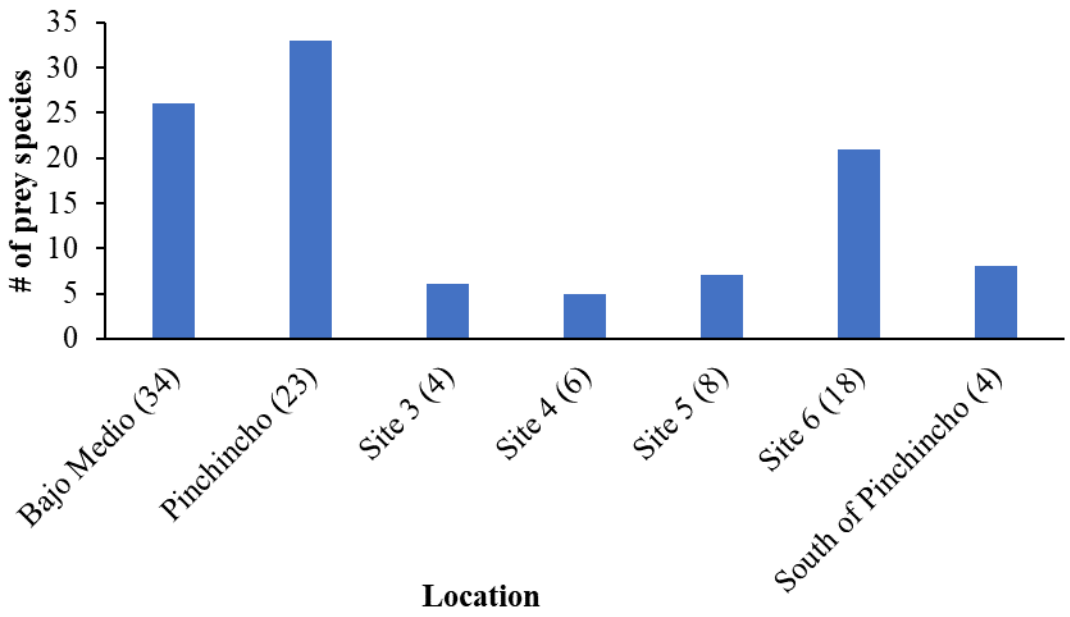

Figure 12 Prey composition (total species number) in the stomach samples of Etelis oculatus at the different locations on the west side of Puerto Rico. The number of samples are in parentheses.

The species composition was significantly different between the size ranges 203-508 mm and 508-1016 mm fork length (Table 8). Smaller (<203 mm fork length) and larger fish (>1016 mm fork length) were not landed during this project, therefore we are missing stomach samples from these ranges. *B. pedaliota*, *S. elongatus* and *H. benoiti* were more common in the stomach contents of larger queen snappers (508-1016 mm), while *D. brachycephalus*, *Myctophum nitidulum*, *D. dumerilii*, *Elagatis bipinnulata*, and *Lepidophanes guentheri* contributed the most to the prey composition of smaller queen snappers (203-508 mm, SIMPER). We did not find any significance of the prey composition between sexes (one-way PERMANOVA, p=0.41). This could be due to the lack of sex data for the samples.

Discussion

The deep-water snappers, silk and queen, are some of the most landed fishes in Puerto Rico (Matos-Carballo 2012). Even though queen snappers are an essential component of the Caribbean commercial fisheries (Bryan et al. 2011), the most recent published analyses of the queen snapper biology in Puerto Rico were carried out more than ten years ago (Rosario et al. 2006). The mean fork length measured in this study was slightly larger than that reported by Rosario et al. (2006), with a mean size of 312.05 ± 66.65 mm. The maximum length of fish caught in their study was less than 700mm, while in this study was slightly over 800 mm.

When comparing the length-frequency distribution of the west coast queen snappers to other places in the Caribbean, the distribution pattern is similar to the Honduras fisheries (Gobert et al. 2010). The fishers in the Lesser Antilles islands, like Barbados (Prescod et al. 1996) and Guadeloupe (Gobert et al. 2010), overall caught larger queen snappers. The size difference between islands could be due to several factors, such as the fishers' gear type, small sample sizes, and time duration during this study. The fishers on the west coast target queen snappers using weighted vertical long lines, unlike in Barbados and Guadeloupe, where they use hand lines and gillnets, respectively (Prescod et al. 1996, Gobert et al. 2010).

Several studies have calculated the relationship between weight and length of the queen snapper (Bohnsack and Harper 1988, Murray et al. 1992, Frota et al. 2004, Rosario et al. 2006). Like past studies, there was a strong linear relationship between queen snapper fish weight and fork length. The power parameter calculated for this study was 2.80, which is similar to values calculated by Rosario et al. 2006 (2.84) and other studies in the south Atlantic and Caribbean, which range from 2.55 (Bohnsack and Harper 1988) to 2.91 (Frota et al. 2004). Therefore, our

study confirms that the queen snapper exhibits isometric growth, given that the power parameter is close to 3 (Bryan et al. 2011).

In western Puerto Rico, the queen snapper fishery is found all year-round. However, fishers usually catch more fish when the water temperatures cool down, with landings increasing between September and March (N. Crespo pers comm.). Based on the GSI values reported by Rosario et al. (2006), queen snappers spawn during this time, between October and November. However, in this study, July collections exhibited the highest GSI values between the west coast sites. July was the only month when queen snappers were not collected during Rosario et al. (2006) study. Many queen snappers, both male and female, were gravid during the July collection. Therefore, queen snappers may spawn during late summer. Fishers have also observed female queen snappers to be gravid during July and August (N. Crespo pers comm.).

Regurgitation of gut contents due to rapid decompression remains a problem for prey identification of deep-water fishes. Most of our stomachs came empty without any big undigested pieces as in previous studies (Haight, et al, 1993). Even when pieces were found, it was difficult to identify the items in the stomachs due to its advance degree of degradation. Given the difficulty in identifying prey items in deep water fishes, we decided to use metabarcoding as regurgitated items likely left behind cells with DNA in the gastrointestinal tract. We were able to record preys in at least 89 samples using metabarcoding.

Both of our molecular approaches suggest *E. oculatus* is a large carnivore that mainly feeds on squids, shrimps, and deep-water fishes. It coincides with earlier studies of its sister species, *E. coruscans*, and *E. carbunculus* that have also been reported as piscivorous fishes (i.e., primary piscivorous feeding guild; Haight, 1993). In fact, *E. oculatus* is classified as a 4.2 on the trophic level on FishBase, suggesting that only larger top predators such as striped marlin or some sharks

are above it in the trophic pyramid (FishBase 2002). Our data and previous reports support the idea that *E. oculatus* likely represents a top predator in deep water environments.

Our approach identified as the most common preys *D. brachycephalus, S. elongatus, B. pedaliota, L. guentheri, M. nitidulum, H. benoiti, A. atlanticus, D. dumerilii, M. selenops, C. atlantica*, and *A. veranyi*. These species mostly belong to three orders of deep-sea fishes. First, we have the Myctophiformes with 28% of the total species identified with both approaches (Table 7). The myctophids, commonly known as lanternfishes, are a diverse group with over 240 species (Helfman 2009). They occur in all seas and are prey of numerous other fishes and marine mammals. The group make up a large fraction of the deep scattering layer – a diverse assemble of the fishes and invertebrates that lives at mesopelagic depths (200–1000 m) during the day and migrate towards the surface at dusk (Helfman et al, 2009). The second order was the Stomiiforms with 18 % of the species identified (Table 7). The Stomiiforms commonly known as dragonfishes and allies, are characterized by inhabiting the mesopelagic and bathypelagic regions in the open water, between 200 and 4000 m depths. During the day, Stomiiforms stay in deep water, and at night migrate to the surface following zooplankton migration patterns and enjoying the plentiful of food in the shallow areas of the ocean. Lastly, we found the Aulopiforms with 8.5 % of the species identified (Table7). This is also a group that is largely found in the open water at mesopelagic habitats. All these species are considered deep-water dwellers of the mesopelagic, bathypelagic and benthic regions of the ocean (Table 9), suggesting that *E. oculatus* can feed in different habitats of the deep ocean.

In addition, we found nine families of Scombriformes, six of them were reported as baits during our study. However, we found three additional families, which suggest *E. oculatus* feeds

on these fishes in their natural habitats. Given the large size of some of these fishes, it seems most likely queen snappers prey on juveniles of these families.

Despite the lack of studies on the diet of deep-water snappers, we found an overlap with the only other study on *Etelis* species (Haight et al. 1993). Haight et al. (1993) found that the main preys of *E. coruscans and E. carbunculus* were mesopelagic lanternfishes and the deep-water demersal cardinalfish. In Hawai'i, those mesopelagic species are a component of the "mesopelagic boundary community" (100-700 m), a band surrounding the islands or banks. If we apply this reasoning to our study, it means that *E. oculatus* is feeding mainly on mesopelagic fishes, mostly Myctophidae, that likely inhabit the mesopelagic boundary. Our data also suggest that *E. oculatus* can feed on other fish species. For instance, we found prey species in the families Scombridae, Phosichthyidae, Scopelarchidae, Gonostomatidae, Alepisauridae, Anguillidae, Caproidae, Carangidae, Chiasmodontidae, Coryphaenidae, Derichthyidae, Epigonidae, Evermamellidae, Howellidae, Macrouridae, Muraenidae, Opisthoproctidae, Phycidae, Pomacanthidae, Pomatomidae, Scombrolabracidae, Sternoptychidae, Synodontidae, Trachichthyidae, and Trichiuridae. We observed some of the families detected in previous studies such as the Mychtophidae, and Synodonidae. Yet, it is clear that our metabarcoding approach provided a broader resolution of the different preys of deep-water snappers, with identifying 31 families total. Our study opens the possibility that the diet of *E. oculatus* is broad and includes fishes with different behaviors that occupy different habitats of the ocean.

The diet of *E. oculatus* also contained invertebrate preys such as three squids (*Abralia veranyi*, *Doryteuthis pealeii*, and *Abalia redfieldi*), two shrimps (*Oplophorus gracilirostris* and *Systellaspis debilis*), and one isopod species. Squids such as the ommastrepid (Humbolt squid) and chiroteuthis, have been previously reported as preys in other *Etelis* species from the Pacific

(Parrish 1987, in Haight 1993). In addition, large crustaceans such as lobsters, shrimps, crabs, amphipods, euphausiids, isopods, and stomatopods have been found to be part of the diet of the deep snappers in the pacific (Parrish1987, Seki and Callahan 1988 in Haight 1993). In our study, one species of squid was used as bait, yet we found two more, suggesting that squids are also part of the natural preys of the queen snapper in Puerto Rico.

Our study strongly suggests that *E. oculatus* is a demersal fish that feeds on benthic vertebrate and invertebrate species with the ability to capture mid-water fishes. We suggest that deep water snappers are a key link between shallow highly productive environments and demersal mostly unproductive areas. The reason is that a large portion of the *E. oculatus* preys are mesopelagic, like the Myctophiformes and Stomiiforms, that daily migrate from deep unproductive areas into shallow rich productive areas following the zooplankton. In essence, it is the zooplankton in the upper layers of the ocean that maintains a major fish community in the mesopelagic environment and by doing so, also supports a highly productive demersal community that maintains healthy stocks of deep-water snappers.

Table 9 Main prey species found in E. oculatus using the metabarcoding approach with ecological information about each species (FishBase 2002).

Specie	Distribution				
Diaphus brachycephalus	Marine	bathypelagic	oceanodromous	depth range 200 - 600 m	Deep-water
Sigmops elongatus	Marine	bathypelagic		depth range 25 - 4740 m	Deep-water
Bonapartia pedaliota	Marine	bathypelagic		depth range 100 - 1200 m	Deep-water
Lepidophanes guentheri	Marine	pelagic-oceanic	oceanodromous	depth range 40 - 750 m	
Myctophum nitidulum	Marine	bathypelagic	oceanodromous	depth range 412 - 1537 m	Deep-water
Hygophum benoiti	Marine	bathypelagic	oceanodromous	depth range 51 - 700 m	Deep-water
Astronesthes atlanticus	Marine	bathypelagic		depth range 300 - 1200 m	
Diaphus dumerilii	Marine	pelagic-oceanic	oceanodromous	depth range - 805 m	
Coccorella atlantica	Marine	bathypelagic	oceanodromous	depth range 50 - 1000 m	Deep-water
Dasyscopelus selenops	Marine	bathypelagic	oceanodromous	depth range 40 - 500 m	Deep-water

Our data indicate that diet composition of species of *E. oculatus* is relatively constant across locations. We have some locations with higher diversity of preys, but at the same time, these locations have many more samples, which prevents us to extricate if higher diversity is due to larger sample sizes or due to a location effect. The highest prey diversity was observed at Pichincho, a seamount located on the far western ridge of Desecheo Island, and a known recreational fishing site for highly migratory pelagic fishes (Appledoorn et al. 2015). As observed during the Okeanos Expedition, high structural relief of the karstic terrain characterizes the seafloor geomorphology at Pichincho (Wagner et al. 2018), and strong bottom currents have eroded and molded some of this karst terrain (Chaytor et al. 2015). The variation in structural relief has allowed for the high diversity and abundance of benthic organisms such as deep-sea corals and sponges. During the expedition, small invertebrates and deep-water fishes, such as the misty grouper (*Hyporthodus mystacinus*) and queen snapper were observed inhabiting caverns and overhangs that dominate this site. A more balanced sampling approach needs to be conducted to understand if there are site differences in prey items of *E. oculatus*.

We did observed variation in species composition of preys across size classes. *B. pedaliota, S. elongatus* and *H. benoiti* were more common in the stomach contents of larger queen

snappers, while *D. brachycephalus*, *Myctophum nitidulum*, *D. dumerilii*, *Elagatis bipinnulata*, and *Lepidophanes guentheri* more common in smaller queen snappers. This difference may be related to an ontogenetic change of *E. oculatus* in the exploitation of different habitats as it changes in size. However, more samples need to be collected of fish smaller than 203 mm fork length and larger than 1016 mm fork length to fully understand the relationship between prey diversity and age of the fish.

A major aspect of this study is our approach. To our knowledge this is the first attempt to use the meta– and barcoding approach to uncover the feeding patterns in a deep-water fish species. Unlike previous cases with analysis of fish gut contents (Haight 1983), most of the fish prey we found were identified to the species level and even some of the most common invertebrate species were also identified to the species level. This high resolution in the identification of prey items in deep-water snappers is atypical and represents a viable alternative to continue learning about the biology of these species of commercial value. The identifiable preys were diverse systematically and ecologically and included Myctophid fishes with some benthic species like shrimps, fishes with demersal habits at a variety of depths, and fishes of the water column (Table 9).

Management recommendations

- Most of the studies, including this one, have not sampled larger queen snappers (>800 mm fork length). A more thorough analysis needs to be conducted to determine the size structure of the queen snapper of Puerto Rico, including the size structure at other locations, especially in the north and east coasts.
- Given the results of this study, the spawning time of queen snappers should be revised. We observed a high mean GSI of 1.08 ± 2.44 during the July collection from 20 samples. Therefore, queen snappers might spawn during late summer. Fishers have observed gravid females during this time (N Crespo pers comm). More samples should be collected during July and August to confirm this possible new spawning time.
- Length-at-maturity is between 233 mm for females and 310 mm for males (Rosario et al. 2006), therefore based on the samples collected, around 76% of the fish sampled in this study were sexually matured individuals. Juveniles were not sampled, and this could be due to the sampling time, site location and depths targeted by west coast fishers. Further studies should be conducted to understand the recruitment dynamics of queen snappers, and if this species is recruitment limited.
- Pichincho has been already designated as an important location for highly migratory species. This seamount may be an important area for forage fish for the queen snappers. More stomach samples need to be collected and analyzed for not only the west coast of Puerto but in the north and east coasts. A more balanced sampling design will allow for site-specific prey descriptions.
- It is essential to incorporate fishers in any future queen snapper research. Researchers collaborating with fishers through a cooperative research program will benefit from a better

quantity and quality of data, and furthermore a better understanding of the biology and ecology of this commercially-important species.

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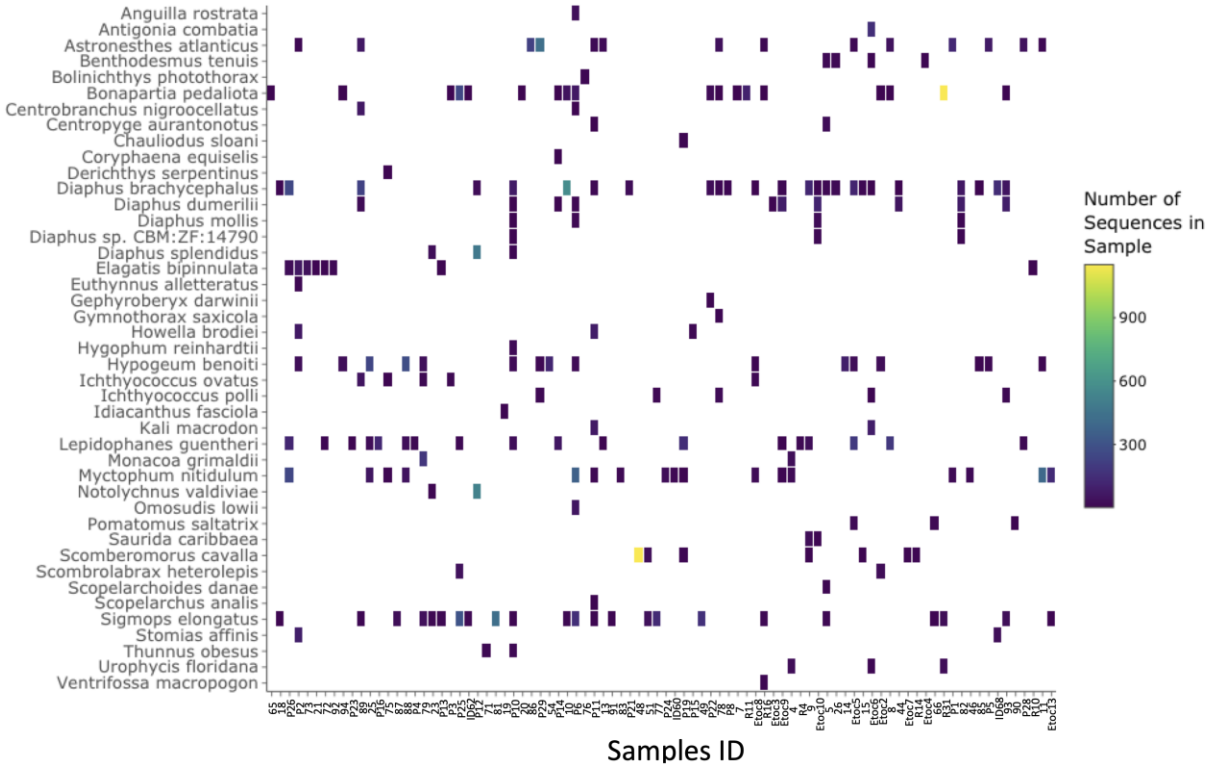
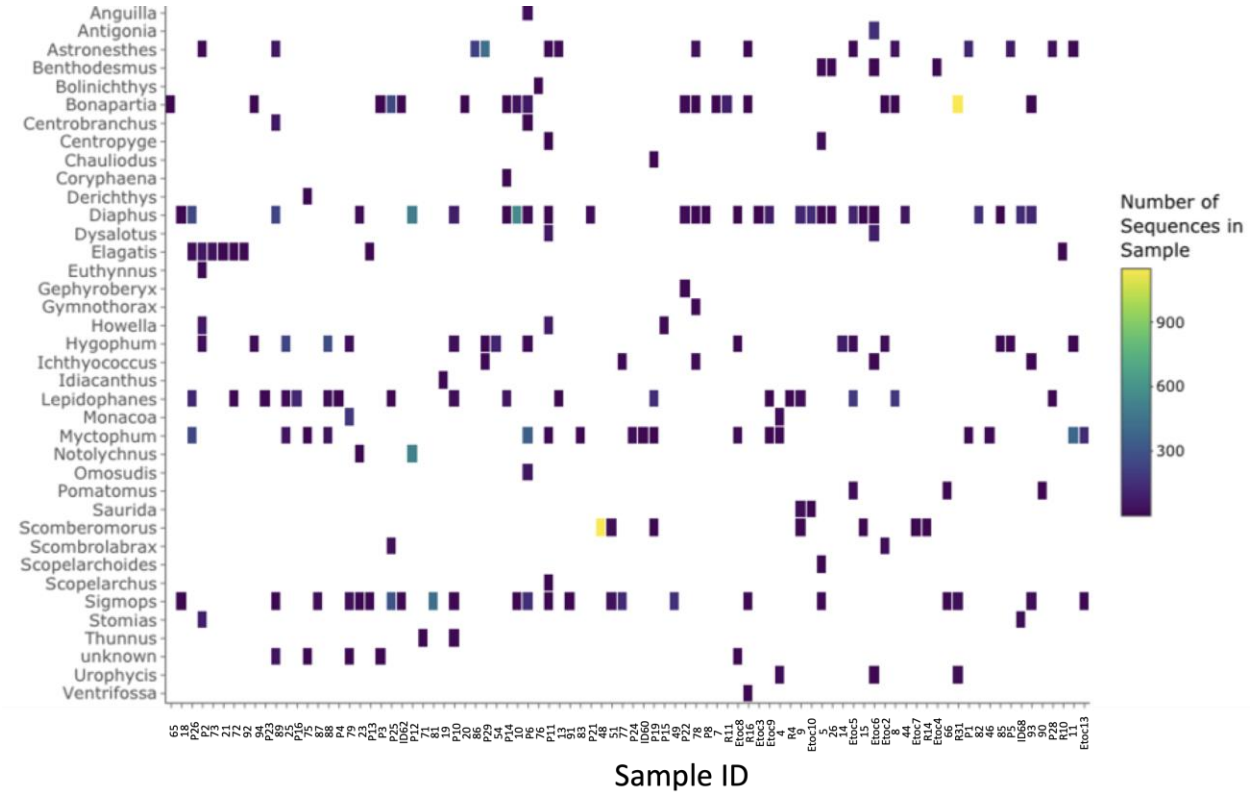
Indices

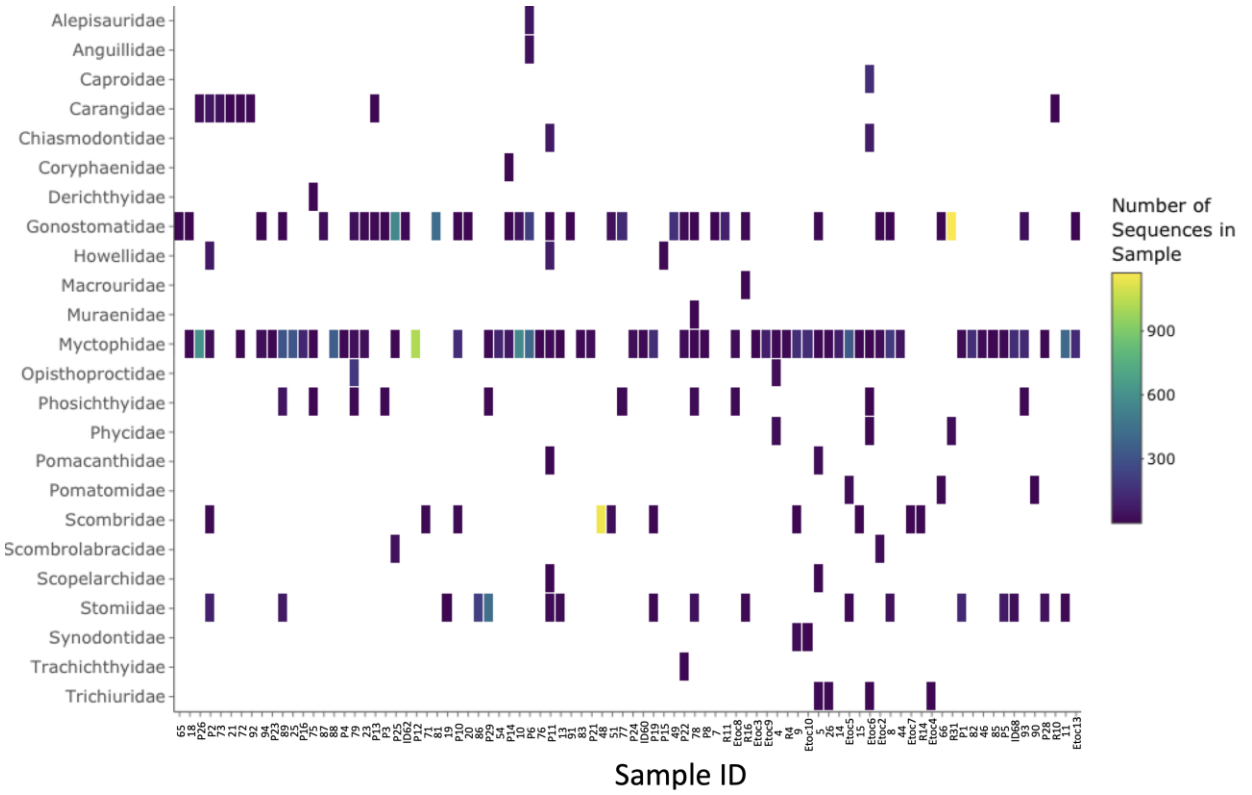
Index 1 Prey species present in the Etelis oculatus stomach content samples using the metabarcoding genetic approach.



Index 2 Prey genera present in the Etelis oculatus stomach content samples using the metabarcoding genetic approach.



Index 3 Prey families present in the Etelis oculatus stomach content samples using the metabarcoding genetic approach.



Index 4 Prey species observed in the stomach contents of Etelis oculatus by extracting DNA from Individual preys using Cytochrome oxidase I (COI).

Abralia veranyi https://www.sealifebase.ca/summary/Abralia-veranyi.html

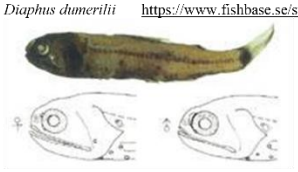
Astronesthes similus https://www.fishbase.se/summary/47625

Abralia redfieldi https://en.wikipedia.org/wiki/Abralia_redfieldi

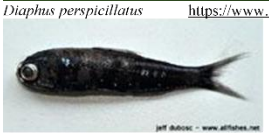
Coccorella atlantica https://www.fishbase.se/summary/Coccorella-atlantica.html

Argyropelecus aculeatus https://www.fishbase.se/summary/Argyropelecus-aculeatus.html

Diaphus dumerilii https://www.fishbase.se/summary/6590



Diaphus perspicillatus https://www.fishbase.se/summary/Diaphus-perspicillatus.html



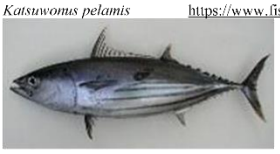
Euthynnus alletteratus https://www.fishbase.se/summary/Euthynnus-alletteratus.html

Doryteuthis (possible pealeii) https://en.wikipedia.org/wiki/Longfin_inshore_squid

Gonostoma elongatum https://www.fishbase.se/summary/Sigmops-elongatus.html

Electrona paucirastra https://www.fishbase.se/summary/6986

Katsuwonus pelamis https://www.fishbase.se/summary/107



Lampadioteuthis megaleia https://en.wikipedia.org/wiki/Lampadioteuthis

Myctophum selenops https://www.fishbase.in/summary/Myctophum-selenops.html

Lepidophanes guentheri https://www.fishbase.se/summary/Lepidophanes-guentheri.html

Opisthonema oglinum https://www.fishbase.se/summary/1486

Myctophum obtusirostre https://www.fishbase.de/summary/Myctophum-obtusirostre.html

Oplophorus gracilirostris https://www.gbif.org/species/2222589

Scomberomorus regalis https://www.fishbase.de/summary/134

Sphyraenops bairdianus https://www.fishbase.se/summary/Sphyraenops-bairdianus.html

Systellaspis debilis https://www.sealifebase.ca/summary/Systellaspis-debilis.html

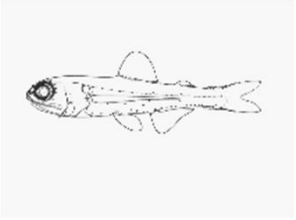
Index 5 Prey species observed in the stomach contents of Etelis oculatus by extracting DNA from Individual preys using metabarcoding approach.

Anguilla rostrata https://fishbase.mnhn.fr/summary/Anguilla-rostrata.html

Bonapartia pedaliota https://www.fishbase.se/summary/9965

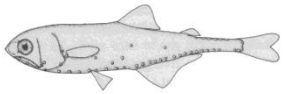
Antigonia combatia https://www.fishbase.de/summary/Antigonia-combatia.html

Bolinichthys photothorax https://www.fishbase.se/summary/11876



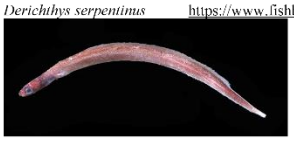
Benthodesmus tenuis https://www.fishbase.se/summary/Benthodesmus-tenuis.html

Centrobranchus nigroocellatus https://www.fishbase.se/summary/Centrobranchus-nigroocellatus.html



Centropyge aurantonotus https://www.fishbase.se/summary/Centropyge-aurantonotus.html

Derichthys serpentinus https://www.fishbase.se/summary/7445

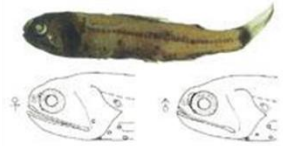


Chauliodus sloani https://www.fishbase.se/summary/Chauliodus-sloani.html

Diaphus brachycephalus https://www.fishbase.se/summary/7434

Coryphaena equiselis https://www.fishbase.se/summary/7

Diaphus dumerilii https://www.fishbase.se/summary/6590



Diaphus mollis https://www.fishbase.se/summary/Diaphus-mollis

Euthynnus alletteratus https://www.fishbase.se/summary/Euthynnus-alletteratus.html

Diaphus splendidus https://www.fishbase.se/summary/10174

Gephyroberyx darwinii https://www.fishbase.se/summary/Gephyroberyx-darwinii

Elagatis bipinnulata https://fishbase.mnhn.fr/summary/412

Gymnothorax saxicola https://www.fishbase.se/summary/Gymnothorax-saxicola.html

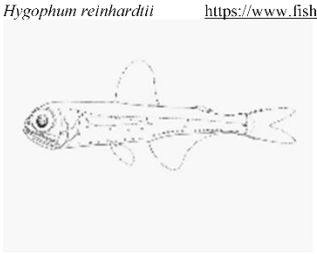
Howella brodiei https://www.fishbase.se/summary/Howella-brodiei.html

Ichthyococcus polli https://www.fishbase.se/summary/Ichthyococcus-polli.html

Hygophum benoiti https://www.fishbase.se/summary/Hygophum-benoiti.html

Ichthyococcus ovatus https://www.fishbase.se/summary/Ichthyococcus-ovatus.html

Hygophum reinhardtii https://www.fishbase.se/summary/4520



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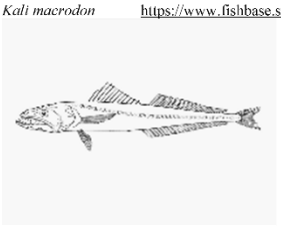
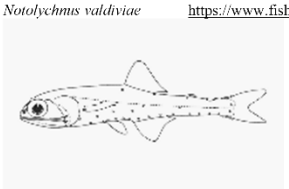


Myctophum nitidulum https://www.fishbase.se/summary/4490

Lepidophanes guentheri https://www.fishbase.se/summary/Lepidophanes-guentheri.html

Notolychnus valdiviae https://www.fishbase.se/summary/4553

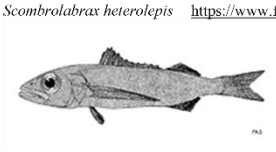


Monacoa grimaldii https://www.fishbase.se/summary/Monacoa-grimaldii.html

Omosudis lowii https://www.fishbase.se/summary/Omosudis-lowii.html

Pomatomus saltatrix https://www.fishbase.de/summary/pomatomus-saltatrix.html

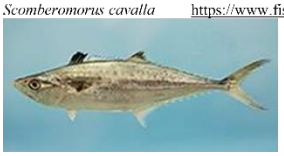
Scombrolabrax heterolepis https://www.fishbase.se/summary/Scombrolabrax-heterolepis.html



Saurida caribbaea https://www.fishbase.de/summary/Saurida-caribbaea.html

Scopelarchoides danae https://www.fishbase.se/summary/16627

Scomberomorus cavalla https://www.fishbase.se/summary/Scomberomorus-cavalla.html



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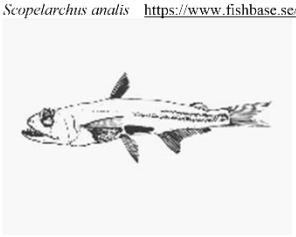

Sigmops elongatus https://www.fishbase.se/summary/7383

Urophycis floridana https://www.fishbase.se/summary/Urophycis-floridana.html

Stomias affinis https://www.fishbase.se/summary/Stomias-affinis.html

Ventrifossa macropogon https://www.fishbase.se/summary/Ventrifossa-macropogon.html

Thunnus obesus https://www.fishbase.se/summary/Thunnus-obesus.html