



Inferring trends in a small-scale, data-limited tropical fishery based on fishery-independent data

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ABSTRACT

Size-based indicators have emerged as useful tools to analyze the status of fisheries which lack fishery dependent data over long time series, such as many coral reef fisheries. In this study, we calculate a number of size-based indicators for the Haitian fishery at the remote Navassa Island, where a reef fish visual census (RVC) data set is available over an 8-year study period (2002–2009). We also calculate the slope of the size spectrum indicator within a Bayesian framework, which allows for potential biases inherent in the RVC method to be accounted for in credibility intervals around parameter estimates. Results of our analyses suggest that stocks targeted by traps declined from 2002 to 2004, followed by a period of increase from 2006 to 2009. The slope of the size spectrum declined from 2002 to 2004 and remained constant for the remainder of the study period, and this pattern was driven by a decrease in abundance of larger species targeted by hook-and-line. Analysis of the Lmax spectrum also indicated a decrease in the occurrence rates of larger species throughout the study period. Our methods can be applied to fisheries in other areas where limited fishery-independent data and no fishery-dependent data are available.

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1. Introduction

The status of fisheries is unknown for up to 70% of targeted species in industrialized nations, and for tropical fisheries the percentage of unassessed stocks is even higher (Beddington et al., 2007). As managers are increasingly required to assess these understudied species, many conventional assessment methods are not applicable as they require large data sets over much of the history of the fishery (Petitgas et al., 2009). Lack of data is a particular problem for coral reef fisheries, which tend to be located largely in developing countries where there exists little financial support for data collection and analysis (Graham et al., 2005). Such insufficiencies in data for reef fisheries have prevented evaluations of their sustainability (Ault et al., 2008). This gap in knowledge on the status of reef species is of particular concern, as a large percentage of human populations in developing countries are reliant on marine resources (Donner and Potere, 2007), and the living standards of coastal populations therefore depend on healthy fisheries.

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Given the importance of coral reef fisheries in this underfunded management context, there is a particular need to develop indicators suited to small scale fisheries with limited data. Fisheries assessments using size spectra were introduced several decades ago (Pope and Knights, 1982; Murawski and Idoine, 1992), and have more recently been tested in both temperate (Daan et al., 2005; Sweeting et al., 2009) and tropical zones (Graham et al., 2005). Size-based indicators (SBIs) based on community metrics, such as mean body length and the slopes of size frequency spectra, show consistent responses to exploitation across systems, and can be calculated based on limited data sets (Jennings and Dulvy, 2005). Average density and length of both communities and individual species are expected to decrease as fishing pressure increases (Shin et al., 2005). Furthermore, empirical studies have shown that the slope of the size frequency spectrum will decrease with increased exploitation (Daan et al., 2005; Graham et al., 2005). This occurs because fishers tend to first target larger-bodied fish, resulting in increased mortality rates on these larger size classes, which reduces both mean size within the community and the proportion of larger fishes in the community (Jennings, 2005).

Many SBIs are developed from fishery-independent fishing surveys such as trawl surveys (e.g., Daan et al., 2005; Sweeting et al., 2009), but such data are unavailable for the large majority of reef fisheries. Therefore, SBIs calculated using underwater visual census data are increasingly valuable (e.g., Graham et al., 2005; Stuart-

Smith et al., 2008). When underwater visual census data are used to calculate SBIs, however, there are additional uncertainties because fish lengths are influenced by both diver effects (Edgar et al., 2004) and habitat attributes (Gust et al., 2001). In this study, we calculate the slopes of size spectra based on a reef fish visual census (RVC) data set, but we improve on past methodologies by calculating indicators in a Bayesian framework, allowing us to quantify diver and habitat effects and calculate unbiased estimates of parameters. The study site is Navassa Island, a territory located 30 km to the west of Haiti, where a limited RVC data set is available based on four research cruises during the period 2002–2009.

Decreases in biomass and fork length of fish trophic and family groups, together with limited observations of escalating fishery activity at Navassa, suggested a decline in the status of the fishery from 2002 to 2004 (Miller et al., 2007). In this study, we calculate a more complete set of SBIs for the full data set encompassing a time line from 2002 to 2009. The goal of the study is to provide some information on trends and status of the fishery, based on this limited data set.

2. Materials and methods

2.1. Study site

Navassa Island (18°24'10" N, 75°0'45" W) is approximately 5-km² in area and is claimed by the USA, as well as by Haiti, but lacks permanent human population. The island is comprised of a raised plateau surrounded by steep cliffs reaching to a submarine terrace of approximately 23–30 m in depth (Miller et al., 2003). A second raised terrace on the island and additional dropoffs and terraces at depth yield an overall 'wedding cake' topography to the region (Miller et al., 2008a). The cliffs surrounding the island preclude the standard coastal mosaic of habitat types such as beaches, mangrove shorelines, and seagrasses. Consequently fish groups dependent on these habitats (e.g., grunts (Haemulidae)) are largely absent from the Navassa assemblage. The primary reef habitats are the steep reef walls formed by the cliffs, as well as patch reefs, spur and groove, and rubble covering the terrace. The island's oceanic position exposes it to substantial physical energy, and thus most of the sampling was carried out on the leeward side of the island (SW), with only occasional sampling past the northwest point being carried out on calmer days (Fig. 1).

Navassa's remote location makes it difficult to access, and information on fishing operations is scarce. The fishery at Navassa, for those Haitian fishers who can afford to make the trip, is an extremely important source of income; in spite of the fact that many of the fishers are to varying degrees also engaged in agricultural and other small (micro) business activities in Haiti. One thousand to 1500 families may be entirely dependent on fisheries related activities (fishing, boat building, equipment repair, gear manufacturing, marketing, etc.) in the region with approximately 300–400 fishers frequenting Navassa Island when not fishing close to home. Navassa's fisheries alone may account for between USD \$200,000 to USD \$500,000 a year to the mainland Haiti economy in the region. Exact figures are extremely difficult to come by due to the enormous number of variables, including the fact that the fishers themselves are unsure of their widely variable annual income (Wiener, 2005).

Distance and the dangers associated with the crossings between Navassa and the Haitian mainland, including high winds and waves, lack of food and water at Navassa, difficulty accessing the island proper, and lack of suitable equipment to reach the island (boats, motors) appear to prevent habitation and therefore reduce levels of exploitation as compared to the mainland. All fishers interviewed from fishing villages in western Haiti stated that fishing at Navassa

was worth the effort and they would all go fish there if they had the necessary equipment (Wiener, 2005). Fishers at Navassa claim they make up to ten trips per year, and some fishers had been visiting the island for more than 40 years. From all of the information gleaned from the fishers, exploitation of Navassa's fisheries by Haitians probably started in earnest around the turn of the 20th century, and most of the fishing pressure on its resources (>50%) appears to come from the village of Anse d'Ainhault (Wiener, 2005).

2.2. Observations of fishing activity

During all four cruises, observations of fishing activity were made, including numbers of boats, numbers of fishers, and gear types. In 2004, 2006, and 2009, the numbers of traps deployed were counted by searching for buoys (plastic bottles and styrofoam blocks) from the research vessel with binoculars and employing a laptop GIS application which recorded placement location around the island (Miller et al., 2008b). In 2009, fisher data collection was improved by sending fishers out with coolers, ice, and handheld GPS units and instructing them to store all catch in the coolers. Fishers returned to the research vessel at the end of each day, where each species was identified and measured to the nearest cm. Using this method we obtained data from two fishing boats over the course of two days. The measured catch was composed of fishes that had been caught in traps with a soak time of approximately one week, as well as from hook-and-line operations.

2.3. RVC data collection and underwater observation of traps

A stationary point count method to visually assess reef fish abundance (Bohnsack and Bannerot, 1986) was used to obtain fishery independent samples. SCUBA divers, at the designated survey point, identified all species within 5 min in an imaginary 7.5-m cylinder, with fishes appearing after 5 min recorded separately (McClellan and Miller, 2003; Brandt et al., 2009). For each species, divers estimated the number of fishes, as well as the minimum, maximum, and average size (cm) observed. The total number of sites surveyed each year was as follows: 110 in 2002, 123 in 2004, 150 in 2006, and 140 in 2009. Eight habitat types were surveyed in the four periods, but the percentage of sites surveyed in each habitat varied from year to year (Table 1). In addition to the standardized RVC sampling, in 2009 a single diver completed underwater visual censuses of 8 fish traps that had been deployed by Haitian fishermen and had been soaking for approximately one week. All trapped fishes were identified to species and length of each fish estimated to the nearest cm.

2.4. Conversion of RVC data to individual lengths

For species where fewer than four fish were observed in the sample, or where four or more fish were observed but were estimated to be the same size (79% of all data entries, Table S1), actual observed lengths of individuals were recorded by divers. However when more than three individuals of different sizes were observed, only the minimum, maximum, and average size of the group of individuals were recorded, and the lengths of individuals within the groups had to be inferred from these data. Size frequency distributions of known fish lengths for each species were inspected and were found to approximate a Poisson distribution. For observations where the number of individuals was >3, the three individuals with known lengths were considered as known individuals, and the remaining individuals were estimated as being distributed as a Poisson distribution with a λ parameter equal to the diver's observed average length, and with minimum (maximum) values truncated accord-

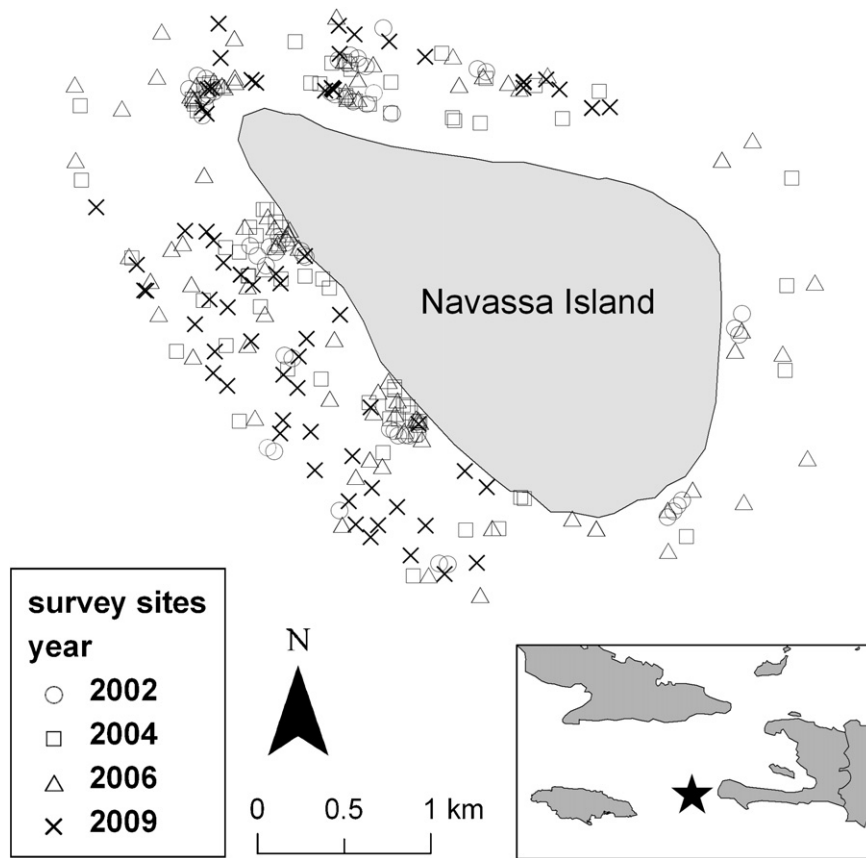


Fig. 1. Map illustrating location and topography of Navassa Island. Contours give depth or elevation in meters.

ing to the diver's observed minimum (maximum). The result is a size frequency distribution with the mode equal to the average value recorded by the diver, which is a good approximation, particularly for large schools of fish where the mean tends towards the mode. Simulated fish lengths using the Poisson distribution were compared against simulated lengths using alternate distributions (triangle, gamma). It was found that the actual distribution used had little influence on the final result; distributions were driven more by the diver's data observations, and the choice of distribution had little effect on inferred length frequencies.

2.5. Classification of species into target subgroups

A list of commercially targeted species was compiled using past reports on the Navassa fishery (Miller et al., 2003; Wiener, 2005), as well as from direct observations of catch data from Haitian fishermen recorded during the four cruises. Species not observed in the catch were excluded from the analyses, as they could not be confirmed as target species. A total of 174 species were observed in RVC counts; 51 of these were identified as commercial species. Non-commercial species included gobies (*Gobiidae*),

Table 1
Sampling design specifying the number of sites surveyed within each habitat type by diver and year. Commercial fish species were observed at 514 of the total 523 sites surveyed.

Year	Diver	Sharp-edged spur and groove	Shallow ledge	Calves	Vertical wall	Wall base	Sand/rubble	Deep low-relief hard bottom	Deep patch reef	Total
2002	1	8	3	6	3	8	1	1	26	56
2002	2	8	3	6	3	8	0	1	25	54
2004	1	5	5	1	4	8	3	3	15	44
2004	3	4	0	0	3	4	1	1	20	33
2004	4	6	1	2	7	8	1	3	17	45
2006	1	4	3	7	0	1	3	4	21	43
2006	3	2	1	5	0	5	3	1	17	34
2006	5	2	1	5	0	1	2	5	17	33
2006	6	3	4	6	1	1	1	4	16	36
2009	3	3	0	0	1	2	0	0	23	29
2009	7	8	0	0	0	2	0	0	14	24
2009	8	0	4	0	1	0	0	0	19	24
2009	9	4	0	0	0	2	0	0	23	29
2009	10	2	0	0	0	1	0	0	19	22
2009	11	0	0	0	0	0	0	0	8	8
Total		59	25	38	23	51	15	23	280	514

blennies (*Blenniidae*), hamlets (*Serranidae*), damselfishes (*Pomacentridae*) and small wrasses (*Labridae*). Three additional species that were listed in the catch data were excluded from the length based analyses. The yellowhead wrasse (*Haliophanes garnoti*, 2340 individuals observed in the RVC), blue chromis (*Chromis cyanus*, 33,198 individuals observed in the RVC) and creole wrasse (*Clepticus parrae*, 20,119 individuals observed in the RVC) were excluded because they were seen only rarely in the catch, and only the largest individuals of these species are retained by the mesh of traps (average body size for all three species was <10 cm).

Species observed in the RVC survey were classified by whether they were likely to be caught by traps, hook-and-line fishing or both. A list of species vulnerable to capture by Antillean Z traps was compiled by including all species that had been observed in fish traps by divers, as well as species that were identified in the catch but not the traps, if they could not have been collected by hook-and-line (e.g., *Acanthuridae* surgeonfishes; *Scaridae* parrotfishes). We added to this list three species of butterflyfishes: *Chaetodon capistratus*, *C. ocellatus*, and *C. striatus*. These were included based on another study of Antillean Z-traps in Haiti (Ferry and Kohler, 1987), which showed that Chaetodontids were the fourth most abundant family in the traps. The absence of butterflyfishes in the Navassa traps (except for a single *Chaetodon striatus*) was likely due to their relatively low abundance at Navassa and the low sample size of traps surveyed. Grunts were also rare at Navassa due to the lack of appropriate habitat. All other families shown to be abundant in the Ferry and Kohler (1987) study were well represented in our trap surveys.

Hook-and-line fishing was not directly observed, although many larger species normally targeted by this method were observed in the fishers' catch and were not normally observed in traps; thus they were likely caught with hook-and-line. Members of five families, *Serranidae* (groupers), *Lutjanidae* (snappers), *Sphyraenidae* (barracudas), *Carangidae* (jacks), and *Haemulidae* (grunts) were assumed to be targeted by hook-and-line fishing based on studies from other regions (Babcock, E.A., pers. comm.). Species within these families that had been observed to enter Antillean Z traps in Navassa were removed from this list so that the effects of trapping would not confound the analyses of the subgroup of species targeted by hook-and-line.

2.6. Calculation of trappability

Trappability, a metric of the susceptibility of a species to traps, was calculated using the methods of Hawkins et al. (2007). If trapping effort had increased (decreased) during the study period, we would then expect to see greatest evidence of decline (recovery) in species with higher trappability values than those species which are less vulnerable to trapping. Trappability is expressed as a ratio of a species' proportional abundance in traps to its proportional abundance in underwater visual surveys, where proportional abundance is defined by the number of individuals of the species divided by the total number of individuals of all species. For our study, proportional abundance in the community was calculated from the standard RVC survey counts for all four years, and proportional abundance of trapped fishes was calculated from the eight underwater visual trap counts. Although our sample size of catch data from fishermen was larger than the sample size from the trap counts, we did not use the former data in calculations of trappability because catch data were composed of undifferentiated trap and hook-and-line catches, nor could we accurately calculate relative abundance from this data set because an unknown portion of the fish were used as bait before the catch was sampled.

Table 2

List of species classified as caught by hook-and-line and not trapped. Includes families known to be susceptible to line fishing (barracudas, groupers, grunts, jacks, and snappers). Species that were either indicated to be trappable in the Hawkins et al. (2007) study or those that entered traps in Navassa were removed from this list.

Species	Family
<i>Sphyraena barracuda</i>	Barracudas
<i>Mycteroperca interstitialis</i>	Groupers
<i>Mycteroperca phenax</i>	Groupers
<i>Mycteroperca tigris</i>	Groupers
<i>Mycteroperca venenosa</i>	Groupers
<i>Epinephelus guttatus</i>	Groupers
<i>Haemulon album</i>	Grunts
<i>Haemulon carbonarium</i>	Grunts
<i>Haemulon sciurus</i>	Grunts
<i>Caranx bartholomaei</i>	Jacks
<i>Caranx lugubris</i>	Jacks
<i>Caranx ruber</i>	Jacks
<i>Seriola dumerili</i>	Jacks
<i>Ocyurus chrysurus</i>	Snappers
<i>Lutjanus analis</i>	Snappers
<i>Lutjanus apodus</i>	Snappers
<i>Lutjanus buccanella</i>	Snappers
<i>Lutjanus jocu</i>	Snappers

2.7. Changes in mean length and density over time

Species-level length and density trends were analyzed for the seven most frequently occurring trapped species and the five most frequently occurring species targeted by hook-and-line. All of these species had occurrence rates in the RVC of >20%; species with lower occurrence were not analyzed due to low statistical power. To analyze changes in length frequency over the four sampled years, we modeled individual fish length using a three-way mixed-effects analysis of variance (ANOVA) with habitat type and diver as random effects and year as a fixed effect, for each of the 10 species independently (R version 2.7.2, R Core Development Team 2008, library lme4). To look at changes in species' density over the four sampled years, we extracted data from the standardized five minute sample period. Because the high number of zero counts prevented transformation of these variables to normality, we used a delta lognormal model to test for differences (Serafy et al., 2007). We modeled lognormal abundances when present with a generalized linear model using habitat type and diver as random effects and year as a fixed effect, and modeled presence/absence data with a logit link generalized linear model using the same random and fixed effects. Separate *P* values are reported for each test, and the back-transformed occurrence and concentration estimates are multiplied to estimate the lognormal fish density (Lo et al., 1992).

We also analyzed changes in density across target groups: (1) the entire fished community, (2) species targeted only by hook-and-line (Table 2), and (3) species targeted only by traps (Table 3). Densities were log-transformed to meet assumptions of normality and a three-way ANOVA was used (year, habitat, and diver as factors; habitat and diver as random effects) to analyze changes in density over time. Due to the presence of many zero counts for the species targeted by hook-and-line, the delta lognormal method described above was used to test for trends in this subgroup.

Because not all habitat types were sampled in every year, our results could have potentially been biased by our unbalanced survey design. To assess the bias introduced by such a design, we reran the above analyses using a balanced subsample of the data set. The balanced data set was created by removing data from habitat types that were not represented in all years, and then randomly drawing from the remaining data with replacement so that each habitat type was sampled the same number of times in each year. Rerunning analyses on changes in mean lengths and densities with the balanced data showed that the unbalanced design had little effect

Table 3
Comparison of trappability (proportional abundance in traps/proportional abundance in visual surveys) of fish species in Navassa and trappability values reported for Jamaica (Hawkins et al., 2007).

Species	Family	Navassa trappability	Jamaica trappability
<i>Acanthostracion polygonia</i> ^a	Cowfishes	37.7	Trapped
<i>Diodon holocanthus</i> ^a	Puffers	31.4	42.1
<i>Cantherhines macrocerus</i> ^a	Filefishes	24.4	Not present
<i>Epinephelus striatus</i> ^a	Groupers	22.0	Not present
<i>Gymnothorax moringa</i> ^a	Moray Eels	18.3	Not present
<i>Lactophrys triqueter</i> ^a	Cowfishes	15.7	0.0
<i>Sparisoma aurofrenatum</i> ^a	Parrotfishes	2.8	0.4
<i>Mulloidichthys martinicus</i> ^a	Goatfishes	1.7	0.0
<i>Holocentrus adscensionis</i> ^a	Squirrelfishes	1.5	0.0
<i>Cephalopholis fulva</i> ^a	Groupers	1.5	0.0
<i>Cephalopholis cruentata</i> ^a	Groupers	1.4	0.3
<i>Pseudupeneus maculatus</i> ^a	Goatfishes	1.4	0.0
<i>Acanthurus bahianus</i> ^a	Surgeonfishes	1.3	3.6
<i>Acanthurus coeruleus</i> ^a	Surgeonfishes	1.3	12.0
<i>Holacanthus tricolor</i> ^a	Angelfishes	0.7	1.3
<i>Xanthichthys ringens</i> ^a	Triggerfishes	0.5	0.0
<i>Scarus taeniopterus</i> ^a	Parrotfishes	0.5	1.2
<i>Holacanthus ciliaris</i>	Angelfishes	0.0	Trapped
<i>Lutjanus apodus</i>	Snappers	0.0	Trapped
<i>Acanthurus chirurgus</i> ^a	Surgeonfishes	0.0	112.2
<i>Sparisoma chrysopterus</i> ^a	Parrotfishes	0.0	18.0
<i>Haemulon flavolineatum</i>	Grunts	0.0	3.5
<i>Sparisoma viride</i> ^a	Parrotfishes	0.0	1.1
<i>Scarus iseri</i>	Parrotfishes	0.0	0.04

Species present in traps but not in visual counts listed as “trapped.”

^a Indicates that the species was included in the subgroup of trapped species for analyses.

on the final outcomes; the direction and approximate magnitude of trends were the same in all cases, although due to smaller sample sizes the balanced subsample supported fewer significant trends. Because the statistical power was increased by using the complete data set, here we report results from the complete unbalanced design.

2.8. Bayesian hierarchical model of slope of size spectrum indicator

The slope of the log transformed size spectrum can serve as an indicator of fishing pressure on fish communities (Daan et al., 2005; Graham et al., 2005). Because our RVC fish length data were influenced by both diver effect and habitat type, we calculated the size spectrum slope indicator using a Bayesian hierarchical model in which diver and habitat effects were modeled as random effects and year was a fixed effect (Royle and Dorazio, 2008). The slope of the size spectrum should be calculated only for size classes well-selected by the gear or sampling methodology (Daan et al., 2005; Jennings and Dulvy, 2005), so we excluded upper and lower size classes that were not observed in all years or had a log-frequency much lower than would be predicted by a linear slope. The size classes used to calculate this indicator were: 10–60 cm for the entire fished community, 10–40 cm for trapped fishes, and 25–60 cm for species caught on hook-and-line, as these size classes were well-represented (Fig. 2).

The observed numbers of individuals in each of the 5-cm length bins ($x_{y,i,j,k}$ where y represents each year, i represents each diver, j represents each habitat type and k represents each size class) is multinomial, so that

$$f(x_{y,i,j}) = \frac{N_{y,i,j}!}{\prod_{k=1}^K x_{y,i,j,k}!} \prod_{k=1}^K (p_{y,i,j,k})^{x_{y,i,j,k}} \quad (1)$$

where $X_{y,i,j}$ is the matrix of $x_{y,i,j,k}$ values for year y with diver i in habitat j , K is the number of size classes, $N_{y,i,j}$ is the total number of observations by year y with diver i in habitat j , and $p_{y,i,j,k}$ is the

probability that an individual fish observed in year y by diver i in habitat j will be in size class k . Because the probabilities of an individual falling into each size class must sum to one, we calculate p as:

$$p_{y,i,j,k} = \frac{\varphi_{y,i,j,k}}{\sum_k \varphi_{y,i,j,k}} \quad (2)$$

and model φ , the proportion of individuals in size class k , as a function of diver and habitat effects:

$$\log(\varphi_{y,i,j,k}) = \alpha_{y,k} + \beta_{i,k} + \gamma_{j,k} \quad (3)$$

where β is the diver effect, γ is the habitat effect, and α is the mean proportion of individuals for each year y in each size class k in the absence of diver and habitat effects (Ntzoufras, 2009). The slope of the natural log-transformed size spectrum for each year is then calculated as the slope of the linear regression of α_k across the midpoint values of size classes k . Significant trends between years are indicated when mean estimates do not fall within the credibility intervals (i.e., posterior probability interval analogous to the frequentist confidence interval) of the estimates for other years.

We implemented our Bayesian model in WinBUGS software (Lunn et al., 2000). For each model, two Monte Carlo Markov Chains were run for 100,000 iterations, which was sufficient to ensure convergence. An initial burn-in period of 1000 iterations was used. Convergence was reached when autocorrelation of both chains was similar, MC error was less than 1% of the standard deviation of the posterior for the slope parameter, and the Gelman–Rubin diagnostic approached one (Brooks and Gelman, 1998).

The Bayesian model was run for the size frequency spectrum of (1) the entire community of targeted species, (2) species targeted by traps only, and (3) species targeted by hook-and-line only. We considered four alternate models which included respectively: (1) diver and habitat effects, where the same diver on multiple cruises was treated as the same observer (8 habitats and 11 divers), (2) diver and habitat effects, where the habitats were grouped into coarser classifications (5 habitats and 11 divers), (3) a model including only habitat effects and no diver effects (8 habitats), and (4) a model including only diver effects and no habitat effects. The deviance information criterion (DIC) was calculated for all mod-

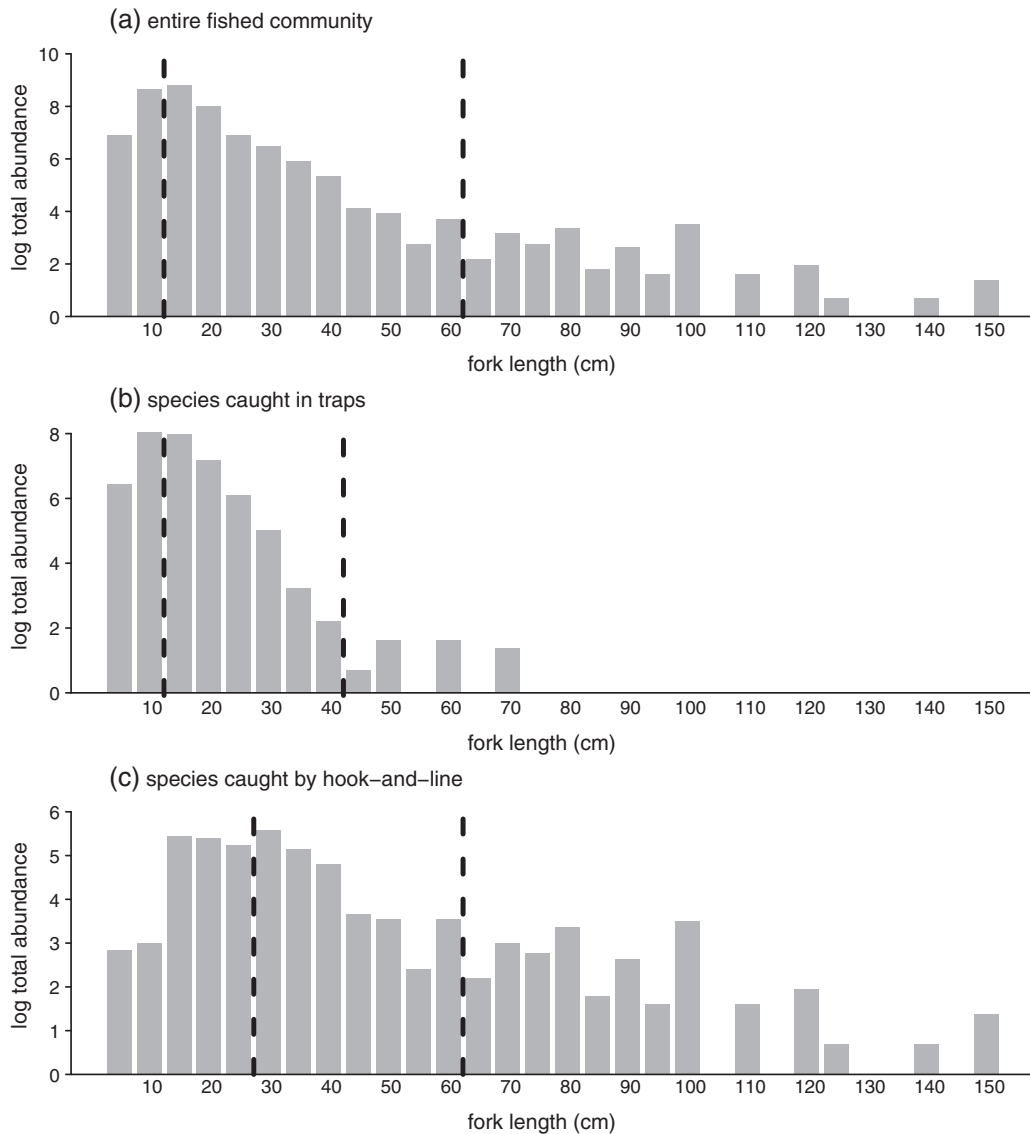


Fig. 2. Natural log scale size frequency histograms for entire fished community (top), trapped species (middle), species caught on hook-and-line (bottom). Combined data from all years and sites are shown. Dashed lines delineate the size classes used in the size spectra analyses.

els using the DIC function in WinBUGS, to determine which model was the most parsimonious. Models with Δ DIC values <2 are supported by the data, while Δ DIC values >10 indicate that the model is not supported (Spiegelhalter et al., 2002).

Again, we assessed the effect of the unbalanced design on the outcome of our results by repeating the Bayesian hierarchical analyses with a subsampled balanced data set with respect to habitat and year. Because of the reduced sample size with the subsampled data set, the model did not converge for two cases: the entire fished community and the subgroup of fishes targeted by hook-and-line. The model did converge for the subgroup of trapped fishes and we found that results were similar regardless of whether the balanced or unbalanced design was used.

2.9. L_{max} spectra

To investigate indirect effects of fishing, particularly on members of larger size classes not included in the slope of size spectra, we analyzed the L_{max} spectra according to the methods of Daan et al. (2005). Because natural mortality rates should be inversely correlated with L_{max} , changes in the L_{max} spectra may indicate

indirect effects of fishing by reflecting changes in total mortality of the species within the community (Daan et al., 2005). Maximum body length (L_{max}) values for each species were extracted from FishBase (Froese and Pauly, 2011). Each species was assigned to one of six L_{max} classes ($L_{max} < 30$ cm, 30–40 cm, 40–55 cm, 55–75 cm, 75–100 cm, and >100 cm); size categories were selected in order to balance the number of species in each L_{max} class. We analyzed the temporal changes in density of fishes within each L_{max} class using a three-way ANOVA (year, habitat, and diver as factors; habitat and diver as random effects). Again, densities were log-transformed and the delta lognormal method was used due to the high number of zero counts; separate P values are reported for presence/absence and density when present.

3. Results

3.1. Observations of fishing activity

Our limited observations of fishing effort are reported in Table 4. The number of active boats and fishers, as well as number of deployed traps and triple mesh nets was highest during the 2004

Table 4
Observations of fishing effort during the study period.

Date of observation	Duration of observation (d)	Measure of fishing effort			Gear in use		
		Total # gear buoys/traps	Total # of boats observed	Total # of fishers observed	Traps	Hook-and-line	Nets
Nov 2002	11	NA	8	44	X	X	–
Nov 2004	13	97	12	66	X	X	X
Apr 2006 ^a	10	7	1	4	X	X	–
Nov 2006	11	46	9	36	X	X	–
Apr 2009	9	25	2	8	X	X	–

^a Observations from Apr 06 are reported in Piniak et al. (2006). No RVC data were available from this observation.

cruise. It is likely that fishing effort fluctuates seasonally as the remote and exposed location of Navassa makes crossing and fishing extremely hazardous during rough seas. Our two observations in April both show substantially lower effort than observations in November. Observations are not necessarily representative of actual fishing activity, as we were only able to obtain snapshots with low temporal resolution.

3.2. Differences in trappability between regions

Trappability values ranged from 0 to 38 (Table 3). Some species, such as the parrotfishes (redtail *Sparisoma chrysopterym*, and stoplight *S. viride*) were not seen in the underwater trap counts but did appear in the fishers' catch, indicating that more samples were needed to fully assess trappability. Despite the low sample size (8 observed traps), there are some notable differences between our study and the Hawkins et al. (2007) study of similar traps deployed in Jamaica. For example, the smooth trunkfish (*Lactophrys triqueter*) was found to be highly trappable (15.71) in our study, and was not reported in traps in Jamaica. Also notable is that the endangered Nassau grouper (*Epinephelus striatus*) was highly trappable (22.0) in our study, but the species was not present in traps or RVC counts in Jamaica. Some of the species found to be moderately trappable in our study (yellow goatfish *Mulloidichthys martinicus*, squirrelfish *Holocentrus adscensionis*, coney *Cephalopholis fulva*, spotted goatfish *Pseudupeneus maculatus*; trappability between 1.4 and 1.7) were also not trapped in the Hawkins et al. (2007) study.

3.3. Individual species trends in length and density

Average length and abundance changed significantly over time for some species (Fig. 3). The four species with trappability values over 1 that were not caught by hook-and-line (redband parrotfish *Sparisoma aurofrenatum*, yellow goatfish *Mulloidichthys martinicus*, ocean surgeonfish *Acanthurus bahianus*, blue tang *A. coeruleus*) showed significant increases in length or abundance from 2004 to 2009. Two trap-caught species with lower trappability values (stoplight parrotfish *Sparisoma viride*, rock beauty *Holacanthus tricolor*) showed no change in length or density over time, while average length of the princess parrotfish *Scarus taeniopterus* fluctuated significantly between years. Two grouper species targeted by both traps and hook-and-line (coney *Cephalopholis fulva* and graysby *C. cruentata*) both showed significant decreases in density during some periods of the study, but increases in length from 2004 to 2009. Two commonly-occurring species targeted only by hook-and-line, the bar jack *Caranx ruber* and the barracuda *Sphyraena barracuda*, showed significant decreases in density from 2004 to 2006 and 2006 to 2009 respectively, while density of the schoolmaster snapper *Lutjanus apodus* decreased from 2006 to 2009.

3.4. Community trends in length and density

Changes in fish density over time, when analyzed at the community level, were only marginally significant. For the target

community as a whole, the effect of year was marginally significant (Fig. 4a, $P=0.057$) and there was an increase in density of targeted fishes in 2009. The subgroup targeted by traps mirrored the trend in the entire fished community with an increase in density in 2009 (Fig. 4b, $P=0.134$). Density of hook-and-line fishes declined between 2004 and 2009 (Fig. 4c). The year effect was significant for presence/absence ($P=0.026$), but not for abundance when present ($P=0.159$).

The deviance information criterion (DIC) values for the five size spectrum models showed that both habitat and diver effects were important (Table 5). The model with the lowest DIC value was the full model, where all 8 habitat groups were included and diver effects were included. There was no support for any of the alternative models, as Δ DIC values were all $\gg 10$. When habitats were grouped into coarser classifications (5 habitat types rather than 8), the Δ DIC of the model was 176.55, indicating that the effect of the 8 habitats on fish lengths were significant. Both habitat effects and diver effects were clearly important, as the models excluding these factors had Δ DIC values of 459.80 and 412.47, respectively. Because there was no support for any of the alternative models, we only report below the parameter estimates generated by the full model (11 divers and 8 habitats).

Bayesian hierarchical estimates of the slope of the log size frequency showed a declining trend for the entire fished community from 2002 to 2004, with little change from 2004 to 2006 and a slight decline from 2006 to 2009 (Fig. 4d). The change in slope from 2002 to 2004 was significant and represents larger individuals and larger species being less abundant in later years (Fig. 5). Decreasing slope can also be an indication of increasing numbers of smaller fishes, and Fig. 5 shows that the slight increases in abundance in the smaller size classes are due to the contributions from the increases in trapped species, particularly in size classes 20–30 cm. For the subgroup of trapped fishes (Fig. 4e), there was no trend over the study period. For the subgroup of species targeted by hook-and-line, there was a significant decline in the slope from 2002 to 2004, but no significant differences were observed from 2004 to 2009 (Fig. 4f).

Analysis of the Lmax spectra showed a slight increase in density of small species from 2006 to 2009, no change in densities of intermediate-sized species, and significant decreases in the occurrence rates of large species (Fig. 6). For analyses of densities when present, significant changes across time were only detected for

Table 5
Results of deviance information criterion (DIC) for choosing the most parsimonious model for slope of the size spectrum for the entire fished community. Δ DIC values >10 indicate no support for the model.

Model	Effective # parameters	DIC	Δ DIC
11 Divers, 8 habitat groups	131.69	3396.51	0.00
11 Divers, 5 habitat groups	111.12	3573.06	176.55
No diver effect, 8 habitat groups	74.45	3808.98	412.47
11 Divers, no habitat effect	91.35	3856.31	459.80

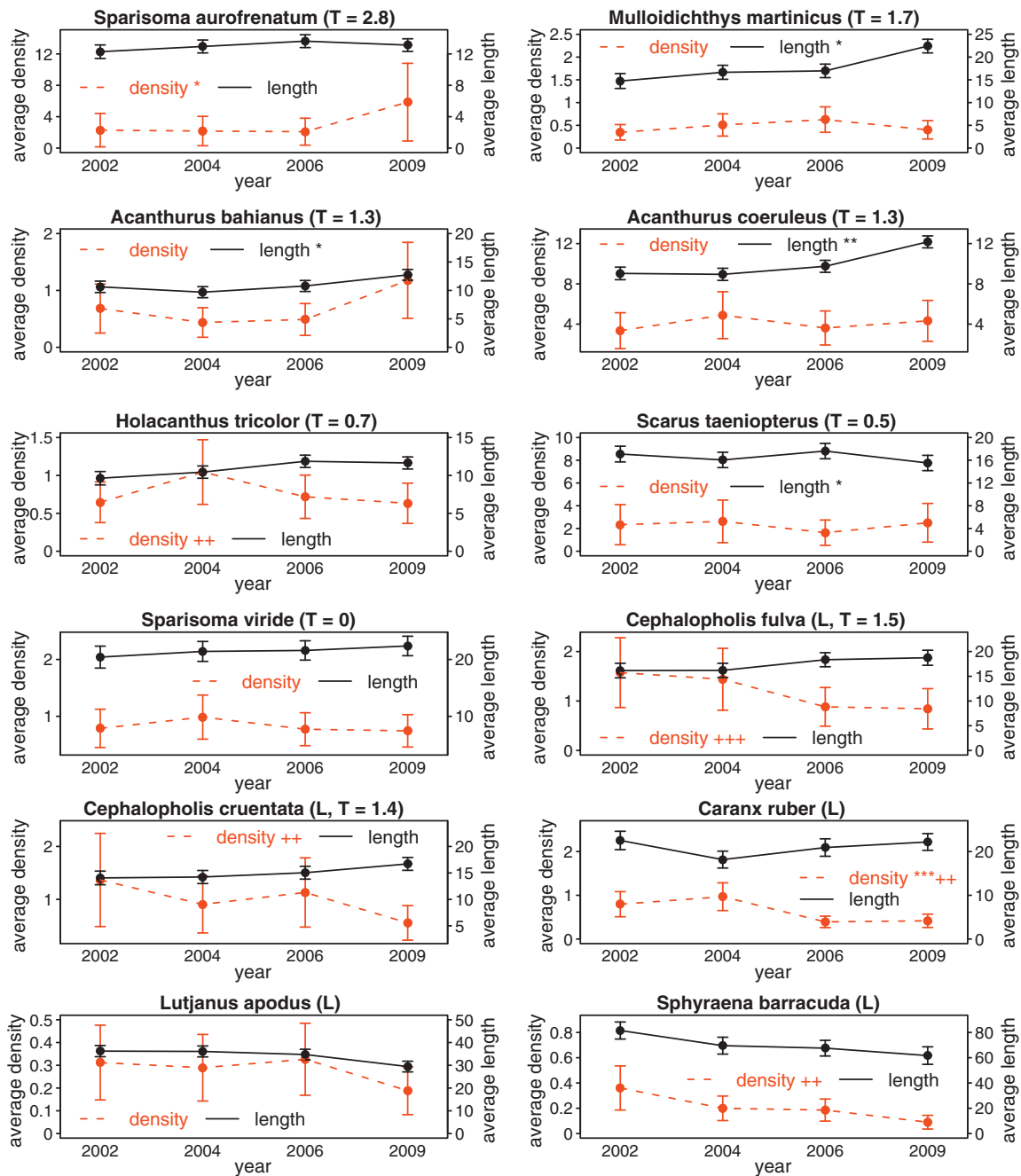


Fig. 3. Average density (number of individuals) per sample and average fork length for individual species (cm). Calculated trappability (T) of each species is indicated; species targeted by hook-and-line indicated with (L). Significance of changes in length and density when present indicated by * symbol; significance of changes in presence/absence indicated + symbol. Error bars are ± 1 S.E. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

species < 30 cm ($P = 0.04$). Changes in density when present were not significant for all Lmax classes > 30 cm ($P > 0.05$). Declines in occurrence rates were significant for fishes in Lmax classes from 40 to 100 cm in years 2006 and 2009, and for fishes > 100 cm in 2009 (Fig. 6).

4. Discussion

Despite the very limited data set available for the Navassa Island fishery, our analyses were able to detect trends in the fished community and even in some of the more abundant individual species throughout the 8-year study period. We detected an overall decline in fish size over the study period, as evidenced by a decrease in the slope of the size spectra, primarily in the interval from 2002 to 2004.

We also detected a decline in the occurrence rates of larger fish species from 2004 to 2009 (Fig. 6). Analyses of changes in fish densities over time at both the species and group level suggest stability in the subgroup of fishes caught only with traps, with increasing densities from 2006 to 2009 (Figs. 3 and 4b). Continued decreases in relative abundances are observed for species targeted by hook-and-line, especially since 2004 (Figs. 3 and 4c). The two small grouper species (graysby and coney) are targeted by both traps and hook-and-line, and both showed significant decreases in density from 2004 to 2006 and 2006 to 2009 respectively, with a slight trend of increasing length from 2004 to 2009 (*Cephalopholis* spp., Fig. 3). These results are consistent with the very limited observations of fishing activity, suggesting cessation of the use of triple mesh nets and a potential decrease in the number of traps since 2004.

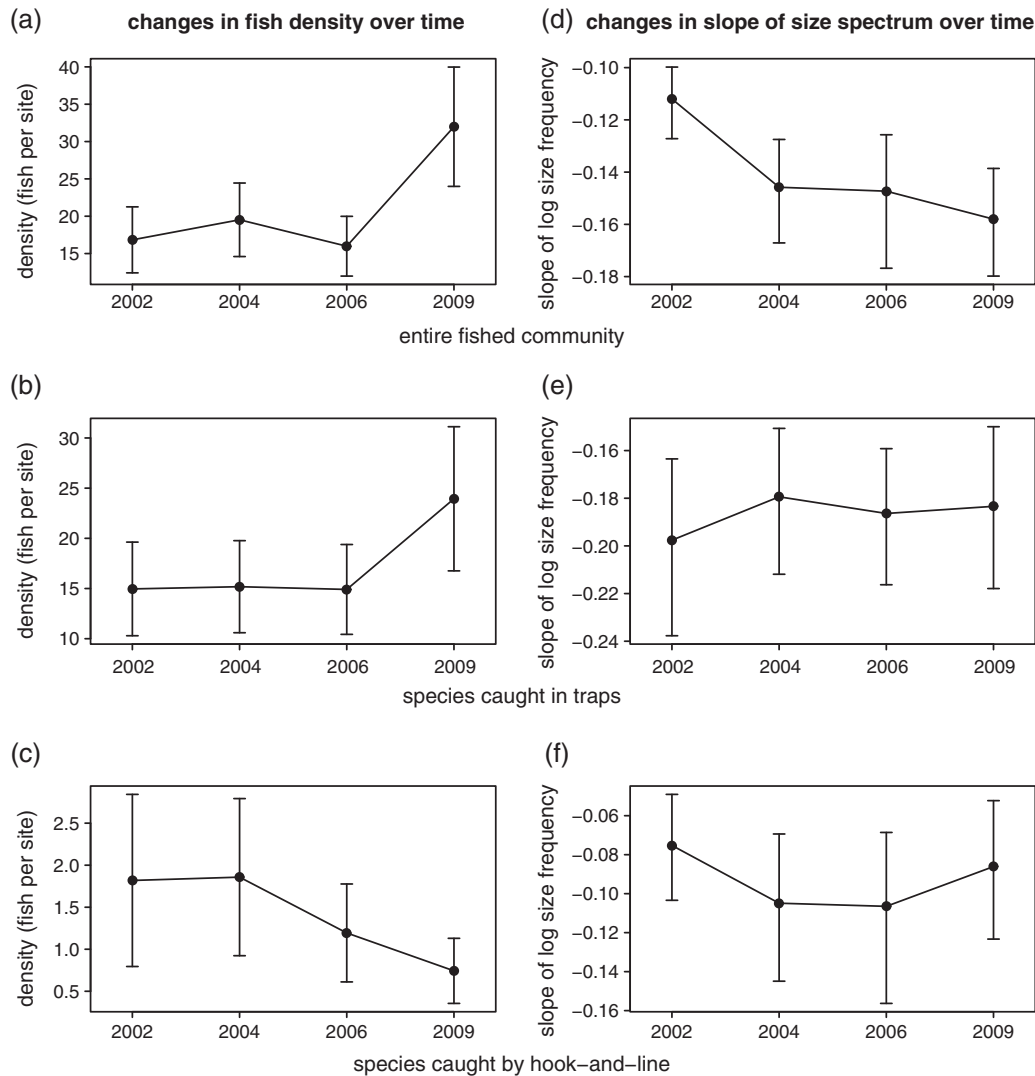


Fig. 4. Changes in density or number of individuals per site (left) and slope of the natural log size frequency spectrum (right) for fish communities. Left: results of 3-way ANOVA (year, diver, and habitat as factors, diver and habitat as random effects). Error bars are ± 1 S.E. (a) Entire fished community: $F_{(1,3)} = 9.07$, $P = 0.057$; (b) trapped species: $F_{(1,3)} = 4.16$, $P = 0.134$; (c) species caught on hook and line: $F_{(1,3)} = 3.47$, $P = 0.159$. Right: results of Bayesian hierarchical model. Error bars are 95% credibility intervals.

The indicators of population status and trends varied among species. For example, average length of the princess parrotfish fluctuated from 2002 to 2009, while all other trapped species showed a stable or increasing trend in average length (Fig. 3). The decreasing size of princess parrotfish during some periods may have been a result of fishing, increased predation on the species or reduced habitat availability for this particular species; it could also be caused by the presence of one or two strong year classes entering the population, although density has not changed.

Length distributions and densities of individual fish populations may potentially fluctuate dramatically due to a range of factors in addition to fishing pressure. Large, stochastic recruitment of individual reef fish species is well known. However, congruent fluctuations among entire assemblages are plausible only to the degree that physio-oceanographic factors (rather than species-specific larval production) determine interannual variation in recruitment. While long term studies of interspecific synchrony in decadal-scale recruitment variability are rare for any region (with the exception of Robertson et al., 1993), the relatively isolated location and uncertain degree of self-recruitment of Navassa makes the likelihood of assemblage-level recruitment pulses difficult to evaluate. Regardless, community-level indicators should be less influenced by stochastic recruitment pulses than individual species and there-

fore may be favorable over species-specific indicators to detect fishing impacts, particularly in data limited situations.

In addition to varying fishing pressure and stochastic recruitment, fluctuations over entire fish assemblages may result from other disturbances such as storm impacts or alterations in basic habitat condition. Tropical cyclones are a relatively common occurrence in the central Caribbean, with six named storms passing within 100 km of Navassa between 2002 and 2008 (as indicated by NOAA's Historic Hurricane Tracks tool; <http://www.csc.noaa.gov/hurricanes/#>, accessed 10 Jan 2011); one in each year from 2005 to 2007, two in 2008, and one in 2002. The strongest of these (at its closest point) was Ernesto in late Aug 2006. This impact was just prior to the 2006 surveys in November, but there were no substantial changes noted between 2004 and 2006 for the entire fished community (Fig. 4a and d); the greatest changes in the assemblage were noted between 2002–2004 (size) and 2006–2009 (density). Other studies indicate that the direct, demographic effects of physical disturbances on reef fish assemblages are short lived or unimportant, while the effects of potential co-incident habitat destruction are enduring (e.g., Syms and Jones, 2000; Adams, 2001). Meanwhile, hurricane damage is only one of many contributors to overall coral reef habitat decline, as documented throughout the Caribbean (Gardner et al., 2003;

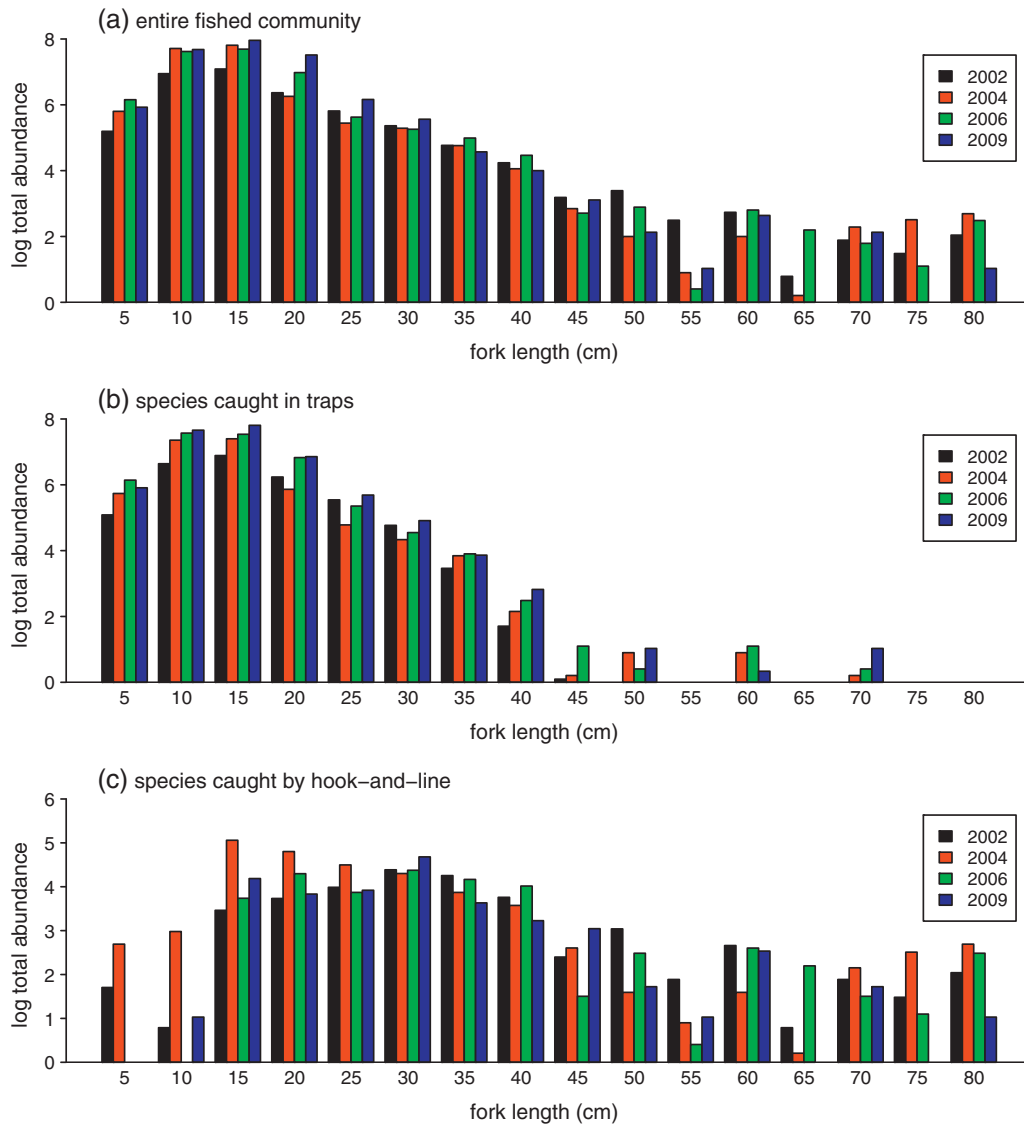


Fig. 5. Natural log scale size frequency histograms separated by year for entire fished community (top), trapped species (middle), species caught on hook-and-line (bottom).

Alvarez-Filip et al., 2009) and in Navassa in particular (Miller et al., 2008b). However, these ubiquitous habitat changes are monotonic and, hence would be expected to relate to monotonic declines in dependent fish assemblages. Such a pattern has been suggested in Caribbean-wide meta-analyses (Paddock et al., 2009) but is not consistent with results of the current study showing recent increases in density and, since 2004, stable size spectrum slope for the entire fished community (Fig. 4a and d) over a period when declines in coral cover and increases in macroalgal cover have been monotonic (Miller et al., 2008b).

Given that we saw increases in some of the important herbivorous fishes (increased density of *S. aurofrenatum* and increased sizes of two *Acanthurus* spp., Fig. 3), we could potentially anticipate a feedback effect to reverse these declining trends in benthic assemblages (e.g., Mumby et al., 2007). However, such a recovery in the benthos may be limited by: (1) overwhelming space occupation by unpalatable macroalgae (Williams et al., 2001; Mumby, 2009), as *Lobophora variegata* constituted over one-third of the average 62% macroalgae cover in Navassa in 2009 (M. Miller, unpubl. data) or (2) poor recruitment of Caribbean reef-building corals. Such factors might preclude herbivores from effecting an anticipated 'reverse phase-shift' (e.g., Bellwood et al., 2004) in this particular system.

The Bayesian hierarchical model estimated a decline in the slope of the size spectrum from 2002 to 2004 and to a lesser extent from 2006 to 2009 for the entire targeted group of species (Fig. 4d), consistent with a pattern expected under increasing fishing pressure and possibly size selective fishing (Sweeting et al., 2009). Within the subgroups of trapped fishes or those targeted by hook-and-line, there were no clear trends in the size spectra over time, except for a slight decline in the slope from 2002 to 2004 for species caught by hook-and-line (Fig. 4e and f). The lack of trends in these subcommunities may be a result of the relationship between size and log abundance being linear across only a small number of size categories. Jennings and Dulvy (2005) showed that the power of surveys to detect trends in size spectra depends on the range of size classes included in the analysis. The slope of the size spectra indicator is also unable to account for information contained in some of larger size classes, which were excluded due to poor representation in all four years. Analysis of the Lmax spectra indicated that occurrence rates of intermediate-sized fishes (40–75 cm) declined significantly from 2004–2009, and that large-sized fishes (>75 cm) declined even more dramatically during the same period. These trends may be due to a lag in the effects of heavy trapping effort during earlier years, or may be a direct result of increasing pressure on larger-sized individuals from hook-and-line fishing.

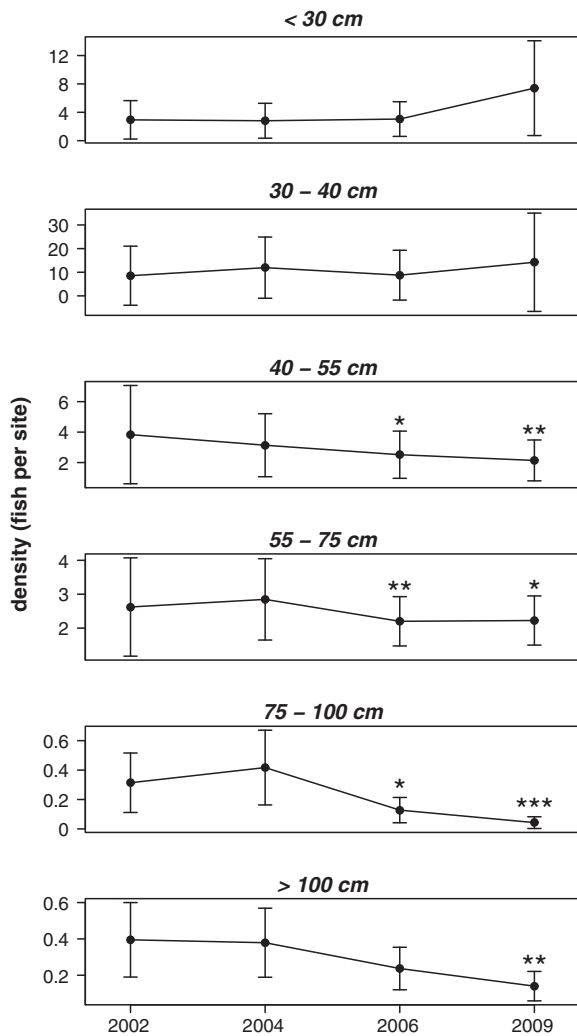


Fig. 6. Average density (number of individuals per sample) of fishes within Lmax size classes. Changes in density when present were only significant for the <30 cm class ($P=0.04$). Significance of changes in presence/absence indicated by * symbol. Error bars are ± 1 S.E. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

In empirical fisheries applications, size spectrum analysis is usually applied to the size of the fish in the commercial catch or those caught in research surveys using fishing gear (e.g., Daan et al., 2005; Gristina et al., 2006; Tsagarakis et al., 2008; Yemane et al., 2008; Sweeting et al., 2009) rather than to underwater visual census survey data, with a few exceptions (e.g. Graham et al., 2005; Stuart-Smith et al., 2008). The size spectrum of harvested species in the underwater visual census data is expected to be steeper than that of the catch, because large numbers of small fish, smaller than the size of recruitment, tend to be seen by divers. The large numbers of smaller fish may also increase the variance of the size spectrum, if recruitment is variable. Nevertheless, high fishing rates, and fisheries targeting larger fish, would both decrease the slope of the size spectrum of fish in the water, as the fishery removes large fish. The size spectrum of fish in the water may be a more direct measure of the impact of fishing on the fish community than the size spectrum of fish in the catch, although the RVC method is still biased by size-selective and species-specific differences in detectability. Further investigations are needed to compare size spectra based on different types of fishery-independent data to assess the utility of SBIs as metrics of fishing pressure.

Analyses of fishes targeted by different types of gear could have been improved with more accurate information on the trappabil-

ity of species at this site. As was shown in Hawkins et al. (2007), species susceptibility varies highly among regions, even when gear types are identical. We found large differences in trappability among sites; for example, surgeonfishes had much lower trappability values in our study compared to the Jamaican study, whereas small-bodied groupers and goatfishes (*Mullidae*) had much higher trappability values in our study. It is important to note that our trappability values were calculated from limited observations of traps, and that a much greater sample size may be needed to accurately estimate trappability. However, a number of species recorded in our traps were not recorded as trapped in the Jamaica study, which had a higher sample size (23 traps). Thus, it appears that some of the differences are due to true differences in trappability and are not an artifact of sample size. Ultimately, our results suggest that our estimates of trappability were at least useful at a gross level; species with higher trappability values (>1) all showed significant increases in length or density from 2004 to 2009, whereas species with lower trappability values (<1) did not show increases in these parameters.

Our study could not resolve the effects of the use of triple-mesh nets on the fished community. This gear is noteworthy because it is known to be damaging to both fish populations and benthic habitat (Mangi and Roberts, 2006), particularly when lost and left to “ghost fish,” as it does not biodegrade like the bamboo traps do. Use of these nets was only observed during the 2004 cruise, and we did not observe any discarded triple mesh nets in 2006 or 2009 (while lost traps were frequently observed), suggesting that indeed the use of this gear had ceased. Interviews with Haitian fishers on the mainland suggest that fishers are aware of the negative impacts of this gear type on fish populations (Wiener, 2005), and it is possible that the gear type was excluded after 2004 through peer pressure within the fishing community. Triple mesh nets were observed to trap larger fishes through entanglement, while medium-bodied and smaller fishes were both gilled in the meshes of various sizes. Furthermore, turtles, lobsters, conch and crabs were also observed to be entangled in these nets. It is likely that the use of this gear had some impact on the fish community, but we could not quantify its specific influence. The effects of these nets are likely to be confounded with any changes in trapping effort that occurred during the study period. While species caught in nets likely included both trapped and line caught fishes, part of the increase in density and size of trapped fishes may be due in part to the elimination of nets after 2004.

Our analyses, together with anecdotal observations of fishing intensity, suggest that there may have been some fluctuations in fishing pressure over the study period; however, the reasons for these potential changes remain unresolved. The amount of fishing effort at Navassa is likely to be extremely variable from week to week depending on weather, fish abundance, other fishing opportunities and other externalities. It is possible that the Navassa fishery undergoes cycles of “boom and bust,” whereby fishers only make the arduous and treacherous voyage to the remote island when the resources are significantly greater compared to mainland such that the risk would be warranted. If the fishery at Navassa becomes depleted sufficiently, fishing effort could subside and resources may undergo some level of recovery. Another interesting point is that 2002, 2006, and 2009, were relatively stable years in terms of political activity in Haiti, whereas in 2004 there was a coup d'état which caused major political and economic destabilization. During times of economic instability, individuals living in coastal areas may turn to the sea as a source of income, and it is possible that numbers of individuals fishing increased in 2004 as a result of the unstable political climate. This is purely speculative, but is worthy of note, as civil strife is often linked to greater ecosystem vulnerability and environmental degradation (Dudley et al., 2002)

and it is important to consider such links when managing ecosystems. We do not have sufficient information to determine whether there were actual changes in fishing pressure and gear use over time, or why these changes might have occurred.

5. Conclusions

Our study shows that valuable information can be extracted from even a limited data set on a remote coral reef fishery. These methods can be applied to other systems where fishery-dependent data are lacking and small amounts of fishery-independent data are available. Trends in the species level could be detected, particularly when occurrence was high (>20%). Other studies have suggested that community-wide SBIs, when coupled with species-specific indices of trends for important and/or vulnerable species, can provide an informative preliminary assessment of the status of the fishery (Jennings, 2005; Hall et al., 2006) and our analyses support this recommendation. Further work should be done to: (1) lengthen the time series over which such analyses are applied, (2) increase observations of traps to obtain more accurate values of species-specific trappability, and (3) gather more fisheries data to improve estimates of total effort. Such research would augment the ability of developing nations to assess and manage coral reef fisheries effectively in a climate of limited funding and monitoring effort for these systems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.fishres.2011.06.010.

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