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ARTICLE

Fishery-Independent Surveys of the Queen Conch Stock in Western Puerto Rico, with an Assessment of Historical Trends and Management Effectiveness

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Abstract
The queen conch *Lobatus gigas* continues to support a commercial fishery in Puerto Rico despite a history of overfishing and low population densities. The goals of this study were to generate density estimates for the queen conch, to assess temporal trends, and to evaluate hypotheses of management interest using generalized linear models. Density data were supplemented by size- and age-class data. Total mean density was 14.1/ha (adults = 7.3/ha; juveniles = 6.6/ha). Year plus habitat and depth (associated effects) were significant factors influencing adult and juvenile density. Lower densities of both juvenile and adult queen conchs were observed in 1997 and 2001 than in 2013, but there have been no differences since 2006. This indicates an improvement in the population, though not recently. A location effect compared sites within the U.S. Exclusive Economic Zone (EEZ), which is closed to fishing, with those in local waters, which are open to fishing. The location term was significant for adults, with lower densities inshore regardless of year. For juveniles, both the location and year × location terms were significant; the EEZ had a higher juvenile density and a proportionally greater density increase (from 2.3/h to 10.0/ha) from 1997 to 2013. Length-frequency diagrams showed an increase in the proportion of adult conchs of 16–20-cm shell length in 2013 relative to 1997. This suggests an effect of the 22.86-cm minimum size limit implemented in 2004. Juveniles comprised 50% of the population in 2013, compared with 70% in 1997, and adults were found in the oldest age-class during the 2013 survey. This suggests an overall decrease in fishing mortality since 1997. Changes in survey methodology are recommended, including but not limited to shortening transects to increase the number of sites, utilizing a two-stage design, not utilizing scooters, standardizing the areas surveyed, and stratifying by depth and habitat.

Queen conch *Lobatus* (= *Strombus*) *gigas* is a valuable commercial and recreational resource in the Caribbean. In Puerto Rico, scuba divers that target queen conchs are among the most successful commercial fishermen (Matos-Caraballo et al. 2012). After the spiny lobster *Panulirus argus*, the queen conch contributes the most to overall

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commercial landings (~11%). In 2007, a total of 65,300-kg meat weight was caught by commercial fishers. At an average price of US$8.34 per kilogram (Matos-Caraballo et al. 2012), the commercial fishery is valued at around $543,000.

Management of this commercially important species throughout the Caribbean is difficult due to a variety of factors. Key among these is that queen conchs change the manner in which they grow. As juveniles they increase in shell length, but about the onset of maturity they cease growing in length and form a broad shell lip that thickens over time (Appeldoorn 1988; Tewfik et al. 1998). As a consequence, the length and biomass of queen conchs are largely fixed at the time of maturation (Appeldoorn 1988). Additionally, there is wide variation in the size at maturity, with a strong environmental influence. Thus, the length and biomass of adults are not a function of age (Appeldoorn 1988). At present, there is no established way to age queen conchs that could be used for assessment in standard growth models. In addition, queen conchs require copulation for reproduction, so that maintaining minimum densities is important, yet the exact densities that are needed are difficult to assess (Stoner and Ray-Culp 2000; Appeldoorn et al. 2011a). In addition, the genetic connectivity of individual stocks is generally not known. Yet queen conchs are vulnerable to overfishing: they are slow moving with limited home ranges (e.g., Delgado and Glazer 2007), and during the extended reproductive season (Avila-Poveda and Baqueiro-Cárdenas 2009) they migrate to shallower waters and preferentially inhabit sandy bottoms where they are conspicuous and easy to catch (Randall 1964; Weil and Laughlin 1984; Coulston et al. 1987). In 1992, following the collapse of queen conch fisheries in a number of countries, queen conchs were listed under Appendix II of the Convention on International Trade in Endangered Species, which requires that exporting countries certify through their local scientific authority that harvest and export are not negatively affecting the stock. This has helped by forcing exporting countries to obtain nondetrimental findings to ensure that exports do not negatively affect the wild population (Theile 2001).

The queen conch resource in Puerto Rico is managed jointly by the territorial and U.S. federal governments. From the shoreline out to 16.87 km (9 nautical miles), the regulations governing harvest are mandated by the territorial government. Beyond 16.87 km is the United States' Exclusive Economic Zone (EEZ), where the federal government imposes and oversees regulations regarding queen conch harvest through the Caribbean Fishery Management Council. In 1997, the U.S. Caribbean EEZ (with the exception of St. Croix) was closed to queen conch fishing. Also at this time, a closed season was implemented in territorial waters (July 1–September 30, amended to August 1–October 31 in 2012). In 2004, additional regulations implemented in local waters included a 22.86-cm (9-in) minimum shell length or 9.5-mm (3/8-in) minimum lip thickness and daily bag limits of 150 per person and 450 per boat.

Puerto Rico's queen conch population is currently overfished but recovering from severe overfishing and loss of habitat in the 1980s. In the mid-1980s one boat trip could average 73 kg of meat, while the same trip in the early 2000s could only average 33 kg (Valle-Esquival 2002). Catch was based on juveniles (Appeldoorn 1991), and fishing mortality was greater than natural mortality (Appeldoorn 1987). A general trend of decreasing catch has been observed since the early 1980s (SEDAR 2007). To combat this, the Puerto Rico Department of Natural and Environmental Resources, through the Southeast Area Monitoring and Assessment Program–Caribbean (SEAMAP–C), has been conducting periodic visual surveys of conch density and size- and age-class structure to aid management. Prior to the standardized SEAMAP surveys, a survey was conducted in 1985–1986, but this was restricted to 81 sites on the southwest corner of the island. Average total density was 8.1/ha (Torres Rosado 1987). The first SEAMAP survey was done in 1997 and covered both the east (29 sites) and west (60 sites) coasts. Average densities were 7.5/ha and 8.5/ha, respectively (Mateo et al. 1998). Sixty sites were again surveyed on the west coast in 2001, where density had increased to 14.4/ha (Appeldoorn 2002). A survey in 2006 added 14 sites on the south coast to the sampling regime and again sampled the west (46 sites) and east (40 sites) coasts (Jiménez 2007). Average densities were 17.7, 22.4, and 46.6/ha, respectively (revised from Jimenez 2007). Direct comparison is complicated by temporal variation, as the four surveys were conducted at different times of the year, ranging from April to December. From 1997 to 2006, a trend of increasing density was noted, though direct statistical comparisons were not made. Improvements in the health of the population were additionally supported by analysis of length- and age-class distributions, which showed a greater proportion of total adults, especially older ones (SEDAR 2007).

The low densities of queen conchs observed throughout the course of these surveys, combined with data from the Bahamas showing that reproductive rates drop at densities less than 50/ha (Stoner and Ray-Culp 2000), suggest that the functional spawning stock of queen conchs in Puerto Rico is critically low. In 2012, a survey of commercially important species at three mesophotic reefs (38–44 m in depth) off the west coast of Puerto Rico found large numbers of adult queen conchs (672 individuals) at one of the sites (Abrir La Sierra; Garcia-Sais et al. 2012). This site is on the insular slope off the western platform of Puerto Rico. Average density over three seasons was 3.3/ha for the wall (slope) habitat, 7.1/ha for the reef-top habitat, and 194.9/ha for the rhodolith habitat (see Garcia-Sais et al. 2012 for habitat classification details). The total adult population estimate for Abrir La Sierra was 29,092 individuals; queen conchs were observed to be reproductively active there, but the extent of this activity was not quantified (Garcia-Sais et al. 2012). This high density of reproductively active queen conchs may be contributing larvae for settlement farther inshore.

The purpose of this study was to resurvey the shallow-water queen conch population off the west coast of Puerto

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Rico as part of the ongoing SEAMAP survey program. Although there is fishing on the east, south, and west coasts, the broad shelf in the west is the primary fishing ground. Additionally, the west coast has the longest time series of past surveys, dating back to 1985–1986 (Torres Rosado 1987). The primary goal of the survey was to generate density estimates and size- and age-class data that could be used to assess trends and current status. However, unlike in past surveys, the analyses of the density data employed generalized linear models to generate more robust statistical comparisons in order to test two hypotheses of management interest:

1. Queen conch densities are continuing to increase (relative to those found by previous studies) in response to management measures limiting fishing effort and catch; and
2. The mean density within the EEZ is higher than that in local waters because the EEZ was closed to fishing for 16 years.

The above density comparisons were augmented by analysis of changes in length- and age-class frequency distributions. Additionally, the spawning stock abundance on the platform (Figure 1) was estimated for comparison with that observed by Garcia-Sais et al. (2012) in deepwater at Abrir La Sierra to evaluate the significance of the latter relative to overall reproductive output off the west coast.

METHODS

Visual surveys.—All SEAMAP surveys for queen conchs in Puerto Rico have utilized areas of expected high and low queen conch density based on interviews with fishers (Mateo et al. 1998). In 2006, fishers were reinterviewed to identify (1) past queen conch fishing grounds, (2) present queen conch fishing grounds, and (3) areas known to have juveniles. These interviews covered the west, east and, south coasts. The resulting maps were digitized into a geographical information systems database using ArcMap, and the pooled area was used as a boundary or frame for the survey area. Individual polygons were fused to form one polygon that was used for site selection. A total of 46 random sites (transect starting coordinates) were chosen off the west coast, within the 27-m isobath (Figure 1). The depth limit was chosen for diver

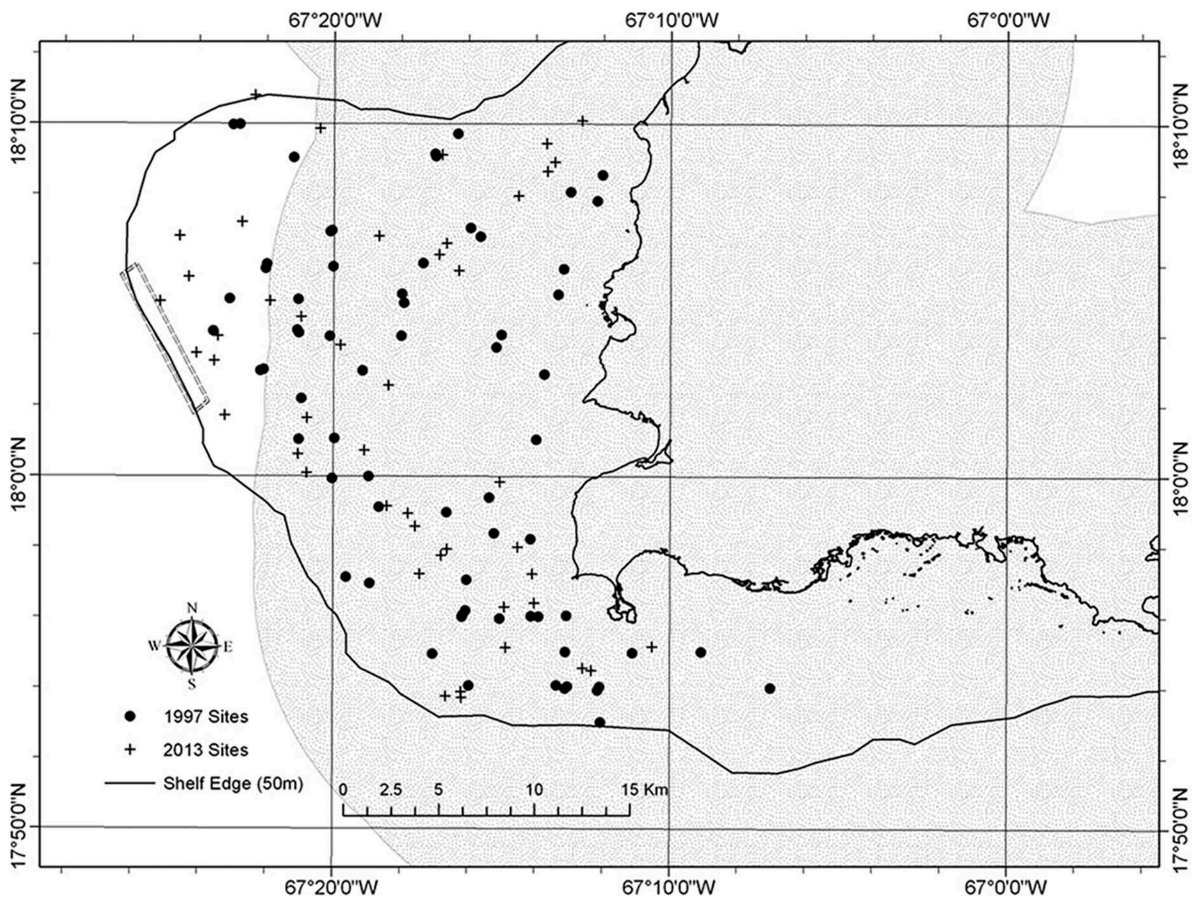

FIGURE 1. Locations of the randomly chosen sampling sites for the 1997 and 2013 queen conch visual surveys on the western platform of Puerto Rico (inside the 50-m isobath). The double-dashed box shows the approximate location of the Abrir La Sierra site surveyed by Garcia-Sais et al. (2012). The gray stippled area represents waters under local jurisdiction.

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safety. The direction of each transect was a preselected random compass heading.

Except for timing, the methods followed by the 2013 survey were identical to those of previous surveys under the SEAMAP protocol to facilitate the comparison of results (see Discussion); the 2013 survey was done during October and November. All of the participating divers were trained in the following: the identification of queen conchs; the use of underwater scooters, including ways to maintain a constant direction and speed as well as safety protocols; length estimation; the identification of age-classes using an established reference collection; and recording all applicable data. Practice transects were employed for training.

At each of the sites, paired visual surveys were done by scuba divers aided by underwater scooters to maximize the distance traveled. Each diver surveyed a 4-m-wide transect of variable length depending on the depth, current, and available dive time, but for a maximum of 45 min. One diver trailed a safety buoy, which helped identify the end point of the transect and allowed the surface support vessel to track the divers; the other diver carried a compass so that the dive pair could follow a straight line along a preset heading. At the end of the transect, divers signaled to the boat by pulling on the buoy line; the boat then approached the buoy and marked the position using GPS. During the survey, habitat, depth, age-class, and estimated siphonal length (to the nearest 1 cm using a 20-cm-long reference object) were recorded for each queen conch along with the time at which these data were obtained and observations of copulation or egg laying. Any observed changes along the transect of depth and habitat type were also recorded. Classifications of habitat were based on the presence of sand, gorgonians (low-relief areas where the underlying hard bottom can be exposed or covered by sand depending on recent bedload transport), the sea grasses *Thalassia testudinum* and *Syringodium filiforme*, algae, reef, hard bottom, or any combination of these. Possible age-classes were juvenile (J), newly mature adult (NMA), adult (A), old adult (OA), and very old adult (VOA); classifications were based on shell appearance and lip thickness (Table 1). To the extent possible, divers attempted to maintain a constant speed along each transect. The length of each transect was calculated in ArcMap by measuring the straight-line distance connecting the starting and ending positions.

TABLE 1. Definitions of adult queen conch age-classes. The numbers in bold italics are the lip thicknesses (mm) of the reference specimens (Appeldoorn et al. 2003).

Age-class (code)	Description
Newly mature adult (NMA)	Flared lip starting to grow or very thin (lip generally less than 5 mm thick); periostrocum tan and clean; lip often thin enough to allow the periostrocum to give color to the underside of the lip (***4, 7***).
Adult (A)	Flared lip fully formed, with minimal to moderate erosion; periostrocum tan but may be covered by or have some algal growth; lip underside generally white with a pink interior (***15, 15***).
Old adult (OA)	Outer lip starting to erode when viewed from the bottom); top of shell still well formed but periostrocum is lost and spines have rounded, with moderate erosion and fouling on the outside shell; lip underside may have a platinum color with a darker pink interior (***30, 33***).
Very old adult (VOA)	Lip very thick and flared portion may be completely eroded away; outer shell highly fouled and eroded, often resulting in shorter total length; viewed from the underside, the lip is squared off; the white portion is often completely eroded and the interior a dark pink (***42, 59***).

Data analysis.—The total area surveyed was calculated by multiplying the length of each transect by its 8-m width (two 4-m transects per site) and summing over all 46 sites. Densities were calculated by dividing the total number of queen conchs observed at each site by the area surveyed. Transects were pooled for a single density estimate per site. For purposes of analysis, each site was classified by the average depth and the dominant habitat type(s) along the transects. Comparisons of both adult and juvenile densities between years (1997, 2001, 2006, and 2013) were made using a generalized linear model that included year, depth, and habitat as fixed effects; for sites at which two habitat types were prevalent, the counts of queen conchs were positively associated with both habitat types. Data for the juvenile model was restricted to densities less than 250/ha. This excluded two sites, site 58 in 2001 and site 6 in 2013. A sensitivity analysis determined these points to be outliers, as they caused distortion in the model estimates and considerably altered the summary statistics and model fit when included. The degrees of freedom for the Pearson chi-square statistic also showed a lack of fit when these points were included in the model. The sample size for the juvenile model was 217 sites, while that for the adult model was 219 sites. The model of total density, which included both juveniles and adults, also excluded the two problematic sites.

The data analysis was performed using SAS, version 9.3 (SAS Institute, Cary, North Carolina). Analyses were conducted using PROC GLIMMIX based on a negative binomial distribution for the counts. This distribution was chosen over a Poisson distribution because it is better equipped to handle overdispersion. The area of each transect was included in the model as an offset term.

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TABLE 2. Descriptive statistics for all queen conch visual surveys in Puerto Rico.

Year	Total number of sites	Sites in local waters	Sites in the U.S. EEZ	Total area surveyed (ha)	Transect average (ha)	Total juveniles	Total adults	Total conchs
1987	81	81	0	40.81	0.2535	224	107	331
1997	67	58	9	51.32	0.3834	207	85	292
2001	60	54	6	23.58	0.3881	89	60	149
2006	46	38	8	25.2	0.5479	240	205	445
2013	45[a]	37	8	37.45	0.814	194	186	380

[a]Site 6 was excluded from the density analysis.

No spatial correlation term was included because the depth and habitat terms explained most of the variability. A separate model included location and year × location terms to compare the mean density of adults and juveniles in local waters versus that in the EEZ. Density plots showing the length distribution for all queen conchs were constructed using shell length for 1997 and 2013. A Kolmogorov–Smirnov test was done to compare the length distributions between 1997 (n = 292 conchs) and 2013 (n = 380). Age-class distributions were constructed for 1997 and 2013 showing the percentage of total queen conchs observed in each of the five age-classes. A Pearson's chi-square test was done to compare the proportions in each age-class between 1997 and 2013. The spawning stock for the west coast was calculated using the pooled density for only the older adult age-classes (adult, old adult, and very old adult) multiplied by estimates of suitable area, i.e., the area of the polygon used for site selection. This spawning stock estimate was compared with the mesophotic population estimate at Abrir La Sierra (Garcia-Sais et al. 2012) to determine the potential contribution of the mesophotic population vis-à-vis the shallow-water stock, assuming equal sex ratios and reproductive output per adult.

RESULTS

Forty-six sites were sampled during the course of the 2013 survey (Table 2). The total area surveyed was 37.45 ha, with transect area averaging 0.814 ha and ranging from 0.3 ha at site 5 to 3.93 ha at site 11 (see Table A.1 in the appendix to this article). The differences in the amount of area covered are based on a variety of factors, including (but not limited to) depth and current. The total number of queen conchs observed was 380: 194 juveniles and 186 adults (Table 2). This does not include the conchs at site 6, where 1,399 juveniles of less than 10-cm shell length were observed. This site was excluded due to statistical distortion effects (see Methods). Elsewhere, juvenile density ranged from 0 at multiple sites to 34.4/ha at site 37; adult density ranged from 0 at multiple sites to 44.7/ha at site 16 (Tables 3, A.2). Total density ranged from 0 at multiple sites to 61.5/ha at site 37. Mean total density was 14.1/ha.

To address the temporal differences in the mean juvenile, adult, and total densities, counts were modeled as a function of year, depth, and habitat. Table 3 lists the mean densities of all past surveys, but those from 1987 were not included in the analyses because of our limited access to the raw data. In this model, year and habitat were significant, but not depth (Table 4). However, in a separate model comparing only year and depth (Table 5), depth became highly significant (P < 0.001). This result occurred because depth and habitat are closely associated.

Transects with mud (estimate = –1.4592), sand (–0.6538), reef (–1.7340) and hard bottom (–0.8467; all P < 0.05) present had significantly lower densities of juvenile queen conchs. Lower mean densities of adults were found on transects with mud (–2.4894; P < 0.05) and sand (–0.4886; P < 0.10), while transects with sea grass were positively associated with the presence of adult conchs (0.6828; P < 0.10).

TABLE 3. Comparison of means and ranges of densities (number/ha) for juvenile, adult, and total queen conchs for all five visual surveys conducted off western Puerto Rico. Where separate juvenile and adult numbers were not reported, the original data were analyzed to calculate these densities. Individual transect densities were not available (NA) for 1987.

	Total		Juvenile		Adult		
Year	Mean	Range	Mean	Range	Mean	Range	Source
1987	8.1	NA	5.5	NA	2.6	NA	Torres Rosado (1987)
1997	8.5	0–247.2	6.2	0–175.1	2.2	0–30.9	Mateo et al. (1998)
2001	14.4	0–509.3	10.1	0–445.6	4.3	0–63.7	Appeldoorn (2002)
2006	22.4	0–125.0	11.4	0–120.0	11.0	0–53.9	Reanalyzed from Jimenez (2007)
2013	14.1	0–61.5	6.7	0–34.4	7.3	0–44.7	This study

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TABLE 4. Model outputs from the analysis of juvenile (J), adult (A), and total queen conch density as a function of year, depth, and habitat type. The numbers in parentheses are either the numbers of juvenile and adult conchs found in that year's survey or the number of transects with the particular habitat type present in all years. The Akaike information criterion (AIC) values and the chi-square values divided by the degrees of freedom indicate the fits of the models; $P \leq 0.10$*, $P \leq 0.05$**.

	Juvenile		Adult		Total	
Effect	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	2.7824**	0.7350	2.1931**	0.5768	3.2425**	0.5293
Year						
1997 (207 J, 85 A)	–0.6852*	0.3729	–1.3249**	0.3022	–0.8880**	0.2807
2001 (89 J, 60 A)	–1.1414**	0.4076	–0.8302**	0.3180	–0.9951**	0.2992
2006 (240 J, 205 A)	0.4046	0.4534	0.3729	0.3354	0.3681	0.3300
Depth	–0.00478	0.008238	–0.00582	0.006645	–0.00800	0.006112
Habitat						
Hard bottom (45)	–0.8467**	0.4420	–0.1281	0.3315	–0.4108	0.3009
Seagrass (47)	0.5996	0.4449	0.6828*	0.3702	0.6777**	0.3324
Reef (21)	–1.7340**	0.4942	–0.08798	0.3499	–0.7048**	0.3239
Sand (45)	–0.6538**	0.3077	–0.4886*	0.2605	–0.4977**	0.2291
Algae (50)	–0.3884	0.3479	0.2711	0.2786	0.01980	0.2505
Gorgonians (21)	0.1498	0.4509	–0.09050	0.3774	0.03976	0.3418
Mud (9)	–1.4592**	0.6639	–2.4894**	1.1427	–1.4944**	0.5544
AIC	890.59		882.04		1,164.05	
χ^2/df	1.57		1.26		1.39	

There was a lower mean density of adult queen conchs in 1997 (–1.3249) and 2001 (–0.8302; both $P < 0.05$) than in 2013. There was no difference between 2006 and 2013 (Table 4). The same pattern was observed for juveniles (1997 versus 2013: –0.6852, $P < 0.10$; 2001 versus 2013: –1.1414, $P < 0.05$).

In 1997, fishing grounds within the U.S. EEZ were permanently closed to queen conch fishing. To test for population differences as a function of management regime (i.e., the closed EEZ versus open local waters), density was modeled as a function of year (1997 or 2013 [reference]), depth, habitat, location, and a year × location interaction term. The year, depth, and habitat terms were included to reduce the unexplained variance. For adults, the location term was significant (–1.4548; $P < 0.05$) but the interaction term was not (Table 6); that is, in both 1997 and 2013 density was higher in the EEZ than in local waters, but the effect of location cannot be separated from the general increase in both areas over time. For juveniles, however, both the location and interaction terms were significant (Table 6), indicating both a higher density in the EEZ and a greater increase in density within the EEZ from 1997 to 2013.

Population changes were also assessed using age-class and length-frequency analyses. There were statistically significant

TABLE 5. Model outputs from the analysis of juvenile (J), adult (A), and total queen conch density as a function of year and depth. The numbers in parentheses are the numbers of conchs found during that year's survey. The Akaike information criterion (AIC) values and the chi-square values divided by the degrees of freedom indicate the fits of the models; $P \leq 0.05$*.

	Juvenile		Adult		Total	
Effect	Estimate	SE	Estimate	SE	Estimate	SE
Year[a]						
1997 (207 J, 85 A)	–0.3243	0.3405	–1.1493*	0.2922	–0.6255*	0.2590
2001 (89 J, 60 A)	–1.0164*	0.3698	–0.706*	0.3039	–0.9305*	0.2772
2006 (240 J, 205 A)	0.3669	0.3638	0.3513	0.2955	0.3519	0.2762
Depth	–0.02626*	0.006345	–0.01913*	0.005882	–0.02463*	0.004928
AIC	904.07		890.07		1,179.24	
χ^2/df	1.63		1.28		1.51	

[a] Reference = 2013.

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TABLE 6. Summary of the outputs from the analysis of juvenile and adult queen conch density as a function of year (1997 versus 2013), depth, habitat, location (local waters versus the U.S. EEZ), and year × location. Only the location and year × location estimates are reported here; because 2013 and the EEZ were the reference points, their estimates were set to 0; $P \leq 0.05$*.

	Adult		Juvenile	
Effect	Estimate	SE	Estimate	SE
Location	–1.4548*	0.4818	–2.5098*	0.5945
Year × location	0.4790	0.7556	2.7471*	0.9087
AIC	439.84		473.85	
χ^2/df	1.18		1.00	

differences in the length-frequency distributions of both juveniles (Kolmogorov–Smirnov D statistic = 0.19303) and adults (0.3757; both $P < 0.05$) in 2013 relative to 1997 (Figure 2). Notably, only 11.6% of the adults were between 16 and 20 cm in 1997, compared with 42.2% in 2013 (Figure 3).

The age-class structure of queen conchs in 2013 was markedly different from that in 1997 (Pearson's $\chi^2 = 50.0427$; $P < 0.001$; Figure 4). One of the most obvious differences is the absence of very old adults (VOA) in 1997. Additionally, in 2013 approximately 50% of the population were juveniles, whereas in 1997 70% were.

The potential importance of the spawning population at mesophotic depths relative to that on the shelf was assessed by comparing the number of full adults on the shelf with the

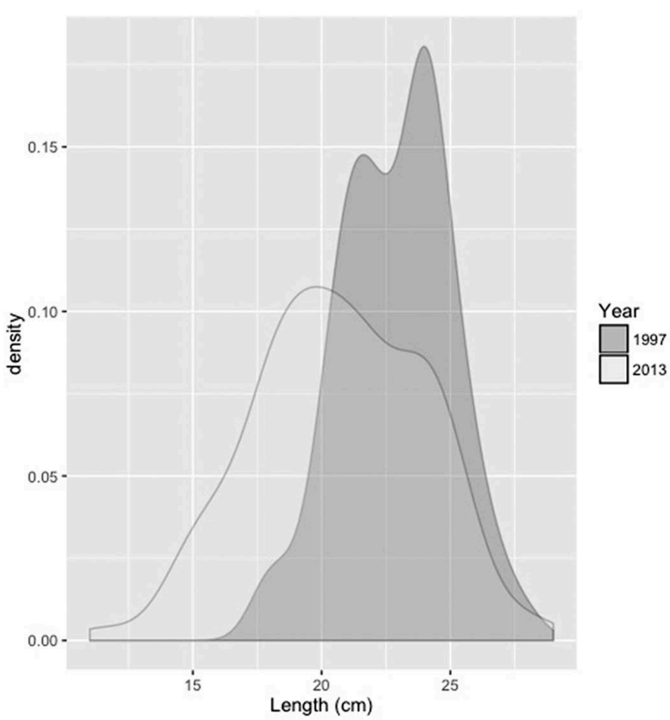

FIGURE 2. Distributions of queen conch shell length in 1997 and 2013.

estimates of Garcia-Sais et al. (2012). The calculated density of spawners (i.e., adults, old adults, and very old adults) on the shelf for the 2013 survey was 4.1 ± 1.6/ha (90% CI). Over the 42,074 ha that were identified as queen conch strata, there was an estimated spawning stock of 104,763–240,241 individuals (mean = 172,705). Therefore, the mesophotic queen conch population at Abrir La Sierra (29,092) only constitutes 14% of the mean spawning population off the west coast of Puerto Rico.

DISCUSSION

The large number of juveniles at site 6, all less than 10 cm in shell length, reflects the emergence of age-1 individuals from a first year of burial (Stoner et al. 1988; Appeldoorn 1990). The varying times of the previous visual surveys (Table 7) and the failure of this phenomenon to be reported for those surveys further justify the exclusion of this site from the statistical analysis. This site is in deepwater (mean transect depth, 22 m) and it has a mixed habitat of sand and algae.

For temporal comparisons, mean densities were modeled using the effects of year, depth, and habitat. Depth and habitat are known to influence both adult and juvenile distributions. Juveniles prefer shallow, sea grass areas with currents (Stoner and Waite 1991; Stoner et al. 1996; Stoner 2003). Adults, on the other hand, utilize multiple habitat types. Sand and algal flats provide nutrition, but adults can also be found feeding in hard-bottom habitats (Torres Rosado 1987; Acosta 2001; Stoner and Davis 2010) and are commonly found in water up to 25 m deep (Stoner and Schwarte 1994). Our findings are consistent with the documented habitat preferences of juveniles. Juveniles were less dense in hard-bottom, reef, sand, and mud habitats. Adults were found at higher densities in sea grass habitats and at lower densities in sand and mud habitats. A large portion of the adults observed were in the NMA category (44.1%), and a majority of those (86.0%, or 37.8% of the total) were found in sea grass habitats. These individuals have a lip and are therefore categorized as adults, but they may not have become reproductively mature and therefore had not yet relocated to the feeding habitats of the older adults (for example, 63% of OA were found in either sand or hard-bottom habitats with algae).

The characteristics of an increasingly healthy queen conch population would include higher adult density (especially in relation to spawning [see below]), an increase in the proportion of older adults, and evidence of sustained recruitment. Thus, the increase in mean adult and juvenile densities from 1997 and 2001 to 2013 is a positive sign, as are the changes observed in the length- and age-class frequency distributions (Figures 2–4). However, despite the continuance of current regulations, no improvements in density or size and age structure were observed from 2006 to 2013.

One of the most striking differences between the 1997 survey and the most recent one is the proportional increase

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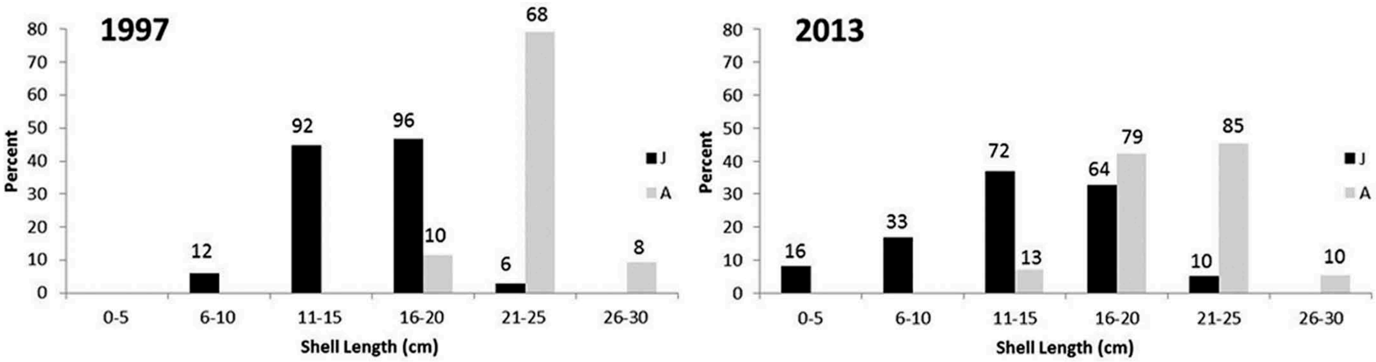

FIGURE 3. Length structures of juvenile (J) and adult (A) queen conchs off the west coast of Puerto Rico in 1997 and 2013. The numbers above the bars are the actual counts.

in smaller queen conchs (i.e., those less than 20 cm; Figure 2). It is possible that the minimum size restrictions put in place in 2004 are responsible for this. These conchs are below the 22.86-cm minimum shell length needed to be harvested legally. Figure 3 shows the significant increase in the number of adults in the 16–20-cm size-class, a difference that is also noticeable in 2006. Queen conchs maturing within this size range would have a fixed shell length that was under the limit and thus would not be eligible for harvest until their shell lip thickness reached 9.5 mm. This provides a minimum of a half year of protection from fishing mortality (Appeldoorn 1988) beyond the protection afforded by the minimum shell length.

Additionally, a greater proportion of the current population (2013) is composed of adults, and these adults are distributed across all age-classes in a manner consistent with a significant decrease in overall total mortality. Unfortunately, because these adult age-classes cannot be readily converted to ages, an exact estimate of mortality is not possible.

Nevertheless, the higher percentage of adults and the presence of older adult age-classes means that there has been a marked increase in the spawning stock. While the average density of the spawning stock is low (see below), a recent field study on the western platform found maximum rates of egg laying and copulation to be 16% and 12%, respectively (Appeldoorn et al. 2011b), suggesting that queen conchs occur locally at sufficiently high densities to maintain reproductive activity.

The appearance of juveniles in the 0–5-cm size-class is also noteworthy. In the 1997 and 2001 surveys, this size-class was not observed at all. But in 2006 such juveniles represented 11.7% of the population, and in 2013 they represented 8.2%. Perhaps this is the result of more sustained recruitment owing to the increase in the number of adults partially protected from harvest.

With respect to the impact of the 1997 closure of the EEZ to fishing, the most interesting result is the difference in the responses of adults and juveniles. Although adults were found at higher densities within the EEZ, this effect was observed in both 1997 and 2013. For juveniles, on the other hand, both the location and interaction terms were significant, thus enabling us to separate the effects of location and year. The density of juveniles in the EEZ increased from 2.3/ha to 10.0/ha (a factor

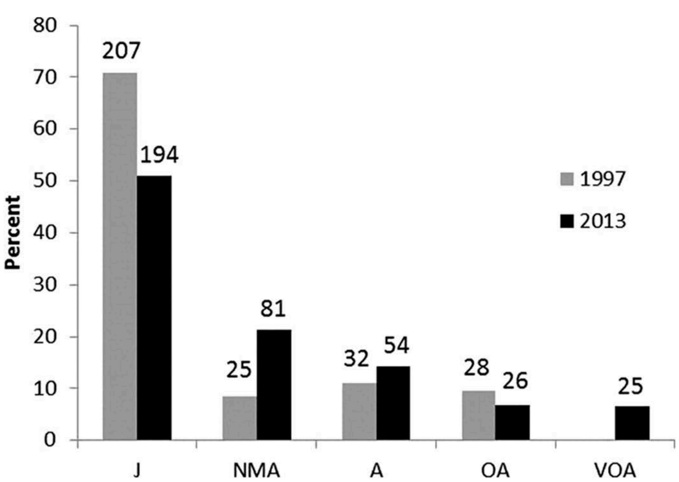

FIGURE 4. Age-class structure of queen conchs off the west coast of Puerto Rico in 1997 and 2013. The numbers above the bars are the actual counts. Abbreviations are as follows: J = juvenile, NMA = newly mature adult, A = adult, OA = old adult, and VOA = very old adult.

TABLE 7. Months in which queen conch visual surveys were conducted for Puerto Rico, by year. In an additional study, in 1987, fieldwork was conducted during every month of the year.

Year	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1997	X						X	X	X
2001	X	X			X	X	X	X	
2006				X	X	X			
2013							X	X	

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of 4.4) from 1997 to 2013, whereas that of juveniles in local waters only increased from 4.0/ha to 6.0/ha (a factor of 1.5). It is possible that this is the result of increased reproductive success on the part of adults in the EEZ that are now protected from fishing.

The inclusion of a more robust statistical analysis than in previous survey reports helps to clarify the trends in the recovery of the queen conch population. Based on increasing densities (Table 4) and the presence of more and older adults, previous investigators have argued that even though the population was overfished it was improving (SEDAR 2007). In the present survey, by contrast, total density did not continue its upward trend and the statistical analysis led to a different conclusion. Though total density is higher since both 1997 and 2001, no significant differences have been found since 2006; indeed, even the increasing trend in total density has been broken. It may be that the protections offered by the current regulations have reached their maximum impact relative to the present level of fishing pressure or that the current sampling design and effort are insufficient to address temporal changes in density in the face of strong habitat and depth effects.

Our results suggest that changes in methodology are needed to draw stronger conclusions about temporal trends and the effectiveness of regulations. Incorporation of the generalized linear model approach into future sampling should have several positive effects. First, it will give survey results a more powerful basis for interpretation. More importantly, however, the statistical model can be used to structure the design of future surveys so as to greatly reduce sample variance and increase sample efficiency (e.g., Smith et al. 2011). For example, the statistical models confirmed what has been known about the importance of habitat (primary) and depth (secondary) in the distribution of queen conchs. Because of this, future sampling methods should be altered to more directly account for these factors. It would be most effective to control for these variables when selecting sampling sites. This can be accomplished in one of two ways: (1) taking great care to choose sites that include a variety of depths and habitat types and then resurveying them year after year; or (2) selecting new sites each year but ensuring that they are stratified over a variety of depths and habitats. Stratifying site selection by habitat (in which each site represents just one habitat type) would make the habitat analysis clearer, but in our case this can only be done by using a detailed habitat map of the entire west and southwest platform, of which there currently is none. However, high-resolution bathymetry (including backscatter) is available for this region, along with the technology for using this to develop detailed habitat maps (Costa et al. 2009; Pittman et al. 2009). With detailed habitat information, it may be beneficial to change the format of SEAMAP sampling to utilize a greater number of small, fixed-area samples rather than the fewer but longer, underwater-scooter-based transects that are currently used. As a consequence, each transect would have only one specific habitat and depth. This would reduce the noise in the data generated by trying to account for these variables in the post hoc analysis. A prime example of this distorting effect concerns the average depths of surveys (Figure 5). The average depth across all sites is less in 1987 and 2006 than in 1997, 2001, and 2013. This raises the question whether higher density represents a true improvement in the population (changes in the adult age-class distribution notwithstanding), because statistical analysis shows that depth is inversely related to density. Changes in the mean depth of the sites probably resulted from (1) the restricted geographical area surveyed in 1987 and (2) the change in sample allocation across the shelf due to the incorporation of redrawn strata in 2006 and the lack of sample allocation outside of those strata.

The power of the test to determine the effectiveness of the EEZ closure is also very limited because the analysis was post hoc. A small and unequal number of sites were chosen in the EEZ, limiting the conclusions that can be drawn from the analysis. To increase its power, the survey would have to be specifically designed to address this issue, adding a much greater number of sampling sites in the EEZ (despite its relatively small area) while keeping the same number of sites in the local areas. This would allow for characterization of the overall population while permitting testing of the closure hypothesis.

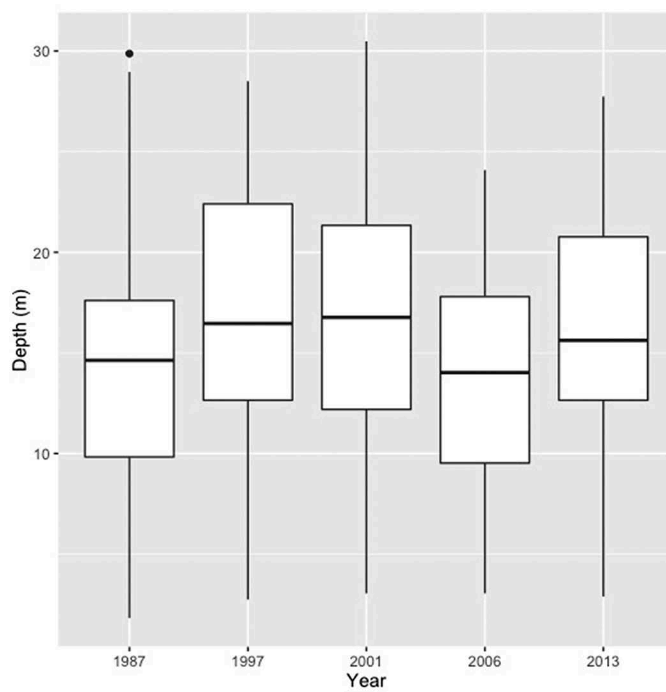

FIGURE 5. Box plots comparing average depth among queen conch visual surveys. The boundaries of the boxes indicate the interquartile range, 75th–25th percentiles. Lines within the boxes indicate the median. The length of the whiskers indicate 1.5× the interquartile range. Data points outside of these are outliers.

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The analysis of the spawning population on the shelf versus that at Abrir La Sierra suggests that the latter, deeper population may constitute only 14% of the total population of spawning adults. The significance of this is not clear, however, because queen conch reproductive output is dependent on a number of factors. One of the most important is adult density (Stoner and Ray-Culp 2000). Queen conchs reproduce through copulation, and given their limited ability to move, maintaining high density is critical to ensuring reproduction. The density reported at Abrir La Sierra (195/ha) is well above the minimum density of 50/ha reported by Stoner and Ray-Culp (2000) needed to avoid Allee effects and approaches the density at which the probability of mating reaches 100% (Stoner et al. 2012). The critical density is known to vary geographically within the Bahamas. The probability of mating reaches 100% at a density of 110/ha in the Exumas but only 90% at densities of 350/ha in Andros and 570/ha in the Berry Islands (Stoner et al. 2012). The density at Abrir La Sierra also exceeds 140/ha, which is considered the population density needed to achieve the maximum sustainable yield elsewhere in the Caribbean (SEDAR 2007; Appeldoorn et al. 2011a). In contrast, the highest individual density estimate observed for mature adult queen conchs on the shelf was only 24.4/ha over a whole transect. Thus, the slope population at Abrir La Sierra may be contributing more larvae than its abundance alone would indicate. However, while Garcia-Sais et al. (2012) reported observing egg deposition at Abrir La Sierra, the rate was not quantified, so no comparisons can be made with those observed at lower depths. Lastly, the dispersal of queen conch larvae may be significantly different for eggs hatched in the deeper waters of the shelf margin than it is for those hatched on top of the platform, but comparative studies are not available to confirm this.

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Appendix: Additional Data

TABLE A.1. Longitude and latitude (decimal degrees) of starting and ending positions for the 2013 paired visual transects. Depth is the average of the starting and ending depths. Habitat types are as follows: 1 = hard bottom/rubble, 2 = sea grass, 3 = reef, 4 = sand, 5 = algae, 6 = gorgonians, and 7 = mud. The station numbers are not sequential because initially selected sites deeper than 27 m were not sampled.

	Starting position		Ending position				
Station	Longitude	Latitude	Longitude	Latitude	Habitat	Depth (m)	Area (h)
1	–67.27755	18.11020	–67.28854	18.11044	4, 5	18.5	0.9304
2	–67.20974	17.90930	–67.20416	17.90814	4, 1	14.7	0.4832
3	–67.34033	18.16436	–67.32837	18.16621	6	20.1	1.024
4	–67.29630	17.98237	–67.28369	17.98374	4, 5	20.4	1.0752
5	–67.30613	18.04306	–67.30534	18.04636	4, 5	24.3	0.3
6	–67.31088	18.11362	–67.30772	18.11775	4, 5	22	0.4528
7	–67.27985	17.96264	–67.27284	17.95759	2, 5	14.6	0.7424
8	–67.28112	18.10493	–67.28001	18.09773	4, 5	10.2	0.6432
9	–67.27983	18.15210	–67.28094	18.16126	3	7.6	0.8
10	–67.22765	18.14433	–67.22371	18.14843	2, 4	7.3	0.4928
11	–67.24194	18.13265	–67.28827	18.13470	2	3	3.9272
12	–67.37877	18.12012	–67.37615	18.10837	4, 6	23.9	1.0632
13	–67.29057	17.95380	–67.29922	17.95381	4, 5	21.3	0.7336
14	–67.39237	18.05451	–67.38200	18.06071	4, 3	20.8	1.0344
15	–67.20541	17.90834	–67.20291	17.90261	4, 5	15.5	0.5496
16	–67.24787	17.91916	–67.24876	17.92464	2, 5	12.8	0.492
17	–67.38714	18.02860	–67.38414	18.03045	4, 5	15.6	0.3016
18	–67.23367	17.94018	–67.24352	17.94197	2	11.5	0.8496
19	–67.35084	18.01042	–67.35601	18.01454	3, 4	18.5	0.5696
20	–67.34944	18.07535	–67.34183	18.08228	4, 1	23.7	0.8904
21	–67.30673	17.98602	–67.29678	17.98479	3	19.2	0.8488
22	–67.41924	18.08263	–67.41341	18.08047	3	16.1	0.528
23	–67.17542	17.91961	–67.17207	17.91564	6, 5	12.6	0.4504
24	–67.22394	18.14887	–67.22942	18.15018	2	8	0.3816
25	–67.36474	18.08293	–67.36566	18.07399	4	27.7	0.7784
27	–67.24203	17.96659	–67.24892	17.96795	4, 5	8.2	0.596
28	–67.40976	18.11349	–67.40544	18.12057	1	24.2	0.7264
29	–67.27746	17.89609	–67.28080	17.92260	1, 6	21.1	2.3648
30	–67.24846	17.93828	–67.25859	17.93848	2, 5	13.2	0.8592
31	–67.23480	17.95396	–67.23985	17.94881	2, 5	10.6	0.5952
32	–67.27705	17.96561	–67.27782	17.96941	2, 4	15.2	0.3424
33	–67.26975	17.89825	–67.26881	17.90867	6, 4	16.7	0.9256
34	–67.31804	18.01221	–67.32545	18.01010	1	15.5	0.6552
35	–67.40501	18.09425	–67.40598	18.08797	6, 3	18.5	0.5928
36	–67.21063	18.16835	–67.20764	18.17109	2, 5	6	0.3976
37	–67.40116	18.05823	–67.39548	18.06139	1, 6	14.9	0.5528
38	–67.29276	17.97640	–67.28926	17.96766	4, 5	22.5	0.828
39	–67.39057	18.06617	–67.39052	18.07480	4, 5	23	0.7648
40	–67.27128	18.09733	–67.27348	18.09109	2, 6	5.9	0.5824
42	–67.26957	17.89536	–67.27339	17.90212	1, 6	18.7	0.68
43	–67.34658	18.00154	–67.35453	18.00716	4, 3	16	0.8384
44	–67.25080	17.99741	–67.23418	17.99046	2	13.5	1.5744
45	–67.34643	18.02754	–67.35651	18.02880	3, 4	21.9	0.8608
46	–67.22816	18.15748	–67.22880	18.15103	2	12.6	0.5728
48	–67.27627	17.98872	–67.26698	17.99150	5, 4, 2	15.3	0.824
50	–67.17708	17.96208	–67.18580	17.95488	2	2.8	0.9752

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TABLE A.2. Counts and calculated densities (number/ha) for each of the 46 sites sampled for the 2013 queen conch survey off western Puerto Rico. The totals and averages do not include the value for site 6, which was treated as an outlier.

	Count						Density		
Site	J	NMA	A	OA	VOA	Total	J	A	Total
1	14	0	1	0	0	15	15.1	1.1	16.1
2	0	0	2	0	0	2	0.0	4.1	4.1
3	13	2	1	0	0	16	12.7	2.9	15.6
4	2	1	2	1	1	7	1.9	4.7	6.5
5	4	0	0	0	0	4	13.3	0.0	13.3
6	1,399	0	0	0	0	1,399	3,089.7	0.0	3,089.7
7	8	0	1	0	0	9	10.8	1.4	12.1
8	4	1	0	0	0	5	6.2	1.6	7.8
9	0	3	1	0	1	5	0.0	6.3	6.3
10	5	5	1	0	0	11	10.2	12.2	22.3
11	4	1	0	0	0	5	1.0	0.3	1.3
12	4	4	1	1	0	10	3.8	5.6	9.4
13	7	0	1	0	0	8	9.5	1.4	10.9
14	2	2	0	0	0	4	1.9	1.9	3.9
15	1	0	1	0	0	2	1.8	1.8	3.6
16	4	10	8	1	3	26	8.1	44.7	52.9
17	1	0	2	2	5	10	3.3	29.8	33.2
18	4	0	0	0	0	4	4.7	0.0	4.7
19	0	0	3	1	0	4	0.0	7.0	7.0
20	0	0	0	0	0	0	0.0	0.0	0.0
21	0	0	0	0	0	0	0.0	0.0	0.0
22	4	2	5	0	0	11	7.6	13.3	20.8
23	10	1	3	3	3	20	22.2	22.2	44.4
24	0	1	0	0	1	2	0.0	5.2	5.2
25	0	0	0	0	0	0	0.0	0.0	0.0
27	0	6	0	2	0	8	0.0	13.4	13.4
28	4	0	1	0	0	5	5.5	1.4	6.9
29	2	0	0	2	3	7	0.9	2.1	3.0
30	8	2	0	2	1	13	9.3	5.8	15.1
31	6	3	1	1	0	11	10.1	8.4	18.5
32	4	1	0	1	0	6	11.7	5.8	17.5
33	11	0	1	0	0	12	11.9	1.1	13.0
34	0	0	1	0	0	1	0.0	1.5	1.5
35	14	8	3	0	3	28	23.6	23.6	47.2
36	7	7	0	3	1	18	17.6	27.7	45.3
37	19	6	8	1	0	34	34.4	27.1	61.5
38	2	1	1	0	1	5	2.4	3.6	6.0
39	0	1	0	2	1	4	0.0	5.2	5.2
40	4	2	0	0	0	6	6.9	3.4	10.3
42	2	1	2	3	0	8	2.9	8.8	11.8
43	0	0	0	0	1	1	0.0	1.2	1.2
44	3	0	0	0	0	3	1.9	0.0	1.9
45	0	0	2	0	0	2	0.0	2.3	2.3
46	17	10	1	0	0	28	29.7	19.2	48.9
48	0	0	0	0	0	0	0.0	0.0	0.0
50	0	0	0	0	0	0	0.0	0.0	0.0
Total	194	81	54	26	25	380			
Average							6.7	7.3	14.1

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