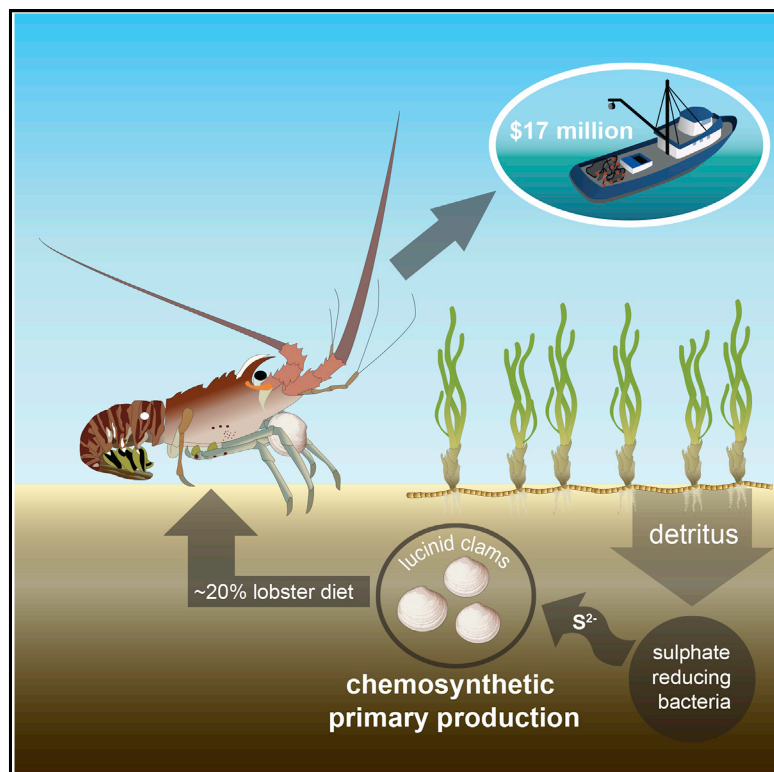
Report

Current Biology

Caribbean Spiny Lobster Fishery Is Underpinned by Trophic Subsidies from Chemosynthetic Primary Production

Graphical Abstract



Highlights

- This is the first stable isotope analysis of the Caribbean spiny lobster diet
- Spiny lobsters obtain 20% of their diet from chemosynthetic food sources
- This is the first demonstration that chemosynthetic primary production supports fisheries
- Seagrass habitats provide chemosynthesis-based ecosystem services

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In Brief

Most of the energetic input into food webs occurs through photosynthesis, but some marine animals get food from symbioses with chemosynthetic bacteria. Higgs et al. show that chemosynthetic primary production from specialized clams in seagrass beds plays a significant role in supporting the economically valuable Caribbean spiny lobster fishery.

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Caribbean Spiny Lobster Fishery Is Underpinned by Trophic Subsidies from Chemosynthetic Primary Production

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SUMMARY

The Caribbean spiny lobster, *Panulirus argus*, is one of the most valuable fisheries commodities in the Central American region, directly employing 50,000 people and generating >US$450 million per year [1]. This industry is particularly important to small island states such as The Bahamas, which exports more lobster than any other country in the region [1]. Several factors contribute to this disproportionally high productivity, principally the extensive shallow-water banks covered in seagrass meadows [2], where fishermen deploy artificial shelters for the lobsters to supplement scarce reef habitat [3]. The surrounding seabed communities are dominated by lucinid bivalve mollusks that live among the seagrass root system [4, 5]. These clams host chemoautotrophic bacterial symbionts in their gills that synthesize organic matter using reduced sulfur compounds, providing nutrition to their hosts [6]. Recent studies have highlighted the important role of the lucinid clam symbiosis in maintaining the health and productivity of seagrass ecosystems [7, 8], but their biomass also represents a potentially abundant, but as yet unquantified, food source to benthic predators [9]. Here we undertake the first analysis of Caribbean spiny lobster diet using a stable isotope approach (carbon, nitrogen, and sulfur) and show that a significant portion of their food (~20% on average) is obtained from chemosynthetic primary production in the form of lucinid clams. This nutritional pathway was previously unrecognized in the spiny lobster's diet, and these results are the first empirical evidence that chemosynthetic primary production contributes to the productivity of commercial fisheries stocks.

RESULTS

Spiny lobsters are foraging generalists in coral reef ecosystems that leave their dens at night to hunt over various habitats around the reef flats [10–12]. Previous studies of the spiny lobster diet have been limited to observational and gut content analyses (see the Supplemental Experimental Procedures), which have a number of known limitations [13]. During sampling operations, large shell middens were frequently observed at the entrance of artificial shelters in seagrass habitats, which mostly (>90%) consisted of shells from the lucinid bivalve, *Codakia orbicularis* (Figure 1A). These shells showed signs of predation where their margins had been chipped away and occasionally small round bore holes were present (Figure 1D). Spiny lobsters at the artificial shelters were directly observed feeding on live *C. orbicularis* specimens on six separate occasions; i.e., the lobsters were holding clams to their mandibles. On four occasions, lobsters were found with *C. orbicularis* specimens actually clamped on to a leg (Figures 1C and 1D). Lobsters were also caught in the process of consuming a range of other prey items, including moon snails (*Sinum maculatum* and *S. perspectivum*), sea stars (*Echinaster echinophorus*, *Astropecten duplicatus*, and juvenile *Oreaster reticulatus*), sea cucumbers (*Holothuria princeps*), a small cowfish (*Acanthostracion polygonius*), and two seahorses (*Hippocampus erectus*).

Stable isotope analysis of potential lobster prey samples clustered into five groupings that were significantly distinct in isotopic space (Figure 2; Table S1): (1) a core "phototrophic" group of photosynthetic primary producers (seagrass and algae) with filter feeders, browsers, and grazers (mollusks, echinoderms, crustaceans, and sponges); (2) a group of "predators" that were ^{15}N and ^{13}C rich relative to group 1 and consisted of a predatory sea star, three predatory gastropod species, three fish species, a shrimp, and a deposit-feeding sea cucumber; (3) a "chemotrophic" group including all samples of the lucinid bivalve *Codakia orbicularis* and three samples of the predatory gastropod *Sinum* that had very low δ^{34}S values relative to all other samples; (4) two samples of the algae *Caulerpa sertularioides* that were strongly ^{13}C depleted relative to all other samples; and (5) a sponge and two annelids living inside of it that had low δ^{15}N values relative to groups 1 and 2.

The stable isotope signatures of all 160 lobster samples fell within the range of values of the five potential food source groups (Figure 2). The carbon and sulfur isotope ratios of lobster tissue samples were concentrated directly between the chemotrophic source and the predator and phototrophic sources. Over half of the lobster samples had δ^{13}C values that were lower than the mean values for the phototrophic, predator, and sponge prey groups (Figure 2A), and 89% of lobster samples had lower

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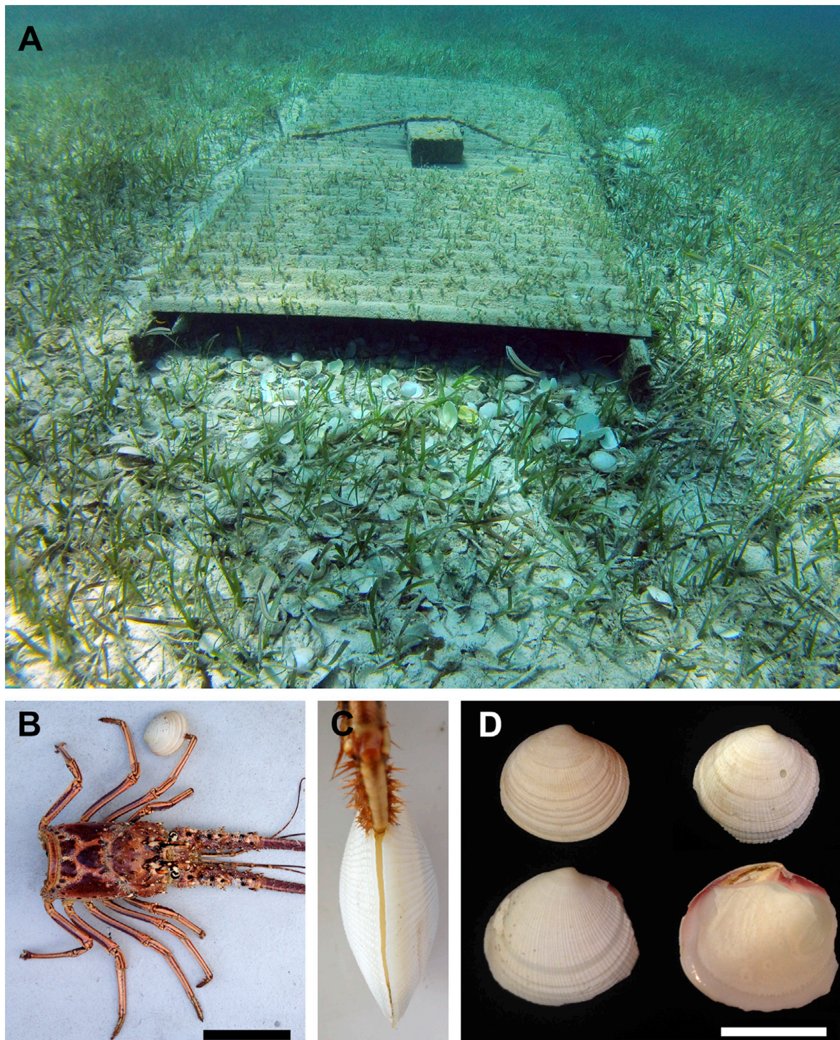

Figure 1. Spiny Lobster, *Panulirus argus*, Predation on *Codakia orbicularis* Clams

(A) An artificial lobster shelter with a shell midden of discarded *C. orbicularis* shells at the entrance.

(B) Lobster carapace with a live *C. orbicularis* clamped on to its leg (scale bar, 10 cm).

(C) Lobster dactylus opening the shell.

(D) Specimens of *C. orbicularis* showing predation damage (shell boring and chipping), with the exception of the top-left specimen, which is undamaged (scale bar, 5 cm).

δ^{34}S values than the mean of the predators group (Figure 2B). The mean δ^{15}N value for the lobsters was 6.14‰ (±0.6‰).

Posterior probabilities from the Bayesian stable isotope mixing model, using the mean and SD values for the five prey groups as sources, indicated that the phototrophic source group overall contributed most to the lobster's diet (42% ± 10%), followed by the predator group (28% ± 5%) and then the chemotrophic group (21% ± 2%), with the sponge and algae groups comprising a minor proportion of the diet (7% ± 4% and 1% ± 1%, respectively). Without prior probability information, the model still estimated that the chemotrophic source constituted 20% (±2%) of the lobsters' diet, although the predator group contribution (44% ± 6%) was estimated to be much higher than that of the phototrophic group (14% ± 19%). The model could not adequately distinguish between the predator and phototrophic sources, which were strongly correlated ($\rho = -0.94$), leading to the large fluctuation in the contribution of the phototrophic source group and wide credible intervals in the absence of prior information.

When lobster samples were grouped according to collection site, substantial differences in the contributions of the three main prey sources were evident (Figure 3). The contribution of chemotrophic food sources to the lobster diet varied from 34% (±6%) in samples from the patch reefs to as little as 12% (±3%) in samples from the southwest bank. As with the pooled analysis, the credible intervals of the posterior probabilities for the chemotrophic source are much narrower than those of the phototrophic and predators groups, indicating a higher degree of confidence in the contribution of the chemotrophic source relative to the phototrophic and predators groups.

DISCUSSION

After the remarkable discovery of deep-sea animal communities fuelled by chemosynthetic primary production in the late 1970s, it became evident that chemosynthetic symbioses were also common in shallow marine environments, across a wide range of taxa [14]. These discoveries soon prompted speculation on the potential importance of chemosynthetic primary production for fisheries stocks [15]. Despite this early recognition, the transfer of chemosynthetic primary production to the wider marine food web has only been quantified relatively recently for deep-sea chemosynthetic habitats [16] and even later for some shallower marine habitats [17, 18]. Recent studies in freshwater systems have also revealed significant chemosynthetic inputs to limnic food webs [19]. Our results provide the first empirical evidence that chemosynthetic primary production plays a significant role in supporting commercially important stocks of marine animals.

Stable isotope analyses of Caribbean spiny lobsters show that they obtain approximately one-fifth of their diet from the chemosynthetic production of lucinid calms, and in some populations this figure is almost doubled. All available evidence indicates that *Codakia orbicularis* production is in turn derived from their chemoautotrophic symbionts [6, 20]. Their sulfur isotope ratios (Figure 2B) are some of the lowest values measured for chemo-symbiotic animals. These values more closely resemble those of gutless solemyid bivalves (−20‰ to −30‰) that entirely rely on their symbionts, rather than the more closely related

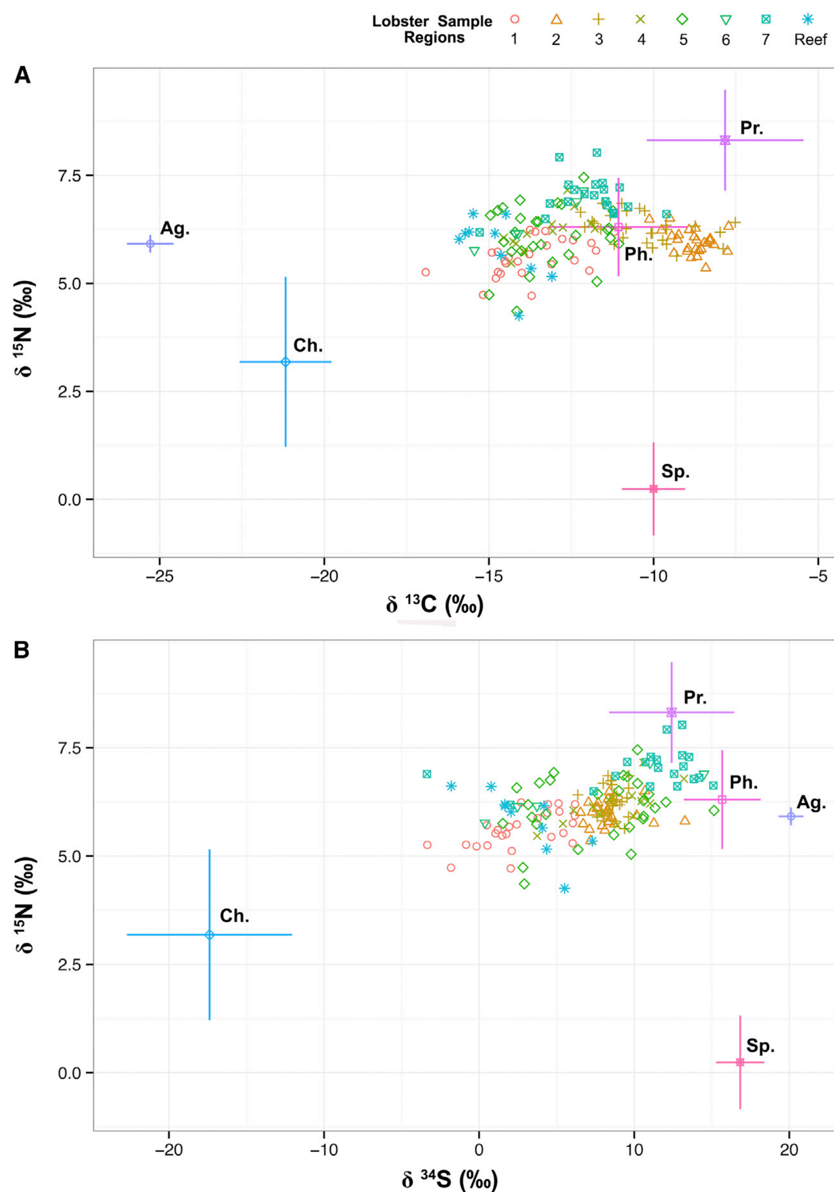

Figure 2. Stable Isotope Tracer Plots for Individual Lobster Samples from Different Regions and Their Potential Food Sources

$\delta^{13}C$ versus $\delta^{15}N$ values (A) and $\delta^{34}S$ versus $\delta^{15}N$ values (B). Individual lobster samples shown as points colored by region. Food source-group values are shown as group means (±SD) and are labeled as follows: Ag, algae; Ch, chemotrophic; Ph, phototrophic; Pr, predator; Sp, sponge. Food source values (Table S1) are corrected according to trophic discrimination factors for each source.

Lucinoma aequizonata (~−6‰) [21], which also feeds heterotrophically [22].

Only one previous study of lobster diet has listed *C. orbicularis* as a prey item (2.8% of diet) [10], despite the abundance of this potential prey in seagrass beds. Our observations of large shell middens explain this discrepancy; since the shells are not consumed, they are unlikely to have been detected in gut content analysis. Large shell middens and direct observations of predation (Figure 1) show that the lobsters are adept at obtaining their prey, which live between 5 and 25 cm below the surface in a dense mat of tough seagrass roots [7]. The shell-chipping method of feeding (Figure 1D) is characteristic of spiny lobster predation [23]. The lobsters seem to selectively feed on the largest clams, since size distributions of shells from three collected middens are all skewed to the upper end of *C. orbicularis* size distributions (Figure 4). Alternatively, smaller shells may be completely crushed, but this seems unlikely given their paucity in gut content studies (Supplemental Experimental Procedures).

Other novel food-web interactions were revealed by the stable isotope analyses. Several individuals of the predatory gastropod *Sinum* (but not all) had isotopic signatures that closely matched those of *Codakia orbicularis* (Table S1), indicating that these gastropods also preyed upon the lucinids. Previous studies have found that ~30% of dead *C. orbicularis* shells are bored in the same manner as those observed at lobster shelters (Figure 1D), but the predator was unknown [4]. *Sinum* moon snails were in turn the most common prey item in our observations of lobster feeding, providing an indirect mode of chemosynthetic carbon assimilation into the lobsters' diet. Despite the lobsters feeding on these and other ^{15}N-rich prey, the mean $\delta^{15}N$ values for adult lobsters surveyed here were ~1% lower than those for juvenile lobsters from hard-bottom habitats [24], consistent with feeding on lucinid clams.

Intriguingly, lobsters living at natural reef habitats showed some of the highest values for chemosynthetic contributions to their diet, along with those from artificial shelters in the northwest part of the banks and sandbores (regions 1 and 6 in Figure 3). All of these habitats are in areas of dense seagrass, whereas regions with low contributions of chemosynthetic production are from areas of relatively low seagrass density (Figure S1). Direct measurement of seagrass density in each region was not undertaken since fishermen do not deploy shelters randomly but always seek the densest seagrass patches in each region (if present). Nevertheless, it is interesting that chemosynthetic contributions to diet seem to mirror seagrass density at the seascape scale, as might be expected given the close relationship between lucinids and seagrass [8]. For a highly mobile and migratory species like *P. argus*, the stable isotope signal integrates spatial and temporal diet assimilation.

The novel dietary pathways identified in this study have several implications for Caribbean spiny lobster management.

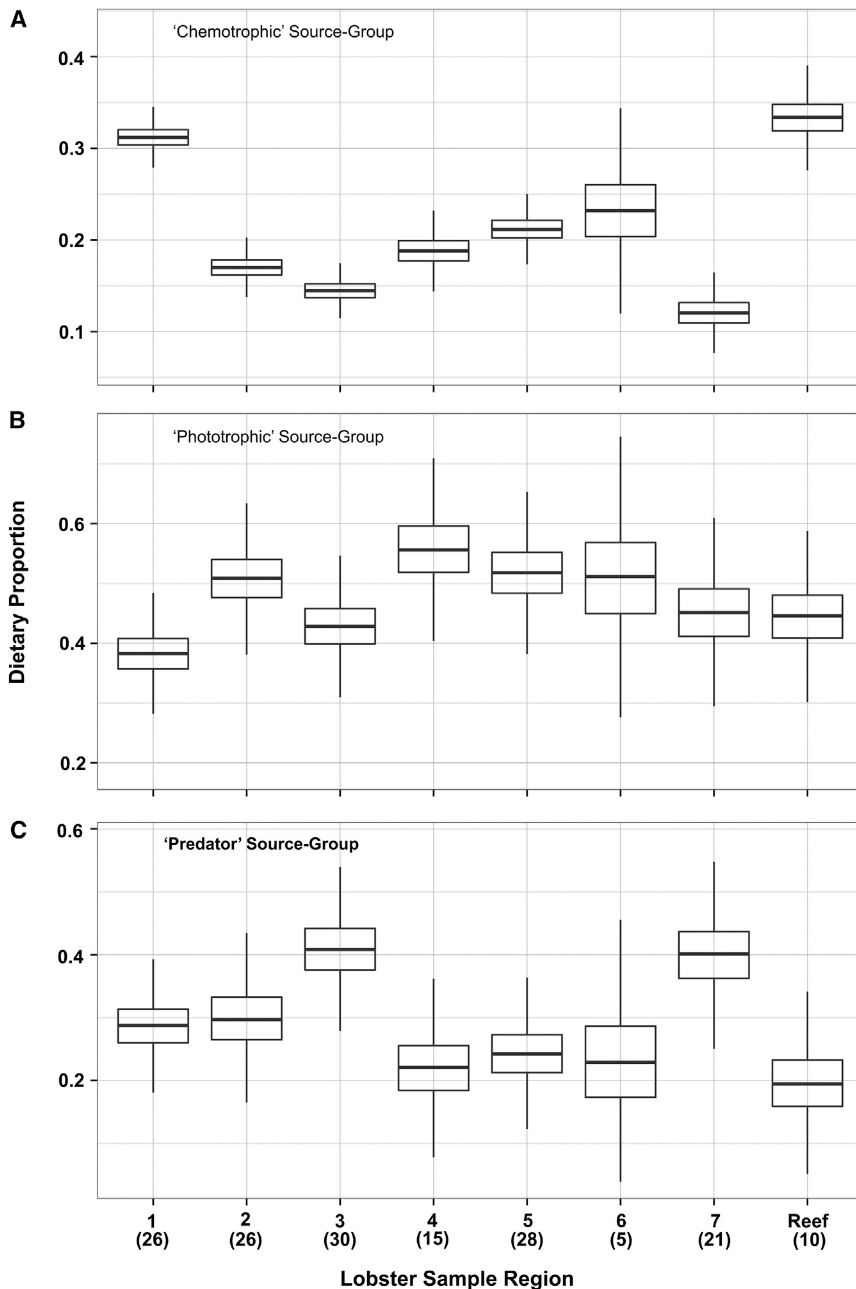

Figure 3. Posterior Probabilities for the Proportional Contribution of each Source Group to the Spiny Lobster Diet for Each Sample Region

Box plots show the median probabilities with 25% and 75% credible intervals. Whiskers show 2.5% and 97.5% credible intervals. Chemotrophic (A), phototrophic (B), and predator (C) source groups are shown. Sample regions shown in Figure S1, and the numbers of lobsters sampled are shown in brackets.

The key role of seagrass habitat and lucinid clams in the ecology of Caribbean spiny lobster emphasize the importance of taking an ecosystem approach to managing lobster stocks [25], with particular regard for seagrass habitat health. Local fishers have long observed that healthy seagrass is the best habitat for their gear and that lobsters prey heavily on *Codakia*. Our results, along with those from previous studies [8], provide a mechanistic understanding for these observations. There is a growing acknowledgment that such "fishers' knowledge" should be given greater prominence in fisheries research and management, especially in data-poor fisheries [26]. Positive moves to do so have already begun with the Bahamas Lobster Fishery Improvement Project [27] and offer the potential for further insights into the dynamics of this important resource.

The significance of chemosynthetic production for spiny lobster stocks may vary around the Caribbean region, but observations of shell middens at lobster habitats in other countries suggest that our results may hold true elsewhere [23, 28]. Further isotopic studies will be able to confirm the significance of chemosynthetic production for other lobster fisheries in the region. In a global context, chemosynthetic production may also be important for other spiny lobster populations such as *Panulirus cygnus*, which has been documented feeding on chemo-symbiotic solemyid and lucinid clams in Australian seagrass beds [29, 30]. Sub-populations of rock lobsters *Jasus edwardsii* in protected New Zealand Fjords also appear to obtain a substantial part of their diet from solemyid clams [31], although it is unclear to what extent these populations contribute to the fished populations.

Spiny lobsters are particularly well adapted to exploiting the high productivity of chemo-symbiotic clams, which are often difficult for other predators to obtain because of their deep-burrowing lifestyle. As such, lobsters play a key role in transferring chemosynthetically fixed carbon from the deep sediment into the wider marine food web. Ultimately, this includes a contribution to human diets and prosperity in the form of lobster biomass that is worth US$17.4 million to the Bahamas fishery alone.

EXPERIMENTAL PROCEDURES

Sample Collection and Treatment

All biological samples were collected during daylight hours in August 2014 from ten selected locations across the Great Bahama Bank, representing a mosaic of different habitats targeted by fishermen (Figure S1).

Tissue samples were taken from 160 lobsters for stable isotope analysis. Where possible, lobsters were sampled from six artificial shelters in each region, with five lobsters sampled from each shelter. Lobster samples from natural reef habitats (patch reef and blue hole) were sampled opportunistically.

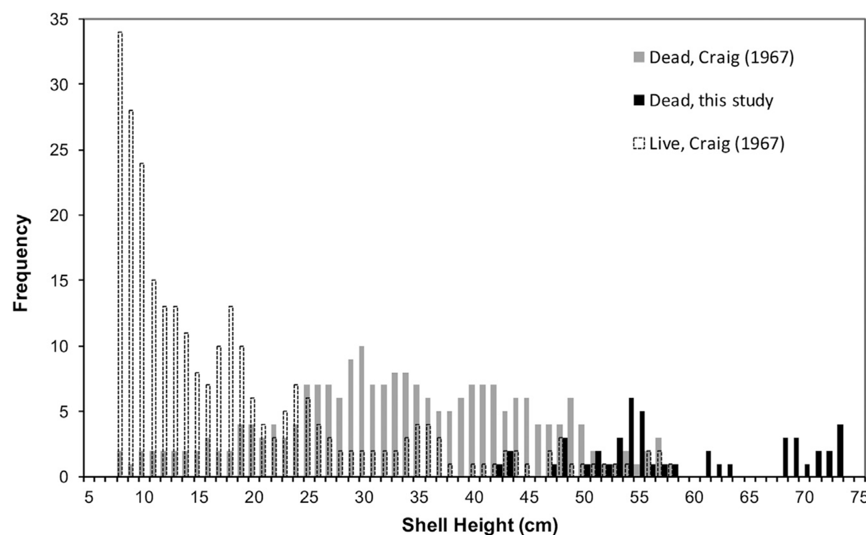

Figure 4. Size-Frequency Distributions of *Codakia orbicularis* Shells Found in Natural Seagrass Populations on the Great Bahama Bank

As reported by Craig [4] for living (dashed bars; n = 289) and dead (light gray bars; n = 209) specimens and shells found in middens at artificial shelters in this study (dark gray; n = 47).

Lobster tissue samples consisted of tail muscle collected from the interior dorsal surface of the carapace, after removal of the tail by fishermen.

Potential prey items were collected by hand, opportunistically by divers from around artificial shelters in proportion to their known frequency in lobster diets, based on a comprehensive literature review (Supplemental Experimental Procedures). Dietary tissue samples consisted of whole organisms for macrofaunal taxa and tissue subsamples for sponges, algae, seagrass, and megafaunal echinoderms. All tissue samples were washed with distilled water, pulverized, and dried at 55°C for at least 24 hr. Samples were then placed in sterile glass containers sealed with plastic caps.

Stable Isotope Analysis

Stable isotope analyses were performed by continuous flow isotope ratio mass spectrometry, using an Elementar Pyrocube elemental analyzer (EA) interfaced with an Isoprime VisION stable isotope ratio mass spectrometer (IRMS). This system has been set up to measure $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ successively in a single sample. Samples for this study were run over five separate measurement runs, including a large set of standards (described in the Supplemental Experimental Procedures).

Statistical Analyses

The total potential prey inventory consisted of 47 different species, with each species represented by 1–11 samples (30 in the case of *Codakia orbicularis*). To generate meaningful results from stable isotope mixing models, it is necessary to group sources when the number of potential sources is so much greater than the number of isotopic tracers [32]. We elected to aggregate samples a priori [33], by undertaking a multivariate cluster analysis on all individual samples to determine which groups of samples were distinguishable in three-dimensional isotopic space (Supplemental Experimental Procedures).

Diet analysis was undertaken in a Bayesian mixing model framework using the SIMMR package developed in the R computing environment [34]. SIMMR was chosen because it is capable of explicitly incorporating prior probabilities into the mixing model, a desirable feature that can reduce the credible intervals of the posterior probability estimates generated by the model [35]. Incorporation of prior probabilities into our model was justified on two grounds. First, there was good information on dietary proportions of *Panulirus argus* prey from previous studies, and second, these studies showed that two of the groups were much less likely constitute significant food sources relative to the other three.

Stable isotope values for individual lobster samples (the consumers) were grouped by region and analyzed as separate groups in the model. Under the SIMMR framework, a correction factor (i.e., discrimination or trophic enrichment factor) is applied to stable isotope values for each source to account for the isotopic fractionation that occurs when consumers assimilate each tracer element from their prey [35]. Discrimination factors for carbon and nitrogen tracers were applied to each source in our model, obtained from experimental studies on the congener species *Panulirus cygnus* [36]. A generic correction factor of +0.5 ± 0.6 was applied to all source values for $\delta^{34}S$, since there are very few controlled feeding studies on sulfur isotope fractionation in biological systems [37]. Correction factors were also incorporated to account for variations in the concentration of each element in source tissues [38]. These values were taken from elemental concentrations measured in the samples themselves, with the exception of sulfur concentrations in the lucinid clams, where a value of 1.4% was used to account for the high elemental sulfur content of the lucinid gills [21], which were unlikely to be assimilated by the lobsters [26].

ACCESSION NUMBERS

The data reported in this paper can be accessed at https://dx.doi.org/10.6084/m9.figshare.4225334.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, one figure, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.10.034.

AUTHOR CONTRIBUTIONS

N.D.H. and M.J.A. conceived and designed the study. N.D.H. collected samples. N.D.H. and J.N. carried out analyses. All authors contributed to the writing of the manuscript.

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