

# Oil platforms off California are among the most productive marine fish habitats globally

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Edited by David W. Schindler, University of Alberta, Edmonton, Canada, and approved September 22, 2014 (received for review June 20, 2014)

**Secondary (i.e., heterotrophic or animal) production is a main pathway of energy flow through an ecosystem as it makes energy available to consumers, including humans. Its estimation can play a valuable role in the examination of linkages between ecosystem functions and services. We found that oil and gas platforms off the coast of California have the highest secondary fish production per unit area of seafloor of any marine habitat that has been studied, about an order of magnitude higher than fish communities from other marine ecosystems. Most previous estimates have come from estuarine environments, generally regarded as one of the most productive ecosystems globally. High rates of fish production on these platforms ultimately result from high levels of recruitment and the subsequent growth of primarily rockfish (genus *Sebastes*) larvae and pelagic juveniles to the substantial amount of complex hard-scape habitat created by the platform structure distributed throughout the water column. The platforms have a high ratio of structural surface area to seafloor surface area, resulting in large amounts of habitat for juvenile and adult demersal fishes over a relatively small footprint of seafloor. Understanding the biological implications of these structures will inform policy related to the decommissioning of existing (e.g., oil and gas platforms) and implementation of emerging (e.g., wind, marine hydrokinetic) energy technologies.**

secondary production | ecosystem-based management | ecosystem services | energy technology | *Sebastes*

**S**econdary production is the sum of new biomass from growth for all individuals in a given area during a unit of time. Some of the original motivations for understanding biological productivity stem from the need to estimate the annual production of fishes that can be taken from a body of water (1, 2). By integrating multiple metrics that can individually reflect aspects of fitness (e.g., density, biomass, growth, fecundity, survivorship, body size, life span), secondary production can be thought of as a general criterion of success for a population (3, 4). Recent studies have extended this idea, using secondary fish production to provide a measure of the productive capacity and economic value of specific habitats within an ecosystem (5, 6) and, in a few instances, to evaluate the efficacy of creating artificial reefs and other forms of habitat restoration (7–9). In ecological studies, static properties such as density or biomass are typical structural response variables, whereas the use of secondary production, a functional measure, has been mostly limited to freshwater and marine benthic invertebrate studies (4). Meanwhile, marine ecologists and fisheries scientists continue to advocate for incorporating more ecosystem-based approaches to managing marine resources (10–12). This includes calls to add more elements of community and trophic ecology to the concept of essential fish habitat (12) and will likely involve the development of functional measures or indicators that incorporate several processes from within an ecosystem (13, 14).

The decommissioning of the >7,500 oil and gas platforms around the world (15, 16) is an unavoidable issue. Understanding the potential effects of the different decommissioning options on the biology of fishes living in such habitats will be important

information to consider in the process. These options include “rigs-to-reefs” approaches where some portion of the platform is left in the water to continue functioning as an artificial reef. A main unresolved issue is the degree to which these types of structures enhance ecosystem function, and in particular secondary fish production, compared with nearby natural reefs (16–20). Additionally, with the current global emphasis on developing sources of renewable energy, deployment of new structures in the marine environment associated with offshore wind and wave energy extraction is increasing (21–23). These deployments may create opportunities to incorporate design elements that may enhance the conservation value and fisheries production associated with these structures.

Here, we compare the annual secondary production of fish communities on oil and gas platforms to those on natural reefs off the coast of southern California (Fig. 1) and to secondary production estimates of fish communities from other marine ecosystems. To calculate the annual secondary production for a fish community, referred to here as “Total Production,” we develop a model based on fisheries-independent density and size structure data of fishes from visual surveys performed from a manned submersible once per year for between 5 and 15 y at each site. We define Total Production of the fish community as the sum of two components: “Somatic Production,” which is the difference between the observed biomass during surveys and the biomass predicted 1 y later using species-specific morphometric, growth, and mortality functions, and “Recruitment Production,” which estimates production from the growth of postlarval and pelagic juvenile fishes that settled or immigrated and survived during a 1-y time interval. Metrics for a “complete platform” were scaled to per square meter of seafloor, i.e., overall values were calculated for an entire platform, and then divided by the surface area of seafloor beneath the footprint of the platform. This permits a more direct comparison among platforms and natural

## Significance

**Secondary production is the formation of new animal biomass from growth for all individuals in a given area during some period of time. It can be a powerful tool for evaluating ecosystem function because it incorporates multiple characteristics of a population or community of organisms such as density, body size, growth, and survivorship into a single metric. Here, we find that fish communities living on the complex hardscape habitat created throughout the water column by the structure of oil and gas platforms off California have the highest secondary production per unit area of seafloor of any marine ecosystem for which similar estimates exist.**

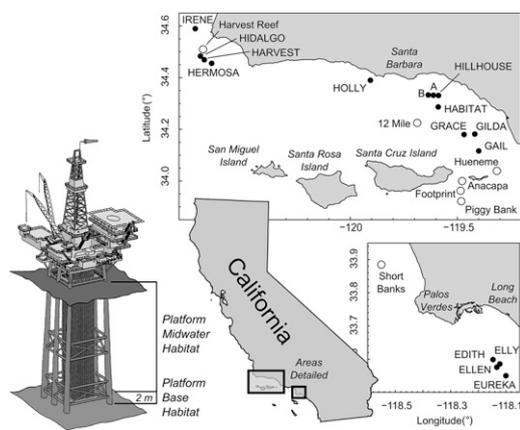
Author contributions: J.T.C., D.J.P., M.L., and A.S.B. designed research; J.T.C., D.J.P., M.L., L.A.Z., C.M.W., J.P.W., and A.S.B. performed research; J.T.C. and D.J.P. analyzed data; and J.T.C., D.J.P., M.L., L.A.Z., and A.S.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1411477111/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1411477111/-DCSupplemental).



**Fig. 1.** Platform diagram and map of the study area. The platform mid-water habitat encompasses the hard substrate of the platform structure from the water surface to 2 m above the seafloor, whereas the platform base habitat is the bottom 2 m of the platform structure. The platform structure consists of outer vertical pilings and horizontal crossbeams (i.e., the platform jacket) and the vertical oil and gas conductors in the center. Note this is a general display diagram and the designs of these structures vary from platform to platform. The 16 platforms (filled circles) and seven natural reefs (open circles) used in the study were surveyed for at least 5 (up to 15) y between 1995 and 2011.

reefs in the present study, and among estimates of secondary production of fishes in other ecosystems from the literature, which are also typically scaled to per square meter of seafloor (Table 1).

## Results and Discussion

Oil and gas platforms off the coast of California have the highest secondary fish production per unit area of seafloor of any marine habitat that has been studied (Table 1). The mean annual Total Production per square meter of seafloor for complete platforms was significantly greater than, and 27.4 times as much as is produced per square meter on natural rocky reefs located at similar depths in the study region (Fig. 2B and Table S1). When platforms are evaluated individually, their average annual Total Production (range, 104.7–886.8  $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ ; Fig. 3) tended to be an order of magnitude higher than that of fish communities in other marine ecosystems where similar types of measurements have been made (range, 0.9–74.2  $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ ; Table 1). High rates of fish production per unit area of seafloor for the complete platforms are achieved because the platform jacket (horizontal crossbeams and vertical pilings) and oil and gas conductors create a complex structure that provides a large surface area of hard substrate throughout the water column (16, 19) (Fig. 1 and Table S2). This results in a high ratio of platform structural surface area to seafloor surface area (range, 5.4–20.2; Table S2), making large amounts of habitat available to juvenile and adult demersal fishes over a relatively small footprint of seafloor (range, 0.2–0.6 ha; Table S2). High structural complexity of hard substrate is often associated with marine habitats that have high abundance and diversity of fishes (24–26). The platform structure supports a diverse community of sessile and motile invertebrates that, along with planktonic food resources, provide the base of the food web for platform fishes (27).

Previous estimates of secondary production for marine fishes have come from more shallow habitats (Table 1). Most are from estuarine environments, generally regarded as one of the most productive ecosystems globally (28). Some estimates also come

**Table 1.** Estimates of secondary production of fishes from various marine ecosystems

Ecosystem	Fish production, $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$	Reference
Oil platforms, California, United States	104.7–886.8*	Present study
Coral reef, Moorea	74.2*	Ref. 59
Estuary, Louisiana, United States	35.0–72.8*	Ref. 60 as cited in ref. 61
Coastal lagoon, (Pacific) Mexico	24.6–66.7*	Ref. 62 as cited in ref. 61
Artificial rocky reef, California, United States	66.5*,†,‡	Ref. 8
Coastal lagoon, Texas, United States	12.1–57.6*	Ref. 63 as cited in ref. 61
Estuary, South Africa	55.9*	Ref. 61
Estuary, California, United States	37.6*,§	Ref. 64
Coastal lagoon, Mexico	34.5*	Ref. 65
Salt marsh, New Jersey, United States	33.5*,¶	Ref. 66
Salt marsh, Delaware, United States	32.4*,¶	Ref. 67 recalculated in ref. 66
Coastal lagoon, Cuba	22.0–27.6*	Ref. 68 as cited in ref. 61
Deep rocky reef, California, United States	4.4–22.4*	Present study
Coastal lagoon, Mexico	20*	Ref. 69 as cited in ref. 61
Eelgrass bed, North Carolina, United States	18.4*,§	Ref. 42
Estuary, Italy	9.0–17.0*	Ref. 70 as cited in ref. 61
Chesapeake Bay, United States	11.2–16.4*,†	Ref. 71
Seagrass bed, southern Australia	2.7–15.8*,§	Ref. 72
Coastal lagoon, Texas, United States	15.4*	Ref. 73
Mangrove habitat, Florida, United States	6.1–12.1¶	Ref. 74
Salt marsh, Massachusetts, United States	6.4*,¶	Ref. 75 recalculated in ref. 66
Soft bottom, California, United States	5.9*,†	Ref. 8
Estuary, Scotland	4.3*	Ref. 76 as cited in ref. 61
Coastal lagoon, Portugal	0.9–2.5*	Ref. 77

After refs. 61 and 78. Also note that, although fish production of 29–901\*  $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$  was reported for Bahamian tidal creeks, surveys were performed at low tide when fishes were aggregated into a fraction of the total available habitat. Therefore, the authors of that study caution against comparing these values with those from other studies (79).

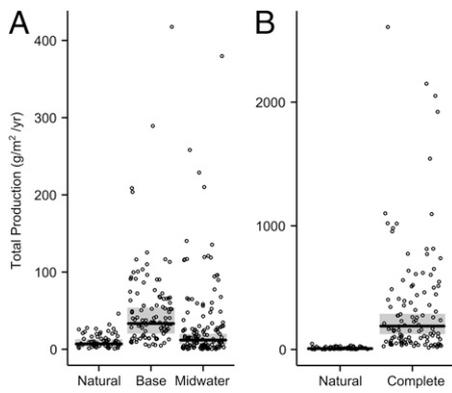
\*Based on summation of production estimates from multiple species in an assemblage.

†Original estimate for partial-year time interval was standardized to a 1-y interval.

‡Original estimate contained gonadal production component; only somatic production component is reported here.

§Original estimate was in grams dry weight and converted to grams wet weight by multiplying by 4 (64).

¶Production estimate for a single species.



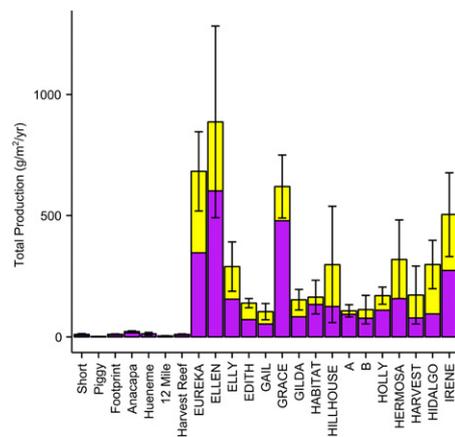
**Fig. 2.** Annual Total Production. (A) Annual production values scaled to per square meter of habitat for natural reefs ( $n = 56$ ) and platform habitat subtypes [base ( $n = 111$ ), midwater ( $n = 132$ )]. (B) Annual production values scaled to per square meter of seafloor for natural reefs ( $n = 56$ ) and complete platforms ( $n = 111$ ). Circles indicate individual data points and are jittered for visibility. Horizontal lines show the backtransformed estimated marginal means. The shaded box represents the 95% confidence intervals (CIs) of the mean. Differences were considered significant if the 95% CIs of their marginal means did not overlap.

from nearshore coral and rocky reefs, studies that typically account only for production of demersal fishes living near the surface of the habitat structure (see references in Table 1); thus, these studies do not account for production throughout the water column and may underestimate total production. These latter estimates may be more comparable to our estimates of production per square meter of transect along the two specific types of platform habitat: the “platform midwater habitat,” which is the platform structure from the water surface to 2 m above the seafloor, and the “platform base habitat,” which is the bottom 2 m of the platform structure (Fig. 1). When these estimates are compared, we still find some annual platform-specific estimates are well above the annual estimates from other ecosystems (see individual points  $>75 \text{ g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$  for base and midwater habitat in Fig. 2A; Table 1). Furthermore, the average annual amounts of production in those habitats for multiple different platforms (i.e., the sum of the two production components for individual platforms presented in Fig. S1) are also similar to or above secondary fish production estimates from the other ecosystems.

The high vertical relief platform midwater habitats of these structures are important nursery grounds for young rockfishes that settle to the platforms as larvae or pelagic juveniles (19, 29). Recruitment Production per square meter of midwater platform habitat (i.e., not scaled to per square meter of seafloor) was 3.7 times as much as that on natural reefs (Table S1). With hard substrate located throughout the water column, platform midwater habitat is likely more readily accessible than natural reefs to the settling fishes that tend to be found in the upper 100 m of the water column during their pelagic stage (30). Recruitment Production and Somatic Production of smaller fishes on platforms is likely further enhanced over natural reefs because predation rates on small fishes may be lower in platform midwater habitats (31), likely due to the relative scarcity of predators compared with natural rocky reefs in the region (19, 29). Increased habitat structure from artificial reefs in Florida has also been shown to reduce predation and increase production of demersal fishes (26). Ultimately, because the surface area of the structure on these California platforms is mostly midwater habitat (average, 96.8%; SE, 0.4%; range, 95.1–98.5%), platform midwater habitat tended to contribute much more than platform base habitat to the complete platform production metrics scaled to per square meter of seafloor (average contribution of platform midwater habitat: Somatic Production: 88.6%; SE, 3.7%; range, 57.7–99.0%; Recruitment Production: 94.9%; SE, 2.8%; range, 67.8–100.0%; Total Production contribution: 91.7%; SE, 2.8%; range, 69.0–99.5%).

As they grow older, rockfishes of many species tend to move into deeper waters (32), and this was evident in the patterns of fish production on the platforms. This ontogenetic habitat use pattern is also likely an important factor that may lead to the previously mentioned reduced predation on platforms, further separating juveniles and smaller adult fishes from the larger piscivorous fishes that may prey upon them. Significantly greater Total Production and Somatic Production values were observed per square meter of platform base habitat than in either natural reef or platform midwater habitat (Fig. 2A and Table S1). The Total Production and Somatic Production values of platform base habitat were 4.8 and 5.2 times as much as that on natural reefs, respectively. The structure at the bases of these platforms form complex “sheltering habitats” created by the large horizontal beams typically at or near the seafloor. They are often partially buried with fallen mussel shells and sediments further increasing the habitat complexity and creating preferred microhabitats for many species of adult rockfishes (33).

The classic “attraction–production debate,” relating to constructing artificial reefs as a fisheries management tool to increase production of exploited fishes, centers primarily around whether hard-bottom habitat is a limiting factor. If so, additional habitat that produces fishes at an equivalent or better rate than natural habitats should result in increased production. However, if it is not limiting, then artificial habitat may only serve to attract and aggregate fishes, making them more easily caught, potentially resulting in further declines in overexploited fisheries (34, 35). Although platforms represent a small contribution to the overall hard substratum in California (18), these structures may be providing a large amount of the hard substrate below a depth of 50 m (17). Therefore, deeper-water platforms may provide considerable hard substrate in soft-bottom outer shelf regions (36). Furthermore, it is clear that juvenile rockfishes are recruiting to and being produced on platforms over multiple years, and these habitats may be valuable in rebuilding populations of bocaccio (*Sebastes paucispinis*), an overfished species in the region (29). A study modeling larval transport dynamics around one platform in this region also found that most juvenile bocaccio that did not recruit to the platform would otherwise have perished (37). Therefore, the platform was not drawing fish away from recruiting to other natural habitats, but providing a net increase in recruitment. This is likely not the case for all species and all platforms, and the isolation of platforms from extensive swaths of natural hard-bottom habitat possibly further contributes to their high rates



**Fig. 3.** Annual Total Production by site. Average of annual values scaled to per square meter of seafloor with SE error bars are divided into Somatic Production (purple) and Recruitment Production (yellow). Sites are ordered from south to north, and platform site names are in capital letters. Note that the base habitat of platforms Habitat, Hillhouse, A, and B were never surveyed and therefore not included in these calculations, so their values will be underestimated.

of production. Production per square meter would likely be reduced if a platform was located adjacent to extensive areas of natural habitat. However, if survival rates of recruiting juveniles to platform midwater habitats were still enhanced over natural habitats, the platform would still act to increase the net production and possibly export adult fishes to surrounding habitats. Additionally, other authors suggest that if artificial structures are designated as no-take areas, then the attraction–production issue may cease to be relevant. This is because the main negative of attraction is that it may make it easier to exploit fishes, and thus protected reefs would only serve to export biomass through spillover and larval export (38). Many operational offshore structures associated with energy production, including some of the platforms in California, currently function as “de facto marine reserves” due to the difficulties of fishing them or safety regulations that limit fishing vessel access all together (22, 23, 39).

Relatively few taxa contributed more than 5% of the Total Production across all habitats (Table S3). This is a common pattern in other ecosystems, where the production of a fish assemblage is typically dominated by a few of the species (see references in Table 1). In all habitats studied here, the biggest contributors were various rockfish species (genus *Sebastes*) and lingcod (*Ophiodon elongatus*). Larger-bodied species such as lingcod and bocaccio, contributed more to production because they have relatively high growth and survival rates (Fig. S2) even though they were not the most abundant species. However, some smaller-bodied species, such as halfbanded rockfish (*S. semicinctus*) and squarespot rockfish (*S. hopkinsi*), also contributed substantial amounts of secondary production because they were very abundant. We should also note that the contributions of species that tend to be more prevalent in shallow water (19, 40) are likely underestimated in our platform estimates because these shallower depths were not well sampled on some platforms (Table S2). However, this effect will be minimized for deeper platforms because shallow depths make up a relatively small proportion of their submerged surface area.

In developing our production model, we made deliberate choices in terms of how we account for changes in the abundance, or turnover, of observed fishes over the 1-y time interval so that our production estimates would tend to be conservative. Studies of secondary fish production commonly estimate fish production as the product of average biomass and specific growth rate over a time interval, typically 1 y (2, 41; see references in Table 1). A key feature of this method is that average biomass over the interval is used. Assuming that samples are taken frequently enough to accurately quantify fish throughout the time interval, this method attempts to directly account for turnover of individuals, or changes due to predation, immigration, and emigration (2, 42). Because the data we used to estimate fish production were only from one sampling event per year, we needed to account for (i) losses due to mortality, (ii) changes due to adult immigration and emigration, and (iii) production from fishes that recruited (i.e., immigration of larval and pelagic juveniles) to the habitat during the time interval. To account for mortality of observed fishes we apply a length- and species-specific annual mortality function (43). This results in very low annual rates of survival for the relatively small size classes for a given species (the effect of this can be seen in Fig. S2), and thus reduces the contribution that the smaller individuals of a given species make to the Somatic Production component of the model. Another particularly conservative feature of our model is that we apply the mortality at the start of the time interval. Therefore, the production from fishes that do not survive the entire interval, but would typically be accounted for in methods where fishes can be sampled on multiple occasions during the time interval (see references in Table 1), is excluded from our estimates. Because rockfishes tend to have high site fidelity (44–46), the calculations of the Somatic Production component also assume immigration and emigration rates are equal. Furthermore, previously observed seasonal changes of the fish communities on platforms, at least for more shallow depths, consisted primarily of the presence

or absence of pelagic species (40) and these types of transient, highly mobile species (e.g., jack mackerel, *Trachurus symmetricus*, Pacific sardine, *Sardinops sagax*) were excluded from the data used for our production estimates. Finally, our Recruitment Production component is also conservative in a similar manner as the mortality function, as it does not include the production of fishes that recruited to the habitat and grew for some period, but died before being observed during the annual survey (6).

Additional aspects of both the survey methodology used to collect the empirical data used in our model and previous studies of organisms on offshore platforms, would further suggest that our complete platform production estimates are likely conservative relative to estimates of fish production from other habitats. First, only fishes within 2 m of the platform exterior were counted during surveys, and fishes in the substantial water volume within the platform structure were not counted. Large numbers of rockfishes were often observed in the water column within the internal structure, particularly during years when fish densities are highest (29). Second, our model uses the same species-specific growth parameters from the literature to estimate fish growth and mortality for all habitats and therefore does not account for variability in growth or mortality across sites or habitat types. However, it has been demonstrated that rockfish and mussels (*Mytilus* spp.), one of the dominant filter-feeding invertebrates on platforms, can grow faster in these offshore artificial environments than in their corresponding natural habitats (47–49). Additionally, as we previously described, predation rates on small fishes may be lower in platform midwater habitats than at natural reefs (31). Therefore, although our model likely underestimates variability among years and sites because it does not account for these potential differences, these factors would again suggest that we are not overestimating the differences between fish production on platforms and fish production from other marine ecosystems in the literature (Table 1).

High interannual variability in rockfish recruitment is well documented (20, 50), and this was evident in the positive skew in the distributions of annual values for all metrics (see ranges in Table S1). As a result, Somatic and Recruitment Production varied highly across space (Fig. S1, see site means) and over time (Fig. S1, see site SEs, which reflect year-to-year variability). A large recruitment event will increase the Recruitment Production component that year. If the strong year class persists (e.g., 29), it will also make a substantial contribution to the Somatic Production component over the subsequent years, with the highest levels of production occurring when a given species reaches intermediate lengths (Fig. S2). Given the high temporal and spatial recruitment variability in fishes across ecosystems (51), and the prevalence of relatively few species contributing the majority of annual secondary production (this study; see references in Table 1), caution should be taken when generalizing secondary production values to an ecosystem or habitat type from a single year of data. Long-term datasets are extremely important to estimate production, an idea that has often been mentioned in the context of estimating the productive potential of artificial habitats (22, 23, 35, 38). This should be considered when designing protocols for making oil and gas platform decommission decisions and monitoring new offshore structures associated with renewable energy production.

Even though oil platforms off the coast of California were not designed to be high production artificial reefs, being among the most productive marine fish habitats that have been studied, they can provide insight into what drives high rates of fish production for both natural and artificial habitats. Management decisions will need to be made regarding (i) the fate of the thousands of platforms that will become economically obsolete over the coming decades (15, 16), and (ii) both the design and policy related to the construction and deployment of offshore renewable energy structures in the marine environment (21–23). Because human activities are threatening fish populations on natural reefs globally (52, 53), understanding the biological productivity of artificial structures is even more critical in terms of conservation of marine resources. Engineering modifications that may increase fish

production could be a consideration during the design process of offshore renewable energy structures to maximize the potential conservation and fishery benefit from their deployment. These could include increasing midwater habitat surface area and complexity for recruiting fishes. If species of interest have a similar ontogenetic habitat pattern as many rockfishes, moving deeper as they grow, then local production may be further increased by providing substantial amounts of complex hard substrate habitat on the seafloor at the base of a structure (16, 19, 22, 39). Recruitment variability will also play a large role in determining the production over time at a given site. Understanding the local and regional oceanography related to larval fish delivery will be an important consideration in terms of how structure location influences fish production (37, 54). In contrast to the limited life spans of structures associated with fossil fuel extraction, estimates for decommissioning renewable energy installations are more flexible and devices have the potential to be maintained in the marine environment for a much longer period (22). This creates the opportunity for adaptive management strategies. Combined with long-term biological monitoring, the designs of these structures can be tested in terms of fish production capabilities. Structures could then be modified as equipment has to be maintained and replaced over the longer term to increase conservation and fishery benefits.

## Methods

**Dataset.** Data for this study were obtained from annual visual surveys conducted during daylight hours in the fall using the manned *Delta* research submersible from 1995 through 2009 and the *Dual Deepworker* in 2010–2011. A researcher aboard the submersibles identified, counted, and estimated the total lengths (to the nearest 5 cm) of all fishes along 2-m-wide belt transects. Because different subsets of sites were surveyed each fall, we used data from the 16 platforms (in bottom depths of 47–224 m) and seven natural reefs (in bottom depths of 44–311 m) (Fig. 1) that had been surveyed for at least 5 y, some of which had been surveyed up to 15 y (Table S2). At platforms, transects ran along the outside of each horizontal beam from near-surface waters to, in most instances, the bottom (Table S2). Because horizontal beam length increases with depth, survey effort is roughly proportional to the surface area of structure at each depth. Platform transects were classified into two habitat subtypes: platform midwater habitat, from water surface to 2 m above the seafloor; and platform base habitat, encompassing the bottom 2 m of the platform (Fig. 1) (19). All of the “natural reef” sites used in the analyses were primarily deep rocky outcrops and banks of high-relief bedrock and boulders of various sizes. At natural reef sites, transects typically ran parallel to rocky ridges chosen at the time of survey from previously acquired seafloor data. Further details on the survey methodology and site descriptions are available elsewhere (19, 29, 32). Annual densities (fish per square meter) at each site for each 5-cm size class in each taxon were calculated for each habitat category (i.e., natural reef, platform base, platform midwater).

**Biological Metrics.** In addition to calculating secondary fish production, we also calculated the total fish density and total fish biomass for each habitat type, site, and year. Observed fish lengths were converted to biomass using species-specific morphometric relationships from the literature (Table S3). To calculate the annual secondary production for a fish community, referred to here as Total Production, we developed a model based on fisheries-independent density and size structure data of fishes from visual surveys performed from a manned submersible once per year. Details of the production model are provided in *SI Methods*.

**Statistical Analyses.** The effect of habitat type on each metric calculated [i.e., density (fish per square meter), biomass (grams per square meter), Somatic Production (grams per square meter per year), Recruit Production (grams per square meter per year), and Total Production (grams per square meter per year)] was evaluated using linear mixed models (LMM). The first set of LMM analyses compared metrics between natural reefs and the complete platform metric. Data from platforms that never had their bases surveyed (i.e., Platform A, B, Habitat, and Hillhouse) were excluded from analyses involving complete platform scaled metrics. A second set of LMM analyses compared metrics among natural reef, platform base, and platform midwater habitat subtypes. Model formulations and the analysis procedure followed Bolker et al. (55) for an unbalanced sampling design with crossed random effects. Models were fitted with the “lmer” function in the “lme4” package (56) in R (57) using restricted maximum likelihood. In each model, habitat type was the fixed factor, combined with a random intercept term for Year and separate random intercept terms for Site within each habitat type. Considering Year as a random factor appears most appropriate due to minimal evidence of temporal autocorrelation in the autocorrelation functions for each site. Additionally, there was limited data from successive years for many sites. To meet normality assumptions, response variables were  $\text{Log}_{10}(x)$  transformed, or  $\text{log}_{10}(x + 1)$  transformed in the case of Recruitment Production due to the presence of zeros. For each habitat type in each model, we calculated estimated marginal means and 95% confidence intervals (CIs) for the means based on 5,000 simulations using the package “arm” (58) in R. Estimated marginal means are predicted means that are calculated from the fitted model and are adjusted appropriately for any other variable in the model. In this case, those are the random factors Site and Year. These values were transformed back to their original scales for reporting. Note that these antilogs of the mean of logged data are estimates of the geometric mean, which also approximates the median on the original scale. Differences were considered significant if the 95% CIs of their marginal means did not overlap.

**ACKNOWLEDGMENTS.** We also thank L. Snook, M. Nishimoto, D. M. Schroeder, T. Lehmann, J. Wilson, S. Hamilton, and H. Kramp. The editor and two anonymous reviewers also provided valuable comments that led to substantial improvements in the article. Study collaboration and funding were provided by the US Department of the Interior, Bureau of Ocean Energy Management, Environmental Studies Program under Agreement M12AC00003.

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