A Structured Deep-water Fish Community in an Isolated Benthic Feature off Southern California

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Abstract

Between September and November in 1995 and 1998–2011, we conducted surveys of demersal fishes and their associated benthic habitats using direct observations from human-occupied vehicles, over the Footprint, an isolated submerged ridge located seawards of the Santa Cruz Island-Anacapa Island Passage, southern California, extending over bottom depths of about 94–500 m. The observed fish fauna, consisting of 127,351 individuals of at least 79 species, was dominated by rockfishes (genus *Sebastes*) (94.5% of individuals, 47% of species). The Footprint is home to a complex of benthic habitats that are occupied by a number of fish assemblages. These were defined by bottom depth, habitat type, and the environmental tolerances and preferences of each species. While the habitat-limited benthic species that occupy the shallower parts of the Footprint are isolated from the Santa Cruz Island and Anacapa Island shelves, the fishes living on the Footprint are not reproductively isolated. Rather, through a web of connections, the fishes of the Footprint are likely well integrated into the Southern California Bight. This connectivity, flowing towards and away from the Footprint, means that events hundreds or thousands of kilometers away may have profound effects on the fish assemblages on this feature. For example, economically important species were relatively uncommon, possibly the result of past overfishing locally and a lack of immigration from other regions.

INTRODUCTION

The Footprint, aptly named for its shape on navigation charts, is a submerged ridge that may be associated with faulting along the southern part of Santa Cruz Island (Gary Greene, pers. comm. to M.L). Located seawards of the Santa Cruz Island-Anacapa Island Passage, in the vicinity of 33.96° N, 119.48° W, the Footprint extends over bottom depths of about 94–500 m and is about 10 km^2 in area (Figure 1). The Footprint is an isolated feature separated by about 8 km from any rocky habitat shallower than 250 m. The top of the feature is composed of extensive beds of cobbles and high-relief boulders. Below this, the upper flanks of the feature are mostly boulders, caves, and crevices. As depth increases, mud becomes more prevalent, comprising about 75% of the habitat in 400 m and deeper (Stierhoff et al. 2013, Yoklavich et al. 2013, Clarke et al. 2020). From surveys of seafloor fishes conducted using a submersible, i.e., human-occupied vehicle (HOV), Yoklavich et al. (2013) estimated a total of 1,953,844 individual fish on the Footprint to a depth of 400 m. From data collected using an autonomous underwater vehicle (AUV) in the same year as Yoklavich et al. (2013), Clark et al. (2020) estimated that the Footprint (to a depth of 500 m) contained between 3,759,089 and 6,507,466 individual fish. In 2003, the Footprint was declared a State Marine Reserve, and recreational and commercial take of all marine resources was prohibited. Many years of manned submersible fish surveys (summarized in Yoklavich et al. 2002, Yoklavich et al. 2007, Love et al. 2009, 2019) have demonstrated that the Footprint is an unusual feature in in southern and central California, as it encompasses a wide depth range and very diverse benthic habitat, in a relatively compact area.

Over the course of 16 years, we surveyed the fish assemblages of the Footprint using a HOV. The Footprint's substantial depth range and diverse habitats within a relatively isolated, circumscribed area, allowed us to inform our understanding of the role that the Footprint plays as fish habitat. The goals of this study are 1) to characterize, based on multi-year surveys, the fish assemblages on this complex feature, 2) to understand the relationship of bottom depth and habitat type in structuring these assemblages and 3) to better understand what might be the level of ecological spatial connectivity (sensu Carr et al. 2017) of fishes both within the Footprint and between the Footprint and other features.

METHODS

HOV SURVEYS

Surveys of demersal fishes and their associated benthic habitats were conducted between September and November in 1995 and 1998–2011, using direct observations from the HOVs *Delta* (Delta Oceanographics) and *Dual Deepworker* (Nuytco Research Ltd.); details regarding these vehicles are found in Love et al. (2009, 2017). Each dive was composed of multiple 15-minute belt transects, directed by a scientific navigator from the support vessel and conducted by a scientific observer inside the HOV during daytime (0800–1700 h). When possible, transects were designed to run along a relatively narrow isobath and no attempt was made to target any particular habitat. Transects were documented with either an externally mounted hi-8 color video camera (1995, 1998–2009) or externally mounted high-definition video camera (2010–2011). The scientific observer within the HOV viewed the transect off the starboard side, verbally recording onto the videotape all fishes 2 m or less above the seafloor. Fishes were enumerated and identified to the lowest possible taxon, and their total lengths were estimated to the nearest 5 cm. Reference light points from two parallel lasers installed 20 cm apart on either side of the external video camera were used to aid size estimates and to delineate the width of the transects. The HOV pilot strived to maintain a height of 2 m above the seafloor and a constant speed of 0.5–1.0 knots, although speed tended to be slower in complex habitats. Segments of transects in which the seafloor was not visible (and thus where the benthic habitat was not visible) were excluded from surveys. Over the years of the study, the transect lengths and habitat patches were estimated in several ways and these are discussed in Love et al. (2009) and Yoklavich et al. (2013). The area of each habitat patch was determined by multiplying length of the patch by the width of the swath (2 m in each year, except for 2011, when the width was 2.5 m). Fish density was calculated for each transect by dividing counts by transect area (length x width) in m^2.

We note that by using this survey methodology 1) we underestimate the densities of very small and cryptic taxa (e.g., gobies), 2) species of a number of families (e.g., Agonidae and Zoarcidae) are difficult to visually identify, and 3) schools of benthopelagic forms such as widow rockfish that can aggregate in the water column above the submersible were not counted. Lastly, studies on the Pacific Coast have demonstrated that if submersibles move at a constant and slow rate of speed, there is little obvious effect on the behavior of most demersal fishes (Murie et al. 1994, Yoklavich et al. 2007, Love et al. 2009, Yoklavich et al. 2013).

ANALYSES

In the laboratory, video transects and the observers' audio annotations were reviewed and fish identifications, counts, and total lengths were confirmed or modified. During this review, fish observations and substratum characterizations were geo-referenced by time markers; thus, each fish was associated with the habitat where it occurred. Habitat patches along each transect were characterized and delineated using the geological definitions of Greene et al. (1999). Substratum types were pinnacle top (code T), rock ridge (R), continuous flat rock (F), boulder (B), cobble (C), pebble (P), gravel (G), sand (S), and mud (M) in order of decreasing particle size or complexity. Habitat patches were categorized using a two-character substratum code: the first character in this code represented the substratum that accounted for at least 50% of the patch, and the second character represented the substratum type that accounted for at least 20% of the patch (e.g., a patch designated as 'BC' comprised at least 50% boulders and at least 20% cobble) (Supplementary Table 1). Because this method of using nine substratum types to classify habitats created too many two-character categories for meaningful interpretations, we grouped 2-character substratum codes into three habitat classes: H (all or predominantly high relief and hard), L (all or predominantly low relief and hard) and S (all or predominantly soft sediment) habitats. We acknowledge that simplifying our patch definitions reduces habitat heterogeneity in the analysis. Thus, the ability to understand some of the more nuanced relationships between species and their habitats (Yoklavich et al. 2000, Anderson and Yoklavich 2007, Love et al. 2009) may have been lost.

To visualize the spatial distribution of each species, we calculated species-specific densities (number/100 m^2) for each transect by dividing counts by transect area (length x width). The densities associated with each transect were mapped for each species in ArcGIS (Esri, Redlands, CA), and symbolized at standardized breaks to allow comparisons among species. To understand rockfish distribution along water depths at different life stages, we separated the young-of-the-year (YOY) from the adult population. YOY rockfishes were defined as 1) any fish identified as "rockfish YOY" and 2) any rockfish that was ≤10 cm long, with the following exceptions: halfbanded, pygmy, shortbelly, and squarespot rockfishes; fishes of the subgenus *Sebastomus*; and “unidentified *Sebastes*” that were ≤5 cm long. Halfbanded, pygmy, and squarespot rockfishes, and some members of the subgenus *Sebastomus* may mature at <10 cm; these taxa may have been part of the "unidentified *Sebastes*" category.

The relationship between fish size and depth was examined for the sixteen species that had the highest density or greatest economic importance (Love 2011). The other species observed in these study were 1) dwarf species whose sizes could not be sufficiently estimated for meaningful analyses, 2) of little or economic importance or 3) so rarely observed that size-depth relationships could not be accurately ascertained. The size of the fish of a given species was weighted by the count of that species within every 25-m depth. Linear regression (lm in R) was used to test the significance in the slopes between fish size and depth.

To examine the effects of the habitats and depth on the species assemblages we performed nonmetric multidimensional scaling (NMDS) analysis on species-specific fish density calculated using Bray-Curtis dissimilarity index (metaMDS in R vegan package). . To control for the sampling effect across different depths and habitats, the sampling unit used in the analysis (the points shown in the Figure 2 NMDS plot) was the average fish densities within 25-m depth bins, extending from 93 to 407 m in depth. The data were zero-filled for fish that were not observed. The data were zero-filled for fish that were not observed. Fish species that occurred in more than 5% of the transects (Love et al. 2009) (Table 1) were used in the analysis. A nonmetric multidimensional scaling (NMDS) analysis was performed using monotone regression convergent solution (metaMDS in R vegan package). The depth bins were grouped into three depth zones (<200 m, 200-300 m, and > 300 m) for better visualization and understanding of the overall trends. The stress value of 0.09 indicated a great fit by choosing the first two ordination axes. Results were converged after 20 iterations. To test for the significant effects of habitat relief and depth on species assemblages, Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations Bray–Curtis distance matrix (Adonis in R vegan package). Because the habitat and depth were both significant factors in the PERMANOVA (see result section), we further ran permutation test for homogeneity of multivariate dispersions (permutest in R vegan package) and the posthoc test (pairwise.adonis in R pairwise Adonis package) to examine the differences among three habitats groups and three depth zones. All analyses were performed using functions in R (R Core Team 2019).

RESULTS

We conducted 60 dives composed of 208 transects and 2852 habitat patches in waters between 93 and 407 m deep. The transects covered an area of 154,948 m^2 (73,430 linear m). A majority of the surveys, as measured by number of transects and area swept, occurred at bottom depths of 100–275 m (Supplementary Table 2). Overall, about 75,752 m^2 of high and hard relief, 45,471 m^2 of low and hard relief, and 33,725 m^2 of soft seafloor were surveyed (Supplementary Table 3). Benthic habitats were not evenly distributed with depth. The crest of the Footprint was composed primarily of low-relief cobble and some high-relief boulders; its sides, to depths of about 275 m, were dominated by larger boulders and other large rocky features; below about 275 m, mud and mud mixed with cobbles predominated (Figure 1, Supplementary Table 3).

Bottom depth and habitat type structured fish assemblages (Figure 2). PERMANOVA test results indicated that both habitat (F=3.41, p =0.001) and depth (F = 12.53, p=0.001) were the important drivers to the fish assemblage, with depth as a stronger driver factor. The multivariate dispersions test suggested that there is no significant difference in the between-site variation in fish community composition among three habitats or depth zones ($p > 0.05$ for the all the permutests). Among three habitats, the posthoc pairwise test revealed the significant difference presented between H and S habitats ($p = 0.012$) but not the other groups. Among three depth zones, all pair of groups were different ($p = 0.001$). Over all habitats, fish densities were highest in depths 125 m and less, declined with depth to 275 m, and then increased slightly below that depth (Figure 3a). In 150 m and shallower, densities were greatest in the highest relief habitat, followed by the low-hard habitat. In general, fish densities at all depths over soft seafloor were relatively low (there was no soft habitat in depths <100 m) and varied little with depth, although there was no soft habitat in depths <100 m (Figure 3b).

We observed a total of 126,181 fishes, of which 94.6% (119,321) were rockfishes. In aggregate, there was a minimum of 77 species, 36 (about 47%) of which were rockfishes (Table 1). High densities of dwarf rockfish taxa dominated the shallowest, rocky parts of the feature. These species included the schooling species halfbanded, pygmy, and squarespot rockfishes, along with the solitary swordspine rockfish (Tables 2, 3). As depths increased, these species gradually became less abundant and were replaced by a suite of benthic and benthic-oriented species, including schooling bocaccio and widow rockfishes, as well as solitary or semi-solitary flag, greenspotted, speckled, and starry rockfishes, and lingcod. However, the densities of a few of the more important economic species (e.g., cowcod and lingcod) were relatively low. In the deeper parts of the feature, characterized primarily by soft seafloor with smaller amounts of low-hard outcrops, poachers, Dover sole, Pacific hake, splitnose and stripetail rockfishes, shortspine combfish, spotted ratfishes, and eelpouts were among the dominant taxa. In very general terms, fish assemblages were structured within three generalized depths (< 200 m, 200–300 m, and > 300 m).

Most species primarily associated with one, or at most two, of the three habitat types (Table 2). Species that were most characteristic of high relief included bocaccio, cowcod, and speckled, starry, and widow rockfishes. Pygmy, squarespot, and swordspine rockfishes were abundant over both high and low hard substrata. Unique among the more abundant fishes, halfbanded rockfish were most dense only over low, hard relief. Typical soft-bottom dwellers included shortbelly rockfish, unidentified poachers, bluebarred prickleback, Pacific hake, Dover sole, and unidentified eelpouts. Some species, while predominantly soft seafloor dwellers, occupied other habitats with some regularity (e.g., splitnose rockfish and shortspine combfish). A few species, such as spotted ratfish, appeared to be true habitat generalists and were characteristic of all three habitats.

Fishes utilized the Footprint at a variety of life stages depending on taxa (examples in Figure 4). For instance, many species were found at all benthic life stages, from YOYs newly recruited from the plankton through adults. Examples of these included pygmy and starry rockfishes, and cowcod. Some species recruited as YOYs elsewhere in habitats shallower than the Footprint, then migrated to the feature later in development through maturity. These included bocaccio and lingcod. A few taxa, such as widow rockfish, recruited as YOYs to the Footprint, but at least some individuals (those not consumed by predators) probably left the feature when mature. Lastly, Pacific hake visited the Footprint only as older juveniles, as neither YOYs nor mature individuals were observed (again, with the caveat that there was some predation on juveniles). A small suite of species (i.e, swordspine rockfish, shortspine combfish, splitnose rockfish, lingcod, cowcod, and flag rockfish) demonstrated an ontogenetic shift in depth distributions, as sizes increased with depth (Supplemental Table 4).

Young-of-the-year rockfishes were a very conspicuous part of the Footprint fish assemblages. We observed 11,439 YOY rockfishes of at least 20 species (Table 4). Of those that could be identified to species, the most abundant YOYs were pygmy, bank, squarespot, and swordspine rockfishes. It is likely that the vast majority of the "unidentified YOYs" category was composed of squarespot, pygmy, and widow rockfishes; at small sizes these lack diagnostic patterns or other identifying marks. Most YOY rockfishes occurred in the shallower parts of the feature, at depths less than 200 m (Table 5), and almost all were associated with either high or low rock reefs (Figure 5). At bottom depths of 175 m or less, YOY *Sebastes* densities were highest in low, but hard, relief patches. Relatively few YOYs were observed over predominantly soft seafloors.

DISCUSSION

The Footprint is a complex and spatially heterogeneous feature, harboring a diverse assemblage of juvenile and adult benthic and benthopelagic fishes. Similar to other areas in southern California (Love et al. 2009), rockfishes, particularly YOYs and dwarf species, dominated the high- and low-relief rocky areas of much of the feature, while characteristic soft seafloor species included various combfishes, eelpouts, poachers, and thornyheads. Three studies of the Footprint fishes, all conducted in 2011 and utilizing three different methodologies (remotely operated vehicle, human-occupied submersible, and AUV; Stierhoff et al. 2013, Yoklavich et al. 2013, and Clarke et al. 2020, respectively) yielded results similar to ours.

We documented a minimum of 77 fish species on this feature. However, this is likely a substantial underestimate as we were unable to differentiate to species members of such families as poachers, eelpouts, and thornyheads. In addition, we did not observe at least several small or relatively cryptic species, such as the yellowchin sculpin (*Icelinus quadriseriatus* (Lockington, 1880)), which from trawl studies are known to be abundant in the general area. We also may have missed the occurrence of a few, uncommon species, that are known from relatively nearby in southern California, such as threadfin bass (*Pronotogrammus multifasciatus* Gill, 1863) and popeye catalufa (*Pristigenys serrula* (Gilbert, 1891)) (Love and Passarelli 2020). Lastly, highly mobile, pelagic, and very transient taxa, that are not closely associated with the Footprint benthos (e.g., anchovies, sardines, jack mackerel, and lanternfishes) were either rarely or not observed. When these potential species are included, total diversity could reach as high as 95–100 species. Despite these limitations, our observations compare well with those of Stierhoff et al. (2013), Yoklavich et al. (2013), and Clarke et al. (2020), and it is likely that the species we documented reflect the typical fish assemblages.

WHAT FACTORS INFLUENCED SPECIES ASSEMBLAGES ON THE FOOTPRINT?

Our analysis demonstrates that the fish assemblages at the Footprint are shaped by bottom depth, along with seafloor structure and the natural history of the various species. Regarding bottom depth, we note that a number of environmental parameters, such as temperature and oxygen, can covary with depth, and it is unclear to what extent either of these (or other parameters) are determinative. For instance, although there have been several studies along the Pacific Coast (e.g., Chu and Tunnicliffe 2015, Keller et al. 2017) that determined the oxygen tolerances of some marine fish species, these tolerances, along with those for temperature, are not well understood for virtually all Pacific Coast fishes.

The physical structure of benthic habitats (i.e., benthic patches) is also a major driver of benthic fish species assemblages (Borland et al. 2020). An array of studies on the benthic fishes in the northeast Pacific (Stein et al. 1992, Yoklavich et al. 2000, Anderson and Yoklavich 2007, Love et al. 2009, Wedding and Yoklavich 2015) has shown that most taxa can be categorized, into one of three categories (using language from Anderson and Yoklavich 2007): “high-relief,” “low-relief,” and “soft” substratum associated species. There is often considerable overlap between the categories, however, particularly between the high- and low-relief species that live over hard substrata. Habitat preferences also can be quite nuanced, making any generalizations problematic. As an example, Love et al. (2006) studied the habitat preferences of benthic fish species living at a depth of about 70 m on a rocky outcrop near Anacapa Island (a few kilometers from the Footprint). They found that while a number of species preferentially occupied high relief, the densities of several species (i.e., bocaccio, flag and vermilion rockfishes) were much higher in those areas where the rocky outcrop had deep crevices. Similarly, Love and York (2006), conducting research on the fishes associated with the bottom crossbeam of California oil and gas drilling platforms, found a suite of species (the “sheltering habitat” guild, including cowcod and vermilion rockfishes) that primarily lived where that crossbeam was undercut, thus creating a long crevice. As another example, even though an overwhelming majority of Dover sole favor mud seafloors, we have, on several occasions, observed them lying directly on rocks. In addition, as we discuss below, on the species level, habitat preferences may be altered by change in densities of predators, competitors, or prey. Habitat preferences also may change as a species matures (Love and Yoklavich 2008). Lastly, we note that habitat associations may be driven by factors that covary, such as preferred prey items.

The interactions of bottom depth, habitat type, and fish habitat preferences lead to partitioning of taxa (Figure 6). As an example, almost all halfbanded rockfishes, a relatively shallow-water species that is almost entirely limited to fields of small boulders and cobbles, live on the crest of the Footprint (Figure 6a). Pygmy rockfishes, limited to a similar depth range co-inhabited the crest with the halfbanded, but also occupy a somewhat broader range of habitats (cobbles, boulders of all sizes, and rock ridges) on the higher-relief, upper flank of the Footprint (Figure 6b). Swordspine rockfish, with habitat preferences similar to pygmies, but with a wider depth preference, also are more commonly found further along the deeper southeast flank of the Footprint than the other two species (Figure 6c). Bocaccio and bank rockfish, two species found primarily over high relief, are typical of species associated with steep drop-offs and fields of large boulders on the feature (Figures 6d, 6e). The deeper seafloor of the Footprint, characterized by small cobbles and boulders and extensive mud fields, is occupied by Dover sole (Figure 6f), Pacific hake (Figure 6g), splitnose rockfish (Figure 6h), and thornyheads (Figure 6i). The relatively few species that are habitat generalists, such as the motile spotted ratfish (Figure 6j), are found over much of the feature. Species that exhibit ontogenetic shifts, also have intraspecific differential patterns of occupation. Larger lingcod, for instance, tend to live in deeper waters and over higher relief than smaller ones (Figures 6k, 6l). Lastly, the tendency for most YOY rockfishes to recruit to shallower, hard substrata, means that the highest densities we observed were on the crest and shallower parts of the drop-off (Figure 6m).

Along with bottom depth, habitat type, and fish natural history, the geographic location of the Footprint, mediated by a broad oceanographic transition zone associated with the convergence of currents from different water masses, may play a role in defining fish assemblages. Benthic fish assemblages at the western-most San Miguel and Santa Rosa Islands differ somewhat from those of eastern-most Santa Cruz and Anacapa Islands (Hubbs 1967, Love et al. 1985). The fish assemblage of the western-most islands, bathed by the relatively cold

California Current, has affinities with that of the Oregonian Province of central and northern California; waters of the eastern two islands harbor an assemblage more characteristic of the warmer southerly Californian Province (Love et al. 1985). The Footprint, located just outside of the Santa Cruz-Anacapa Island Passage, is predominantly inhabited by Californian Province species (e.g., swordspine rockfish) or by species with relatively wide geographic ranges (e.g., bocaccio, halfbanded, and pygmy rockfishes). Some characteristic Oregonian species (i.e., wolf-eel, and redbanded, rosethorn, and yelloweye rockfishes) were observed at low densities. The yellowtail rockfish (*Sebastes flavidus* (Ayres, 1862)), a species that is abundant west of the Footprint at Santa Rosa Island (at depths and in habitats similar to that of the Footprint), is absent from the Footprint. Similarly, a suite of species that are abundant 100 kilometers to the south (i.e., freckled, honeycomb, and Mexican rockfishes) are uncommon at the Footprint.

THE INFLUENCE OF GEOLOGIC TIME AND HUMAN ACTIVITY ON FOOTPRINT HABITAT PATCHES

The Footprint is composed of mosaics of habitat patches that may fluctuate across the entire feature and, very importantly, over time (Pittman 2018, Jackson et al. 2018). Just as habitat patches can be viewed from different spatial perspectives, they also can be viewed from various temporal ones. As an example, at least as recently as 13,000–20,000 years ago, the crest of the Footprint was above sea level (Reeder-Myers et al. 2015). However, although the Footprint as we know it today is of relatively recent origin, and while the specific locations of the various patch types were different in the past, all of the habitat types present today (e.g., ridges, boulders, cobble, and mud) were probably present in the past.

Human activities also can have a profound effect on number, size, and type of habitat patches and the organisms associated with them, either through habitat disruption or by direct removal of various fishes (Boivin et al. 2016; Saul and Pittman 2018). To what extent has human activity, particularly fishing, altered the structure and function of various habitat patches of the Footprint, and how representative are the resultant patterns of species and species assemblages observed by Stierhoff et al. (2013), Yoklavich et al. (2013), Clarke et al. (2020), and in our study? Specifically, to what extent are we viewing the ecological patterns on the Footprint through the lens of a shifting baseline (Pauly 1995, Soga and Gaston 2018)?

Because it is located well offshore, it is unlikely that the Footprint has been directly subject to the environmental perturbations (e.g., urban runoff, sewage effluent, and ocean dumping) that influence many nearshore, mainland marine habitats. Because of its rough terrain, the Footprint also has not been subject to intensive benthic trawling that can lead to habitat disruption (although we have noted a few gillnet and trawl nets, longlines, and some monofilament fishing line during our surveys). However, through observations conducted from 1963–1982, the senior author documented the removal of tens of thousands of bocaccio, many hundreds of cowcod and lingcod, and extremely large numbers of other rockfish species, such as chilipepper, and greenspotted and bank rockfishes through intensive hook and line fishing by recreational anglers (primarily aboard commercial passenger fishing vessels) and, to a lesser extent, commercial fishermen (M. Love, unpubl. obs.). While this fishing probably had a comparatively minor effect on bottom topography (although it may have had a substantial effect on structure-forming invertebrates, such as corals and sponges), it could have drastically reduced the populations of certain fish species.

How might the removal of very large numbers of large predatory fishes alter the ecological function of some habitat patches and of the Footprint as a whole? As an example, our research (and that of Stierhoff et al. 2013, Yoklavich et al. 2013, and Clarke et al. 2020) found very high densities of small, “weedy” rockfish species (e.g., pygmy, squarespot, and swordspine) associated with the rocky areas on, and near, the crest of the Footprint. Does this represent a “natural” state, one that reflects the habitat preferences of these small fishes, or are these very high densities a consequence of the decreased densities of larger, more predatory species, whose depletion has served to release from predation these smaller species which could then occupy previously off-limits habitats (as discussed in Love et al. 2009)? While there is a rich literature on the habitat preferences of California rockfishes (e.g., Yoklavich et al. 2000, Anderson and Yoklavich 2007, Love et al. 2009), it is undeniable that after many years of intense fishing pressure off central and southern California (He and Field 2017, Cope et al. 2021), the fish assemblages on virtually all rocky banks and outcrops have been substantially altered (e.g., Yoklavich et al. 2000, Love and Yoklavich 2006) . We know of only one study from off California, from depths comparable to those of the Footprint, that documented the fish assemblages on what was probably an unfished reef. Yoklavich et al. (2000) reported on the fish assemblages associated with five similar rock outcrops surrounded by mud on the steep sides of Soquel Canyon, central California. Four of the five sites had been fished to a greater or lesser degree, and one small site likely served as a natural refuge from fishing. This latter site sits on the steep sides of a submarine canyon (where trawling would not occur) and is not visible with the bottom imaging equipment that is found on commercial and recreational vessels, making it appear to be soft mud, and not attractive either to hook-and-line or to commercial traps fishermen. In addition, at this site we observed none of the debris that is associated with fishing operations (e.g., lost gear, bottles and cans). While large, predatory species (e.g., bocaccio, cowcod, and yelloweye rockfish) occurred at all five sites, they were far more abundant and larger on the unfished outcrop. Importantly, Yoklavich et al. (2000) noted that the “abundance of

S. helvomaculatus [rosethorn rockfish, a relatively small species] was significantly *lower* [our italics]…at those sites having high numbers of larger species and less fishing activity…" Thus, it is possible that, prior to human alterations, the shallower parts of the Footprint may have been dominated by larger individuals, with relatively low densities of younger fishes or dwarf species in adjacent habitats (Baskett et al. 2006, O'Farrell et al. 2009).

However, it is important to note that while characteristics (such as size, amount, and type) of the habitat patches may be altered, and therefore the proportion of each species on those patches may change through species- and size-selective capture, the basic species adaptations to depth, that have evolved over millennia likely have not been altered over the last century. Thus, it can be argued that while the *intensity* of the ecological functions (based on the densities of taxa) might have been altered, the *types* of functions (based on the diversity of taxa) remain the same. For example, the Footprint still is a site where economically important species reproduce and their larvae are exported throughout the Southern California Bight. The difference is that in our study the *magnitude* of larvae exported by, for instance, bocaccio, cowcod and other heavily-fished species, is likely much less compared to that before these species were overfished in the mid to late 20th century. On the other hand, the export of larvae from the "weedy" species may now be much larger, if their densities have increased over time.

We note that there have likely been substantial changes to the densities of some of these species since the end of our study in 2011. As examples, between 2011 and 2017 off California, the estimated spawning output of bocaccio increased by 70% and of cowcod by 33% (E.J. Dick, pers. comm., He and Field 2017, Dick and He 2019). Because the Footprint is an MPA, it is reasonable to assume that the populations of these species also have increased over this time. But what about the population trajectories of the most important dwarf species, squarespot, pygmy, and swordspine rockfishes? No stock assessments have been made of pygmy and swordspine rockfishes, but one of squarespot rockfish found a significant decline in the years following 2015 (Cope et al. 2021). However, because this was ascribed to "high removals" by recreational anglers (Cope et al. 2021), and because the Footprint is an MPA, it is not clear of the squarespot rockfish on that feature suffered a similar decline. Moreover, a survey of rockfish larvae in the vicinity of a large southern California MPA (not including the Footprint) found that densities of six of eight economically important rockfish taxa (including bocaccio, but not cowcod) increased between 1998 and 2013, implying that larval export of these species had increased over time (Thompson et al. 2017).

ECOLOGICAL CONNECTIVITY

Connectivity between and among marine systems includes both biological (i.e., eggs, larvae, juvenile, and adult organisms) and the physical (i.e., nutrients, gasses, and inorganic chemicals) components (Bouillon and Connolly 2009, Boström et al. 2018, Olds et al. 2018), and is scale dependent (Jackson et al. 2018). Although fish connectivity may be relatively constrained on some isolated features (e.g., González-Irusta et al. 2021), our study implies that many of the fish species associated with the Footprint likely exhibit substantial connectivity both among habitat patches and between the Footprint and other marine environments. This connectivity may be either one- or two-way depending on taxa and life stage.

LOCAL-SCALE CONNECTIVITY AT THE FOOTPRINT

While we know relatively little about the movements of fishes within or among habitat patches on the Footprint, we can make some inferences: 1) Our research demonstrates that some species move deeper as they mature. This is a widespread behavior observed in demersal fishes along the Pacific Coast (Stein et al. 1992, Love et al. 2009). 2) There also is some amount of ontogenetic movement between habitats, albeit this is poorly understood. As an example, YOY cowcod recruit from the plankton to cobbles or cobbles with small boulders; as they mature, they move into high-relief habitats, such as boulders and rock ridges (Love and Yoklavich 2008). 3) While some species are primarily limited to one habitat type, others, such as spotted ratfish, combfishes, and halfbanded rockfish, very likely move about substantially, both within and between habitat types. 4) It is likely that some species have a limited home range or are even territorial. This is particularly the case with the more benthic-oriented species, like starry and rosy rockfishes. On the other hand, the more aggregating species (e.g., chilipepper, squarespot, and widow rockfishes) are less sedentary and likely have greater home ranges.

CONNECTIVITY WITH OTHER AREAS

Current patterns in the southern California Bight are extremely dynamic and based on the Regional Ocean Modeling System models, fish eggs and larvae produced throughout this system travel substantial distances before the young settle out (Nishimoto et al. 2019). Thus, it is highly likely that virtually all of the fish species living on the Footprint produce pelagic eggs or larvae that are not retained but rather are carried away by currents. Exceptions include the benthic, and fully formed, young of the viviparous surfperches, family Embiotocidae, (i.e., pink perch and shiner perch), and perhaps the young of such families as the eelpouts, which produce large demersal eggs, well-developed larvae at hatching, that may not disperse great distances (William Watson, pers. comm. 29 October 2021). Populations of these taxa, particularly of the surfperches, are likely at least partially self-sustaining. Similarly, it is highly probable that many of the fishes living on the Footprint are derived from larvae carried to the Footprint from other areas. By contrast, for at least some species (e.g., bocaccio, lingcod, and Pacific hake), most of the source individuals are not derived from larval settlement, but rather originate as young juveniles that have settled elsewhere and migrated to the feature (either swimming in open water without benthic habitat references or swimming very deep, following the bottom) (Figure 4). By the same token, the Footprint exports not only larvae, but also older juveniles of such species as Pacific hake and widow rockfish (Figure 4).

The movement of fishes off and on the Footprint is species-specific. Below its rocky crest and upper sides, much of the Footprint seafloor becomes a patchwork of areas increasingly composed of mud, along with smaller, isolated, areas of rocks. It is likely that most of the relatively shallow-dwelling (250 m or less), rocky-substrata specialist species are effectively isolated both by depth and available habitat; species such as halfbanded, pygmy, squarespot, starry, and swordspine rockfishes rarely, if ever, leave the feature. Species that live over a wide depth range, are habitat generalists, or are not strongly associated with the seafloor probably are more motile and move on and off the feature. Examples of these taxa include spotted ratfish, as well as various flatfishes, poachers, thornyheads, and combfishes. While the mobility of most of these species is unknown, Dover sole conduct ontogenetic movements (Vetter et al. 1994), seasonal inshore and offshore migrations (Hagerman 1952), and likely move in response to local conditions (Mearns and Sherwood 1974). Similarly, it is likely that these species also visit the Footprint from other sites. Special circumstances apply to both shortbelly rockfish and Pacific hake, and perhaps widow rockfish, which live on the Footprint only during limited parts of their juvenile and early adult life cycles.

Assuming that the larvae of most species, the juveniles of at least a few taxa, and the adults of many others leave the Footprint in various ways, how far-reaching might be this feature's influence, that is its *threshold distance* (Berkström et al. 2020)? In this instance, threshold distances are likely both species- and life stage-dependent. Rockfish larvae and pelagic juveniles, for instance, may remain in the plankton for 3–6 months and, in the case of splitnose rockfish, up to one year (Love et al. 2002), during which time they may travel hundreds of kilometers. We note that while this may be the case for more offshore species (i.e., the species inhabiting the Footprint), the larvae of some nearshore rockfishes may remain near their natal grounds (Taylor and Watson 2004). Pacific hake are wide ranging and juveniles from southern California migrate northward, in later years potentially moving as far north as British Columbia (Bailey et al. 1982, Hamel et al. 2015). Thus, the influence of Footprint on fish populations may, potentially, be felt along much of the Pacific Coast. Similarly, fish populations well away from the Footprint may influence those on the Footprint, through the same mechanisms.

CONCLUSIONS AND THE FUTURE OF FOOTPRINT FISH ASSEMBLAGES

Within its relatively limited confines, the Footprint is home to a complex of benthic habitats that are occupied by a number of fish assemblages. These assemblages are defined by bottom depth, habitat type, and the environmental tolerances and preferences of each species. Rockfishes, particularly some of the dwarf species, are the dominant group, and economically important species are relatively uncommon, probably the result of past overfishing. While the habitat-limited benthic species that occupy the shallower parts of the Footprint are isolated from the Santa Cruz Island and Anacapa Island shelves, the fishes occupying the Footprint are not reproductively isolated. Rather, through a web of connections, the fishes of the Footprint are likely well integrated into the Southern California Bight. This connectivity, flowing towards and away from the Footprint, means that events hundreds or thousands of kilometers away may have profound effects on the fish assemblages on this feature. For instance, a reduction of the adult California Current Pacific hake population caused by overfishing hundreds of kilometers to the north might reduce the number of juvenile hake available as prey on the Footprint.

How might the future ecological functions of the Footprint change, given the dynamic nature of environmental parameters and thus of fish assemblages, and the often substantial role that human activities play in affecting marine habitats? There are several factors and forces that may alter the fish assemblages, and therefore alter the ecological functions of the fishes of the Footprint. In particular, we foresee two processes, the Footprint's MPA designation and global climate change, that will likely lead to changes in the fish assemblages on the Footprint and to the ecological role that the Footprint plays.

The fish assemblages and the densities of various taxa have likely changed over time, due both to geologic forces and to human-induced changes. Up to the present, the primary role that humans have played has likely been through intensive fishing of economically important taxa on the Footprint. It might be argued that we do not know the ecological functions provided by the Footprint before biological surveys at the feature were initiated, because of substantial alterations in the fish assemblages. But we can speculate that prior to overfishing the Footprint was a substantial exporter of larvae, compared to many other southern California features, of economically important species, species that are now badly depleted on the Footprint.

As noted previously, at least on a state-wide basis, the populations of both bocaccio and cowcod have increased in the years following this study and thus, if that pattern has been followed at the Footprint, we would expect that larval production of these species has also increased. And while we are unsure about the population statuses at this feature of smaller, prey species, increased predation may have led to a decrease in their densities and a concomitant decrease in their larval export (e.g., Baskett et al. 2006). A follow up visual survey of the Footprint would help elucidate what changes, if any, have occurred with both previously overfished economic species and the dwarf species that may have taken advantage of a potential release from predation.

Arguably, it is the consequences of climate change that may have the largest effect on the species assemblages of the Footprint, Regarding the marine systems off the northeast Pacific, the term "climate change" covers a range of environmental perturbations (briefly summarized in Carr et al. 2017), including shoaling hypoxia, decreasing pH, and warming water temperatures. Some of the effects of climate change may include alterations in the abundance and distribution of organisms, and disruptions and reorganizations of both assemblages and ecosystems. All of these have the potential for altering both the character of the Footprint species assemblages and its ecological role in the marine environment. As an example, increasing seasonal and long-term hypoxia has been occurring in the northeast Pacific (Keller et al. 2010, Chu and Tunnicliffe 2015). This is causing habitat compression by reducing the viable habitats for a range of fishes and invertebrates (Chu and Tunnicliffe 2015, Ross et al. 2020). Specifically at the Footprint, Meyer-Gutbrod et al. (2021) found that, from 1995 to 2009, some rockfish species have moved shallower, perhaps in response to increasing hypoxia. Ultimately, hypoxia shoaling at the Footprint will result in the loss of some habitat for those taxa that require relatively high oxygen concentrations, such as lingcod, chilipepper, and greenstriped rockfish (Keller et al. 2017). We note that this has already occurred at a seamount off British Columbia, where rougheye rockfish (*Sebastes aleutianus* (Jordan & Evermann, 1898) are now "inhabiting primarily the upper half of their preferred depth range…seemingly to avoid the OMZ [the shoaling oxygen minimum zone]" (Ross et al. 2020). On the other hand, this same process might provide an opportunity for habitat expansion for those fish species that can tolerate, or require, low oxygen conditions (e.g., Pacific hake, slender sole, Dover sole, and thornyheads; Chu and Tunnicliffe 2015, Keller et al. 2017).

Climate-driven events that affect ecosystems external to the Footprint also may have an effect on this feature's fish assemblages. For instance, ocean currents may shift, altering the direction and final locations of larvae exported from the Footprint and the spatial and temporal variability of recruitment to the feature (Fox et al. 2016). Increased water temperatures may influence the fish assemblages to include more southern species. A widespread decline in kelp beds may impact nearshore bocaccio YOY recruitment, lower the number of juveniles that migrate to the Footprint, and decrease both subsequent adult densities and larval export.

It has long been recognized that marine habitats, and by association their organismal assemblages, are, by their very nature, dynamic – they change in response to a myriad of intrinsic and extrinsic factors (Pickett and Thompson 1978). And while we better understand the variable nature of some of these factors (e.g., the various aspects of climate change, extrinsic fishing pressure, oceanographic conditions), others likely remain to be elucidated. Suffice it to say that changes in the fish assemblages of the Footprint have occurred in the recent past and may continue to occur in the near future.

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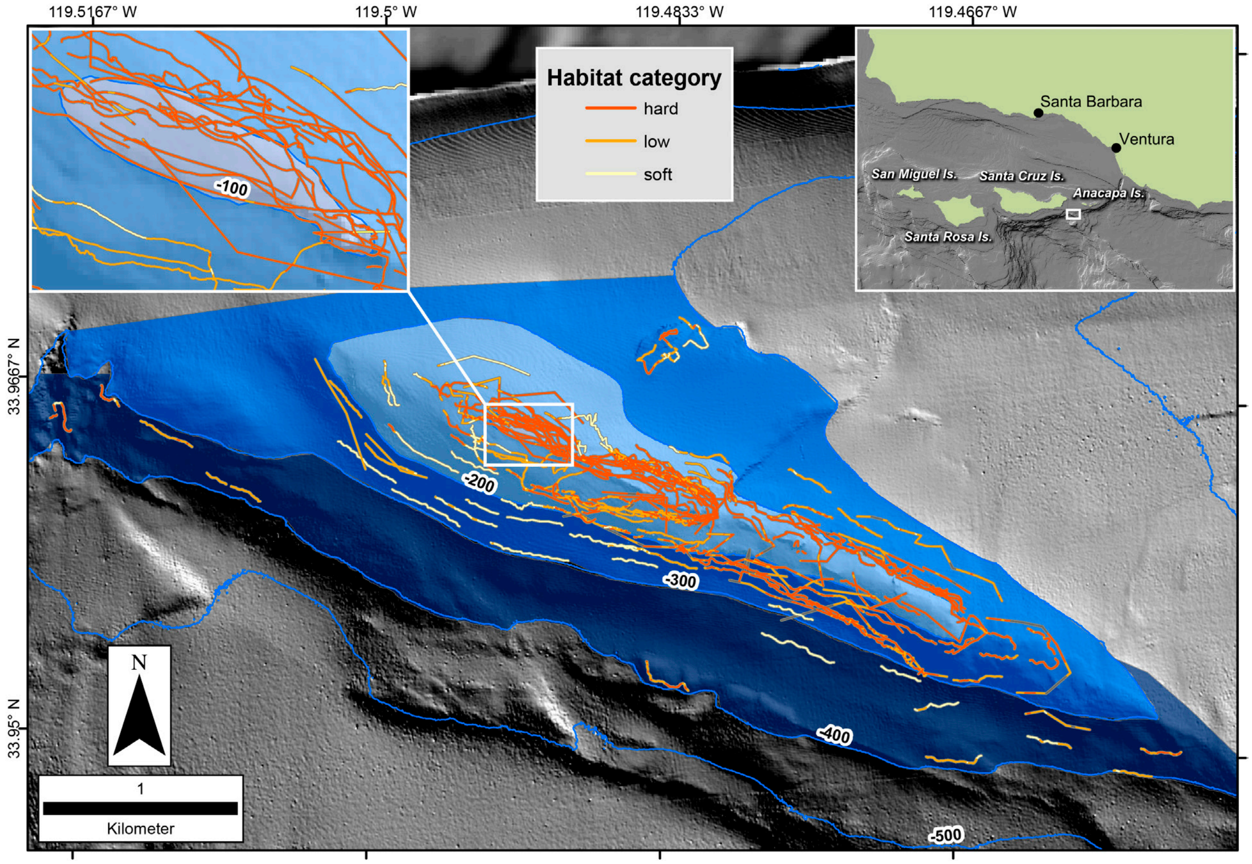

Figure 1. Location of the Footprint (right insert) in Southern California. The main figure shows the location of each transect, 1995, 1998–2011, coded by habitat type. Definitions of habitat types are found in Supplementary Table 1. The left insert shows the location of transects in the shallowest, <100 m, part of the feature.

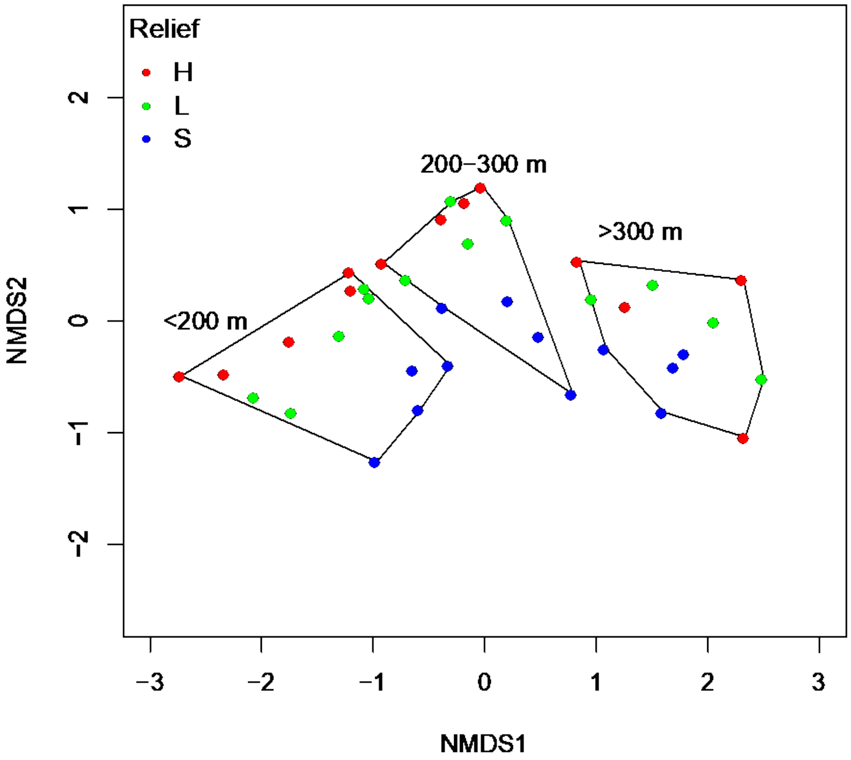

Figure 2. A non-metric multidimension scaling (NMDS) analysis of habitat types and depth categories based on species densities (fish per 100 m^2) and species occurring in more than 5% of the transects.

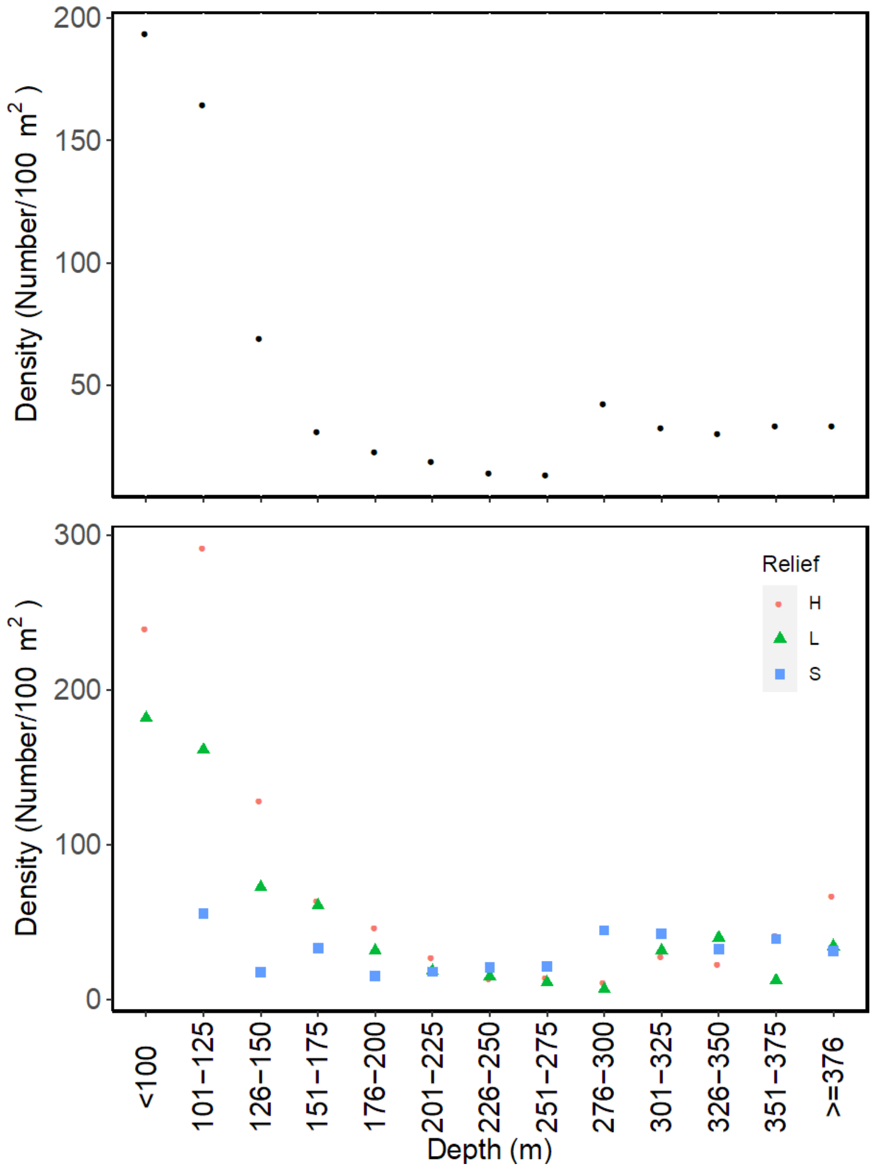

Figure 3. A) Overall fish densities by depth. B) Overall fish densities in each habitat class by depth on the Footprint, 1995, 1998-2011. H = high-hard, L = low-hard, S = soft. Definitions of habitat types are found in Supplementary Table 1. The mean value is the weighted mean among patches. There was no S habitat in <100 m.

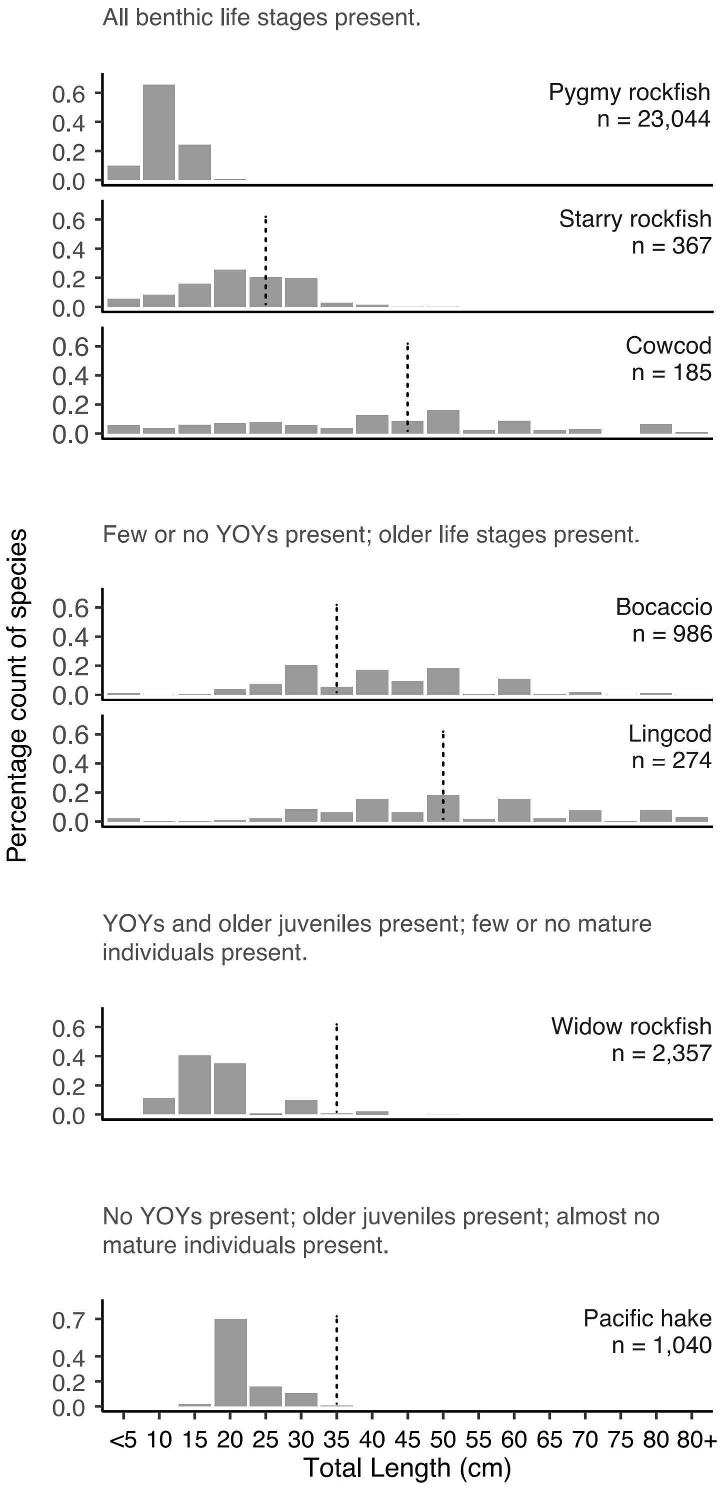

Figure 4. Size frequencies of selected species observed on the Footprint, 1995, 1998–2011. Vertical lines delineate size at 50% maturity, rounded to the nearest cm. “YOY” refers to young-of-the-year. Size at 50% maturity for pygmy rockfish is unknown, however it is likely to be about 10 cm total length. Lengths at 50% maturity are based on data from Love (2011).

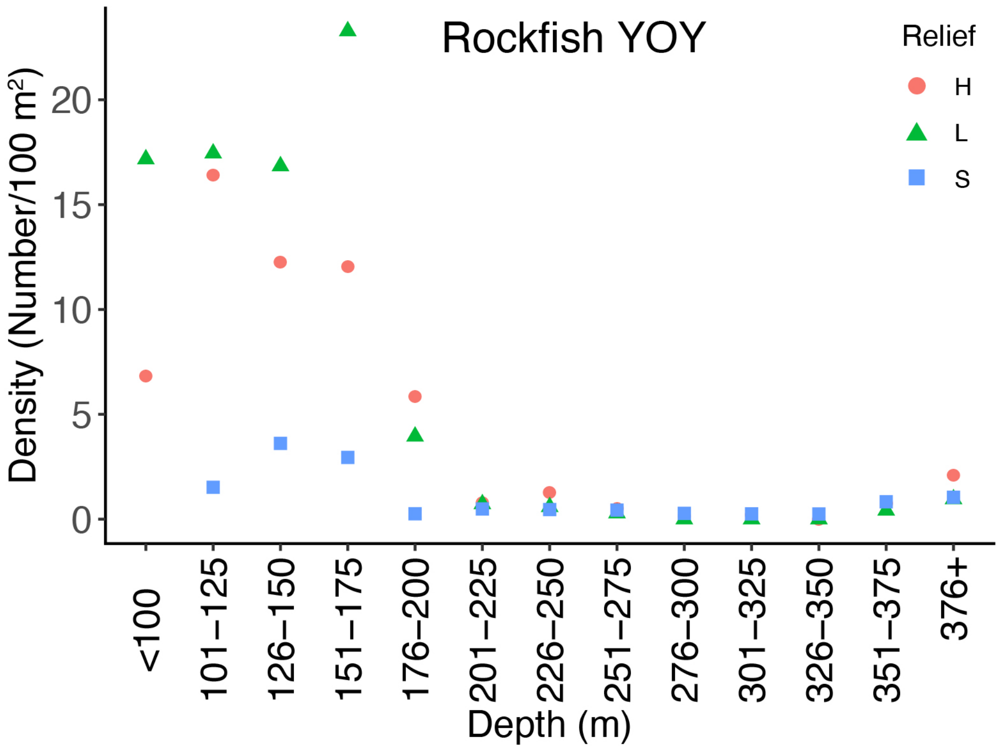

Figure 5. Overall YOY rockfish densities observed on the Footprint, 1995, 1998–2011, in each habitat type by depth. There is no S habitat type in <100 m. Size classes of YOY rockfish by species are described in the methods section of the text.

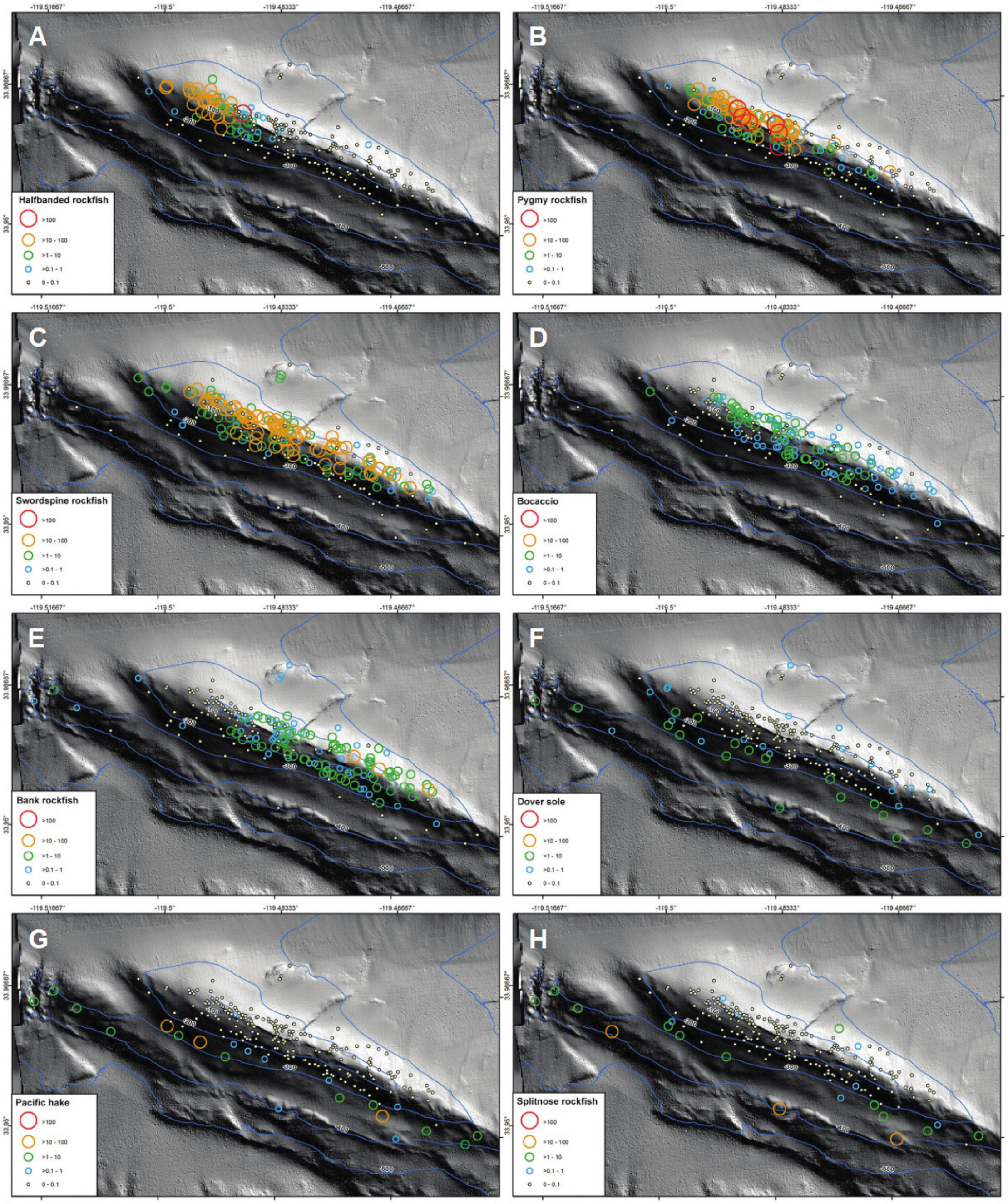

Figure 6. Densities (number/100 m^2 per transect) of selected species observed at the Footprint, 1995, 1998–2011.

Table 1. All fish species and species groups observed on the Footprint, 1995, 1998–2011, listed by density (individuals per 100 m^2). Species denoted by an asterisk (*) are of economic value, either in the commercial or recreational fisheries, or both. The total number of transects is 213.

Common Name	**Scientific Name**	**Density**	**Number**	**Frequency of Occurrence**
Squarespot rockfish	*Sebastes hopkinsi* (Cramer, 1895)	23.09	35395	93
Pygmy rockfish	*Sebastes wilsoni* (Gilbert, 1915)	15.04	23044	109
Swordspine rockfish	*Sebastes ensifer* Chen, 1971	10.74	16466	143
Unidentified *Sebastomus*	*Sebastomus* spp.[1]	10.03	15370	186
Halfbanded rockfish	*Sebastes semicinctus* (Gilbert, 1897)	5.14	7881	63
Unidentified young-of-the-year	*Sebastes* YOY[2]	3.72	5694	119
Unidentified rockfishes	*Sebastes* spp.	1.6	2448	161
*Widow rockfish	*Sebastes entomelas* (Jordan & Gilbert, 1880)	1.54	2357	35
*Bank rockfish	*Sebastes rufus* (Eigenmann & Eigenmann, 1890)	1.41	2163	123
Pinkrose rockfish	*Sebastes simulator* Chen, 1971	1.34	2048	100
Shortbelly rockfish	*Sebastes jordani* (Gilbert, 1896)	1.09	1678	50
Shortspine combfish	*Zaniolepis frenata* Eigenmann & Eigenmann, 1889	1.03	1575	159
Unidentified poachers	Agonidae	0.89	1365	54
*Pacific hake	*Merluccius productus* (Ayres, 1855)	0.68	1040	21
*Bocaccio	*Sebastes paucispinis* Ayres, 1854	0.64	986	126
Splitnose rockfish	*Sebastes diploproa* (Gilbert, 1890)	0.6	925	21
*Speckled rockfish	*Sebastes ovalis* (Ayres, 1862)	0.53	811	66
*Dover sole	*Microstomus pacificus* (Lockington, 1879)	0.29	439	38
Spotted ratfish	*Hydrolagus colliei* (Lay & Bennett, 1830)	0.27	418	126
*Starry rockfish	*Sebastes constellatus* (Jordan & Gilbert, 1880)	0.24	367	87
Unidentified combfish	*Zaniolepis* spp.[3]	0.23	360	88
*Greenspotted rockfish	*Sebastes chlorostictus* (Jordan & Gilbert, 1880)	0.19	289	85
*Lingcod	*Ophiodon elongatus* Girard, 1854	0.18	274	106
Stripetail rockfish	*Sebastes saxicola* (Gilbert, 1890)	0.18	272	26
*Cowcod	*Sebastes levis* (Eigenmann & Eigenmann, 1889)	0.12	185	100
Unidentified bony fishes	Osteichthyes	0.12	182	84
Bearded eelpout	*Lyconema barbatum* Gilbert, 1896	0.11	170	10
Bluebarred prickleback	*Plectobranchus evides* Gilbert, 1890	0.11	170	25
Rosethorn rockfish	*Sebastes helvomaculatus* Ayres, 1859	0.08	116	21
Unidentified thornyhead	*Sebastolobus* spp.[4]	0.07	105	12
*Flag rockfish	*Sebastes rubrivinctus* (Jordan & Gilbert, 1890)	0.07	101	65
*Greenblotched rockfish	*Sebastes rosenblatti* Chen, 1971	0.07	100	57
Unidentified flatfishes	Pleuronectiformes	0.06	88	38
Unidentified sculpins	Cottidae	0.05	80	31
Unidentified pricklebacks	Stichaeidae[5]	0.05	79	15
*Blackgill rockfish	*Sebastes melanostomus* (Eigenmann & Eigenmann, 1890)	0.05	77	21
*Aurora rockfish	*Sebastes aurora* (Gilbert, 1890)	0.05	74	10
Sharpchin rockfish	*Sebastes zacentrus* (Gilbert, 1890)	0.05	73	17
Rosy rockfish	*Sebastes rosaceus* Girard 1854	0.05	70	25
Unidentified *Icelinus* Sculpins	*Icelinus* spp.[6]	0.04	67	17

Common Name	**Scientific Name**	**Density**	**Number**	**Frequency of Occurrence**
Ronquil	*Rathbunella* spp.[7]	0.04	65	12
*Vermilion rockfish	*Sebastes miniatus* (Jordan & Gilbert, 1880)[8]	0.04	60	29
Bigfin eelpout	*Lycodes cortezianus* (Gilbert, 1890)	0.04	55	14
*Rex sole	*Glyptocephalus zachirus* Lockington, 1879	0.03	51	15
*Chilipepper	*Sebastes goodei* (Eigenmann & Eigenmann, 1890)	0.03	48	19
Greenstriped rockfish	*Sebastes elongatus* Ayres, 1859	0.03	47	27
Whitespotted rockfish	*Sebastes moseri* Eitner, Kimbrell, & Vetter 1999	0.03	44	9
Unidentified eelpouts	Zoarcidae	0.02	36	11
Unidentified sanddab	*Citharichthys* spp.	0.02	36	7
Dwarf-red rockfish	*Sebastes rufinanus* Lea & Fitch, 1972	0.02	32	11
Slender sole	*Lyopsetta exilis* (Jordan & Gilbert, 1880)	0.02	31	9
*Chameleon rockfish	*Sebastes phillipsi* (Fitch, 1964)	0.02	29	4
*Pink rockfish	*Sebastes eos* (Eigenmann & Eigenmann, 1890)	0.02	27	15
Longspine combfish	*Zaniolepis latipinnis* Girard, 1858	0.02	27	14
*Bronzespotted rockfish	*Sebastes gilli* (Eigenmann, 1891)	0.01	19	15
Unidentified hagfish	*Eptatretus* spp.[9]	0.01	17	9
*Longnose skate	*Beringraja rhina* (Jordan & Gilbert, 1880)	0.01	16	14
*Darkblotched rockfish	*Sebastes crameri* (Jordan, 1897)	0.01	15	6
*Shortspine thornyhead	*Sebastolobus alascanus* Bean, 1890	0.01	12	3
Blackeye goby	*Rhinogobiops nicholsii* (Bean, 1882)	0.01	10	7
*Petrale sole	*Eopsetta jordani* (Lockington, 1879)	0.01	10	9
*Sablefish	*Anoplopoma fimbria* (Pallas, 1814)	0.01	10	2
*English sole	*Parophrys vetulus* Girard, 1854	0.01	9	8
Sandpaper skate	*Bathyraja kincaidii* (Garman, 1908))	0.01	9	6
Unidentified lanternfishes	Myctophidae	0.01	8	5
Pacific electric ray	*Tetronarce californica* (Ayres, 1855)	<0.01	6	6
Honeycomb rockfish	*Sebastes umbrosus* (Jordan & Gilbert, 1892)	<0.01	5	3
Spotted cusk-eel	*Chilara taylori* (Girard, 1858)	<0.01	4	2
Unidentified cusk-eels	Ophidiidae[10]	<0.01	4	3
*Pacific sanddab	*Citharichthys sordidus* (Girard, 1854)	<0.01	4	2
Pink seaperch	*Zalembius rosaceus* (Jordan & Gilbert, 1880)	<0.01	3	3
Blacktail snailfish	*Careproctus melanurus* Gilbert, 1892	<0.01	3	2
*Pacific hagfish	*Eptatretus stoutii* (Lockington, 1878)	<0.01	2	2
California smoothtongue	*Leuroglossus stilbius* Gilbert, 1890	<0.01	2	1
Starry skate	*Beringraja stellata* (Jordan & Gilbert, 1880)	<0.01	2	2
Unidentified skates	Arhynchobatidae or Rajidae	<0.01	2	2
Blacktip poacher	*Xeneretmus triacanthus* (Gilbert, 1890)	<0.01	2	1
*Yelloweye rockfish	*Sebastes ruberrimus* (Cramer, 1895)	<0.01	2	2
Pacific argentine	*Argentina sialis* Gilbert, 1890	<0.01	1	1
Shiner perch	*Cymatogaster aggregata* Gilbert, 1854	<0.01	1	1
Swell shark	*Cephaloscyllium ventriosum* (Garman, 1880)	<0.01	1	1
*Canary rockfish	*Sebastes pinniger* (Gill, 1864)	<0.01	1	1
Freckled rockfish	*Sebastes lentiginosus* Chen, 1971	<0.01	1	1
Bluntnose sixgill shark	*Hexanchus griseus* (Bonnaterre, 1788)	<0.01	1	1

Common Name	**Scientific Name**	**Density**	**Number**	**Frequency of Occurrence**
Threadfin sculpin	*Icelinus filamentosus* Gilbert, 1890	<0.01	1	1
Spotfin sculpin	*Icelinus tenuis* Gilbert, 1890	<0.01	1	1
*Mexican rockfish	*Sebastes macdonaldi* (Eigenmann & Beeson, 1893)	<0.01	1	1
Plainfin midshipman	*Porichthys notatus* Girard, 1854	<0.01	1	1
*Big skate	*Beringraja binoculata* (Girard, 1855)	<0.01	1	1
California skate	*Beringraja inornata* (Jordan & Gilbert, 1881)	<0.01	1	1
Red brotula	*Brosmophycis marginata* (Ayres, 1854)	<0.01	1	1
Southern rock sole	*Lepidopsetta bilineata* (Ayres, 1855)	<0.01	1	1
Wolf-eel	*Anarrhichthys ocellatus* Ayres, 1855	<0.01	1	1
Total		82.3	126,181	

[1] Primarily swordspine and pinkrose rockfishes, but perhaps including greenspotted, greenblotched, pink, and rosethorn rockfishes.

[2] Young-of-the-year.

[3] Longspine and shortspine combfishe*s*.

[4] Shortspine and longspine (*Sebastolobus altivelis* Gilbert, 1896) thornyheads.

[5] Likely primarily saddled prickleback (*Lumpenopsis clitella* Hastings & Walker, 2003).

[6] Threadfin and spotfin sculpins.

[7] Perhaps both stripefin (*Rathbunella alleni* Gilbert, 1904) and bluebanded (*Rathbunella hypoplecta* Gilbert, 1890) ronquils.

[8] Likely both vermilion rockfish and sunset rockfish (*Sebastes crocotulus*).

[9] Primarily Pacific hagfish, but possibly black hagfish (*Eptatretus deani* Evermann & Goldsborough, 1907).

[10] Spotted cusk-eel and basketweave cusk-eel (*Ophidion scrippsae* (Hubbs, 1916)).

Table 2. Overall densities (individuals per 100 m^2) of fishes observed on the Footprint, 1995, 1998–2011, by habitat type. H = high, L = low, and S = soft. Habitat categories are described in Supplement Table 1. Species are ordered by density in the H habitat category.

Species	**H**	**L**	**S**
Squarespot rockfish	32.22	24.87	0.13
Pygmy rockfish	18.74	19.79	0.28
Swordspine rockfish	13	13.9	1.41
Unidentified *Sebastomus*	10.08	15.93	1.98
Unidentified YOY rockfishes	4	5.76	0.33
Widow rockfish	3.01	0.21	0
Bank rockfish	2.65	0.31	0.1
Unidentified rockfishes	2.41	1.29	0.18
Pinkrose rockfish	1.85	1.1	0.5
Bocaccio	1.15	0.24	0.04
Speckled rockfish	1.01	0.1	0.02
Shortbelly rockfish	0.69	0.2	3.21
Shortspine combfish	0.45	0.91	2.48
Starry rockfish	0.38	0.17	0.01
Spotted ratfish	0.28	0.32	0.2
Splitnose rockfish	0.27	0.38	1.67
Lingcod	0.24	0.2	0.03
Cowcod	0.21	13.25	5.34
Halfbanded rockfish	0.19	0.1	0.01
Unidentified combfish	0.17	0.24	0.37
Unidentified fishes	0.12	0.13	0.11
Rosethorn rockfish	0.11	0.05	0.04
Greenspotted rockfish	0.1	0.34	0.18
Vermilion rockfish	0.08	<0.01	0
Sharpchin rockfish	0.07	0.02	0.03
Flag rockfish	0.07	0.09	0.02
Greenblotched rockfish	0.06	0.06	0.08
Whitespotted rockfish	0.06	<0.01	0
Rosy rockfish	0.05	0.07	<0.01
Stripetail rockfish	0.05	0.09	0.58
Unidentified poachers	0.05	0.08	3.89
Chilipepper	0.04	0.03	<0.01
Bluebarred prickleback	0.04	<0.01	0.41
Pacific hake	0.04	0.04	2.98
Dwarf-red rockfish	0.04	<0.01	0
Chameleon rockfish	0.04	<0.01	0
Dover sole	0.03	0.04	1.2
Pink rockfish	0.03	<0.01	0.01
Blackgill rockfish	0.03	0.01	0.15
Longspine combfish	0.03	<0.01	0.02

Species	**H**	**L**	**S**
Unidentified pricklebacks	0.03	0.01	0.17
Bronzespotted rockfish	0.02	0	<0.01
Aurora rockfish	0.02	0.02	0.14
Unidentified sculpins	0.02	0.05	0.12
Unidentified *Icelinus*	0.02	<0.01	0.14
Greenstriped rockfish	0.02	0.01	0.08
Unidentified *Rathbunella*	0.02	0.04	0.11
Unidentified hagfish	0.02	<0.01	<0.01
Darkblotched rockfish	0.01	<0.01	<0.01
Longnose skate	0.01	0	0.02
Unidentified thornyheads	<0.01	0.06	0.22
Blackeye goby	<0.01	0.01	0
Unidentified flatfishes	<0.01	0.02	0.23
Pacific electric ray	<0.01	<0.01	<0.01
Shortspine thornyhead	<0.01	<0.01	0.02
Yelloweye rockfish	<0.01	0	0
Honeycomb rockfish	<0.01	<0.01	0
Pacific hagfish	<0.01	0	0
Southern rock sole	<0.01	0	0
Starry skate	<0.01	0	<0.01
Freckled rockfish	<0.01	0	0
Bluntnose sixgill shark	<0.01	0	0
Wolf-eel	<0.01	0	0
Big skate	<0.01	0	0
Rex sole	<0.01	0.01	0.14
Canary rockfish	<0.01	0	0
Mexican rockfish	<0.01	0	0
Pacific argentine	0	0	<0.01
Shiner perch	0	0	<0.01
Blacktail snailfish	0	0	<0.01
Pacific sanddab	0	0	0.01
Spotted cusk-eel	0	0	0.01
Swell shark	0	<0.01	0
Unidentified cusk-eels	0	0	0.01
Petrale sole	0	0	0.03
Unidentified eelpouts	0	0	0.11
Threadfin sculpin	0	<0.01	0
Spotfin sculpin	0	0	<0.01
Bearded eelpout	0	0	0.51
Bigfin eelpout	0	0.02	0.14
Slender sole	0	0	0.09
California smoothtongue	0	0	<0.01
Unidentified lanternfishes	0	<0.01	0.02
Plainfish midshipman	0	<0.01	0

Species	**H**	**L**	**S**
English sole	0	<0.01	0.02
California skate	0	<0.01	0
Sandpaper skate	0	<0.01	0.02
Red brotula	0	<0.01	0
Sablefish	0	<0.01	0.03
Unidentified sanddabs	0	<0.01	0.1
Unidentified skates	0	0	<0.01
Blacktip poacher	0	0	<0.01
Pink seaperch	0	<0.01	<0.01

Table 3. Mean depth and depth range of fishes observed (including only those taxa that were observed at least five times) on the Footprint, 1995, 1998–2011. Taxa are ordered by mean depth, shallowest to deepest. Numbers and frequency of occurrence of each taxa are found in Table 1. Other than "Unidentified YOYs" only taxa that were identified to species are included in this list.

Species	Mean Depth (m)	Depth Range (m)
Blackeye goby	115	98–177
Squarespot rockfish	115	93–175
Rosy rockfish	116	97–210
Halfbanded rockfish	121	94–278
Pygmy rockfish	124	94–200
Starry rockfish	129	94–222
Speckled rockfish	129	93–210
Widow rockfish	130	94–208
Whitespotted rockfish	131	98–217
Pacific sanddab	132	109–200
Pacific electric ray	135	97–207
Flag rockfish	138	94–220
Freckled rockfish	143	143–143
Vermilion rockfish	143	98–246
Dwarf-red rockfish	144	98–217
Greenspotted rockfish	145	96–319
Unidentified YOY rockfishes	147	93–359
Chilipepper	136	98–267
Swordspine rockfish	155	94–260
Lingcod	156	95–285
Cowcod	162	95–270
Bocaccio	156	93–315
Longspine combfish	159	107–213
Rosethorn rockfish	179	125–367
Spotted ratfish	182	95–321
Shortspine combfish	183	95–376
Spotted cuskeel	195	125–328
Darkblotched rockfish	217	98–265
Bank rockfish	206	102–367
Greenstriped rockfish	211	121–259
Pinkrose rockfish	212	98–368
Greenblotched rockfish	221	94–367
Sharpchin rockfish	227	201–315
Bronzespotted rockfish	233	192–296
Pink rockfish	248	146–297
Stripetail rockfish	255	98–309
Shortbelly rockfish	262	99–368

Species	Mean Depth (m)	Depth Range (m)
Bluebarred prickleback	265	192–331
Slender sole	288	124–331
Dover sole	299	153–407
Bearded eelpout	305	226–347
Petrale sole	315	238–377
English sole	319	294–358
Pacific hake	320	208–407
Bering skate	327	294–390
Aurora rockfish	332	271–392
Rex sole	346	251–407
Blackgill rockfish	349	229–392
Bigfin eelpout	354	266–407
Splitnose rockfish	357	112–392

Table 4. Young-of-the-year (YOY) rockfishes observed on the Footprint, 1995, 1998–2011, ordered by mean depth (m). See Methods for definitions of YOY rockfishes.

Species	**Total Number**	**Mean Depth**	**Minimum Depth**	**Maximum Depth**
Canary rockfish	1	102	102	102
Squarespot rockfish	217	113	95	148
Halfbanded rockfish	61	116	97	145
Chilipepper	4	122	109	146
Starry rockfish	21	124	99	170
Pygmy rockfish	2230	127	96	200
Greenspotted rockfish	36	131	98	210
Widow rockfish	242	132	96	203
Swordspine rockfish	265	132	110	201
Speckled rockfish	45	139	110	173
Cowcod	18	143	95	220
Unidentified YOY	5694	147	93	359
Unidentified *Sebastomus*	8	153	128	190
Greenstriped rockfish	2035	153	96	359
Shortbelly rockfish	36	166	100	244
Bank rockfish	405	185	115	270
Bocaccio	12	190	135	252
Unidentified rockfishes	38	200	98	381
Pinkrose rockfish	14	234	147	270
Blackgill rockfish	9	271	229	308
Stripetail rockfish	9	276	234	308
Aurora rockfish	31	365	272	407
Splitnose rockfish	8	377	357	392

Supplementary Table 1. Categories used in the habitat analyses.

Habitat categories	Substratum types
H	BB, BR, BT, RR, RB, RT, TT, TB, TR, BG, RG, BP, RP, BC, RC, TG, TP, TC, TF, BF, RF, RS, RM, BS, BM, TS, TM
L	CB, CR, GB, GR, PB, PR, FB, FR, FT CC, FC, FF, PP, GG, CF, CG, CP, FP, GC, GP, PC, CS, CM, FS, FM, GS, GM, PS, PM
S	SH SR, MR, SB, MB, ST, MT, SC, MC, SG, MG, MF, SF, MP, SP, SS, MM, SM, MS

The three habitat categories, H (high relief), L (low relief), and S (soft sediment) comprise subcategories consisting of combinations of the following substratum types: pinnacle top (T), rock ridge (R), boulder (B), continuous flat rock (F), cobble (C), pebble (P), gravel (G), sand (S), and mud (M). Category H includes all combinations with pinnacle top, rock ridge, and boulder as the primary substratum. Category L includes all combinations with continuous flat rock, cobble, pebble, and gravel as the primary substratum. Category S includes all combinations with sand or mud as the primary substratum.

Supplementary Table 2. Distribution, by depth, of transects conducted from 1995, 1998–2011 on the Footprint.

Depth (m)	Number of Transects	Area (m^2)
93–100	9	5955
101–125	41	30,144
126–150	35	29,238
151–175	17	12,448
176–200	26	17,711
201–225	24	19,337
226–250	18	13,778
251–275	18	11,587
276–300	4	2890
301–325	7	5857
326–350	2	1713
351–375	3	2085
376–407	4	2818

Supplementary Table 3. Habitat distributions by area (m^2) of surveys conducted at the Footprint, 1995, 1998–2011.

Habitat categories (e.g., HH, HL) are described in Supplementary Table 1 and in text.

Habitat distribution by area (m^2)

Depth Interval	HH	HL	HS	LH	LL	LS	SH	SL	SS
(94–100)	619.7	492.6	0.0	1912.1	3510.6	316.5	0.0	0.0	0.0
(101–125)	7452.8	2586.7	223.2	4134.1	8233.5	2811.3	63.7	19441.6	1239.6
(126–150]	11066.6	5193.8	1568.2	1501.1	1743.4	3951.5	176.3	1218.2	2599.4
(151–175]	3675.1	2213.0	774.4	1254.5	748.4	1658.8	88.7	1263.7	1479.7
(176–200]	5913.3	2295.8	1492.4	1609.7	1643.1	1233.7	423.2	456.6	1662.3
(201–225]	9419.0	4558.7	2539.1	734.7	930.0	2054.3	338.5	1117.3	246.8
(226–250]	2669.6	2672.0	1120.9	919.5	145.4	556.0	380.1	1211.7	1900.5
(251–275]	1404.7	1636.0	1644.0	690.6	324.2	1037.2	881.9	1078.5	2535.9
(276–300]	412.1	283.3	239.4	91.8	84.8	385.2	297.4	501.3	1685.2
(301–325]	354.6	65.0	221.0	60.0	0.0	227.5	172.0	998.0	2776.9
(326–350]	15.0	7.5	12.5	0.0	0.0	15.0	2.5	107.5	1910.0
(351–375]	647.5	17.5	5.0	120.0	82.5	97.5	350.0	587.5	117.5
(376–425]	45.0	120.0	75.0	170.0	0.0	482.5	215.0	1150.0	550.0
Total	43,695.0	22,141.9	9915.1	13,198.1	17,445.9	14,827.0	3389.3	11,631.9	18,703.8

Relief distribution in percent (%) and area (m^2). Categories H, L, and S are described in Supplementary Table 1.

Depth Interval	H%	L%	S%	H area	L area	S area
(94–100]	16.2	83.8	0.0	1112.3	5739.2	0.0
(101–125]	35.8	52.9	11.3	10,262.7	15,178.9	3244.9
(126–150]	61.4	24.8	13.8	17,828.6	7196.0	3993.9
(151–175]	50.6	27.8	21.5	6662.5	3661.7	2832.1
(176–200]	58.8	26.8	15.2	9701.5	4486.5	2542.0
(201–225]	75.3	17.0	7.7	16,516.8	3719.0	1702.5
(226–250]	55.8	14.0	30.2	6462.6	1620.9	3492.3
(251–275]	41.7	18.3	40.0	4684.7	2052.0	4496.4
(276–300]	23.5	14.1	62.4	934.8	561.8	2628.7
(301–325]	13.1	5.9	80.9	640.6	287.5	2483.8
(326–350]	1.7	0.7	97.6	35.0	15.0	2020.0
(351–375]	33.1	14.8	52.1	670.0	300.0	1055.0
(376–425]	8.5	23.2	68.2	240.0	652.5	1915.0
Total	NA	NA	NA	75,752.1	45,471.0	33,724.8

Supplementary Table 4. The linear regression relationship between fish size and bottom depth for fish species with the highest densities or of greatest economic importance. A positive slope value suggests that size increases with depth.

Species	**intercept**	**slope**	**p-slope**	**r^2**	**Sample size**	**Significant?**
Squarespot rockfish	14.734	-0.0020	0.9310	0.0029	5	no
Pygmy rockfish	9.461	0.0082	0.7161	0.0505	5	no
Swordspine rockfish	11.014	0.0313	0.0001	0.9382	8	yes
Halfbanded rockfish	8.750	0.0340	0.0230	0.6767	7	yes
Widow rockfish	12.165	0.0963	0.1822	0.3938	6	no
Shortbelly rockfish	16.735	0.0056	0.4779	0.0648	10	no
Bank rockfish	14.650	0.0365	0.0931	0.3122	10	no
Shortspine combfish	14.418	0.0176	0.0133	0.4738	12	yes
Bocaccio	41.207	-0.0085	0.8241	0.0075	9	no
Splitnose rockfish	8.207	0.0309	0.0133	0.6077	9	yes
Speckled rockfish	20.177	0.0342	0.5219	0.1094	6	no
Starry rockfish	15.598	0.0543	0.1038	0.5241	6	no
Lingcod	33.197	0.1127	0.0113	0.6337	9	yes
Stripetail rockfish	15.131	0.0070	0.5849	0.0637	7	no
Cowcod	14.878	0.1581	0.0186	0.6303	8	yes
Flag rockfish	9.685	0.0914	0.0111	0.8327	6	yes