



Trophic ecology of the gopher rockfish *Sebastes carnatus* inside and outside of central California marine protected areas

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ABSTRACT: Marine protected areas (MPAs) can potentially alter food web dynamics by increasing the density of fishes within their borders. Such increases in the density of potential competitors can cause generalist predators to contract the scope of their diets. This study investigated the effects of increased conspecific fish density on the diets of gopher rockfish *Sebastes carnatus* at a 35 yr old MPA in Point Lobos, California, and at 4 newly established MPAs in Año Nuevo, Point Lobos, Piedras Blancas, and Point Buchon in central California. Analyses were conducted for 707 stomachs collected from 2007 to 2009. Diets did not differ inside versus outside the old Point Lobos MPA in terms of prey richness, evenness, composition, or gopher rockfish trophic level. However, fish outside the MPA had greater levels of individual specialization. No consistent differences in these metrics were observed inside versus outside the 4 new MPAs, although prey composition and evenness did differ significantly among geographic locations. Diets at Año Nuevo, the most northern and shallow location, consisted predominantly of *Cancer* spp. and porcelain crabs (Porcellanidae), while diets from southern, deeper locations were dominated by brittle stars (Ophiuroidea). The case study of the old Point Lobos MPA indicates that fish feeding ecology may not change in an MPA after several decades. Differences in prey observed among geographic locations suggest variation in the community composition among central California's new MPAs, which may influence the effect of each MPA on food web dynamics over time.

KEY WORDS: Diet · Marine reserves · Feeding ecology · Sebastidae · Kelp forests

INTRODUCTION

The decline of many fisheries and coastal marine ecosystems around the world has prompted the increasing adoption of marine protected areas (MPAs) as ecosystem-based management practices that can protect both marine species and ecosystem services (Allison et al. 1998, Crowder et al. 2008). Fishing directly alters marine ecosystems through the removal of fishes and indirectly alters them through changes in marine food webs resulting from the loss

of predators and prey (Botsford et al. 1997, Pinnegar et al. 2000). In turn, MPAs that exclude fishing pressure within their borders can directly affect marine communities by increasing the density and size of fishes (McClanahan & Arthur 2001, Halpern & Warner 2002, Micheli et al. 2004, Guidetti & Sala 2007, Tetreault & Ambrose 2007, Lester et al. 2009). A greater abundance of predators inside MPAs can subsequently trigger indirect effects that cascade down multiple trophic levels via predator–prey interactions, sometimes altering community structure by

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changing the abundance and distribution of prey species and primary producers (Babcock et al. 1999, Guidetti 2006, Mumby et al. 2007).

Recognizing the need to protect California's marine species and habitats from human impacts, the California Department of Fish and Game passed the Marine Life Protection Act in 1999, which called for a network of MPAs to span the California coast. The first section of this statewide network was established in central California in April 2007, when the California Fish and Game Commission adopted 29 MPAs between Pigeon Point and Point Conception. These MPAs, effective as of September 2007, include 13 no-take state marine reserves that prohibit all commercial and recreational fishing within their borders and 15 state marine conservation areas, which permit limited fishing. In addition to creating new MPAs, the act expanded the pre-existing Point Lobos State Marine Reserve, which has been closed to fishing since 1973. As one of the oldest no-take marine reserves in the USA, Point Lobos offers a unique opportunity to examine the long-term effects of fishing exclusion inside an MPA, including potential effects on marine food webs.

Studying fish feeding habits inside and outside of MPAs provides a means to investigate potential indirect effects of increased fish density on marine food webs. While previous studies have looked for the effects of MPAs across trophic levels, such as the effects of specialist predators on the distribution of their prey and organisms at lower trophic levels (Babcock et al. 1999, McClanahan 2000, Fanshawe et al. 2003, Guidetti 2006, Clemente et al. 2009), few studies have focused within a trophic level to investigate the indirect effects of fishing exclusion on a single predator's feeding habits (Badalamenti et al. 2008, Fanelli et al. 2009, 2010, Sinopoli et al. 2012). The increased density of competitors inside MPAs is one potential factor that could cause within-trophic-level diet changes. Manipulative experiments using three-spined sticklebacks *Gasterosteus aculeatus* have demonstrated that increased densities of conspecifics can lead to increased diet specialization (Svanbäck & Bolnick 2007), supporting the theory that competing populations will diverge from each other in resource use (Brown & Wilson 1956). Changes in a single species' diet can therefore be used to infer changes in ecological relationships between a predator and its prey as well as the indirect effects of increased competitor densities in MPAs.

The gopher rockfish *Sebastes carnatus* was chosen to investigate potential changes in feeding ecology at 4 MPAs located in central California: Año Nuevo,

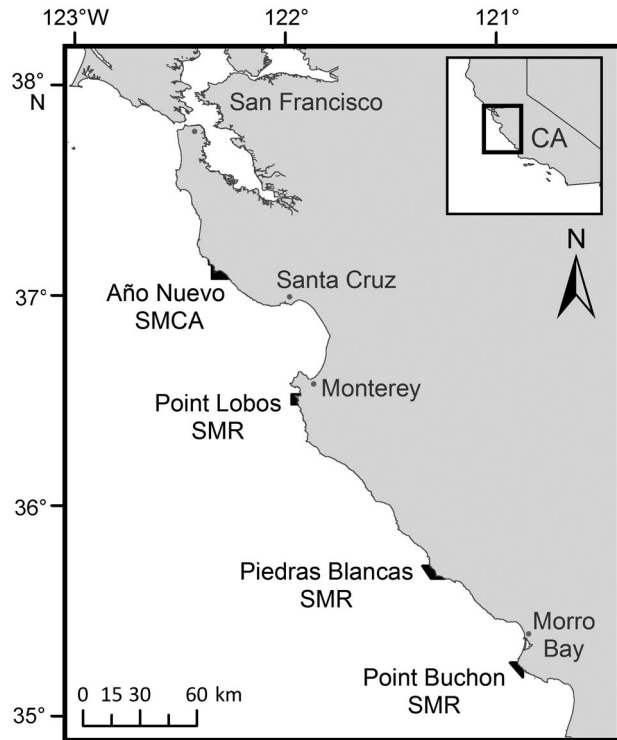


Fig. 1. Marine protected areas (MPAs) in 4 geographic locations within the central California study area (shown in inset). MPAs include the Año Nuevo State Marine Conservation Area (SMCA) and the Point Lobos, Piedras Blancas, and Point Buchon state marine reserves (SMRs)

Point Lobos, Piedras Blancas, and Point Buchon (Fig. 1). The gopher rockfish is one of the most commonly occurring nearshore fishes in central California (Yochum et al. 2011) and is frequently caught in recreational and commercial live-fish fisheries (Key et al. 2005). Its abundance, territorial behavior, restricted movements, and generalist feeding habits (Larson 1980) make it a good candidate to investigate localized changes in food web structure that may occur in protected areas.

Differences in gopher rockfish density at the study locations enable an investigation of potential MPA effects. Baseline monitoring surveys from 2007 to 2009 in the MPAs chosen for this study documented significantly greater gopher rockfish densities inside MPAs compared to nearby fished areas at 3 of the 4 study locations (Starr et al. 2010, 2015). At the Point Lobos MPA, established in 1973, these differences in gopher rockfish density inside versus outside the MPA could possibly be a result of more than 30 yr of MPA protection; however, at the new MPAs, these differences represent a pre-existing baseline rather than a direct result of the new MPAs themselves.

Nevertheless, pre-existing differences in fish density inside and outside of MPAs still provide an opportunity to examine the effects of differing fish densities on feeding ecology. Such effects could be amplified if fish densities increase in the MPAs over time.

The goal of this study was to investigate the effects of fishing exclusion and increased conspecific densities on the feeding ecology of the gopher rockfish in central California MPAs. Specific objectives were to (1) assess the long-term effects of fishing exclusion by comparing gopher rockfish diets inside and outside of an MPA that has been established for more than 30 yr, (2) assess the short-term effects of fishing exclusion across the central California region by comparing gopher rockfish diets inside and outside of 4 newly established MPAs, and (3) explore environmental factors that could potentially contribute to variation in gopher rockfish diet.

MATERIALS AND METHODS

Study areas and sample collection

This study investigated 4 MPAs and 4 corresponding reference areas surveyed by the California Collaborative Fisheries Research Program (CCFRP, Starr et al. 2015). Each MPA and reference area pair was located in a different geographic location (Fig. 1): Año Nuevo, Point Lobos, Piedras Blancas, and Point Buchon. These locations contain extensive nearshore rocky habitats representative of the central California coastal region. The 3 southernmost MPAs are state marine reserves that prohibit all fishing. The Año Nuevo MPA is a state marine conservation area that prohibits all fishing but permits the hand harvest of giant kelp; however, kelp harvesting in this area has never occurred. To assess the impacts of excluding fishing pressure inside the MPAs, a reference area that had no restrictions on fishing was sampled near each MPA for comparison. Each reference area shared similar size, depth, habitat, and oceanographic conditions with the nearby MPA (Yochum et al. 2011). The Point Lobos MPA, established in 2007, encompasses the pre-existing Point Lobos Ecological Reserve (Fig. 2), which was closed to fishing in 1973. The area encompassed by the 1973 boundary will hereafter be referred to as the old Point Lobos MPA, and the area inside the extended 2007 boundary will be referred to as the new Point Lobos MPA.

Within each MPA and reference area, grid cells measuring 500 × 500 m were delineated as part of the

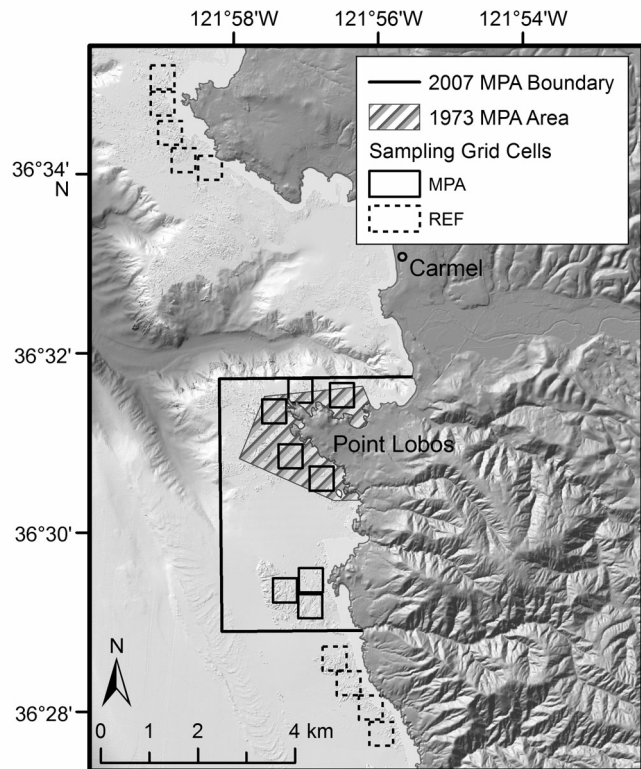


Fig. 2. Marine protected area (MPA) and reference (REF) area sampling sites at Point Lobos. Grid cells measuring 500 × 500 m were established in both the MPAs and REF areas. The shaded area denotes the boundary of the old Point Lobos MPA, closed to fishing in 1973. The solid line denotes the expanded boundary of the new Point Lobos MPA, established in 2007. Dotted lines represent grid cells in the unprotected REF areas

CCFRP sampling protocol, with similar numbers of grid cells located in the MPA and reference areas at each geographic location (Wendt & Starr 2009, Starr et al. 2010). At Point Lobos, grid cells were delineated in both the old and new sections of the MPA. Gopher rockfish were collected with hook-and-line and trapping gear in the summer and fall of 2007 to 2009 as part of monitoring surveys conducted by the CCFRP (Wendt & Starr 2009, Yochum et al. 2011). The great majority of samples were collected during hook-and-line surveys. Each location was sampled for 4 d each month from August to October 2007, from July to September 2008, and in July and August 2009. The Piedras Blancas MPA and corresponding reference area were added to the survey in 2008; thus, no fish were collected at Piedras Blancas in 2007. Four of the grid cells in a given MPA or reference area were randomly chosen and sampled each day, and a portion of the gopher rockfish catch was retained haphazardly.

Care was taken to retain fish, whenever possible, that did not show extruded stomachs or regurgitated stomach contents. Any prey items found in the oral cavity were saved with the fish to be included in later dietary analysis. The retained fish were euthanized and placed on ice until the boat returned to shore, at which point they were frozen. Fish lengths and weights were measured to account for potential biases in feeding related to fish size. The total and standard lengths of each fish were measured to the nearest 1.0 cm, and total fish weight was measured to the nearest 1.0 g. Total lengths were compared inside and outside of MPAs using a randomized block design. The independent variable was whether an area was designated as an MPA or as a reference area. The dependent variable was total fish length for 31 fish randomly selected from each area to account for differences in sample size. A reference area was paired geographically with each of the 4 MPAs, allowing geographic location to be used as a blocking factor in a randomized complete block (RCB) ANOVA.

Fish were later partially thawed, and stomachs were removed and refrozen for later analysis. Fish with empty stomachs were excluded from analysis. Stomachs were thawed individually at room temperature, and the contents were examined with a dissecting microscope. The prey items of each stomach were identified to the lowest possible taxonomic level following Carlton (2007), enumerated, and weighed wet to the nearest 0.001 g after blotting away excess moisture. Bait used to catch fish was easily identified and thus excluded from dietary analysis. To minimize the effect of potential partial regurgitation, stomachs that contained less than 0.1 g of prey were considered empty and excluded from further dietary analysis. Prey were counted using the minimum number of individual prey items represented by the body parts present (Lance et al. 2001).

Determining long-term effects of fishing exclusion at Point Lobos

A difference in gopher rockfish density inside and outside of the old Point Lobos MPA provided the basis for investigating potential MPA effects on diet (Fig. 3, Starr et al. 2010, 2015). Diets were compared between fish collected at the old Point Lobos MPA and corresponding reference areas to assess the effects of increased conspecific densities after more than 30 yr of fishing closure. Diets were compared using the following metrics: (1) richness, (2) even-

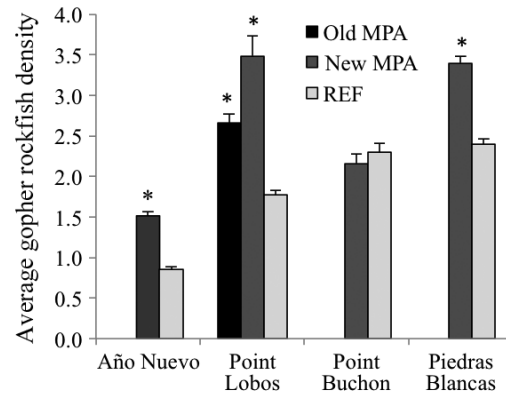


Fig. 3. Average gopher rockfish density at all study areas from 2007 to 2009 measured in catch per angler hour with hook and line. Vertical bars represent standard error. Asterisks indicate significant difference between marine protected areas (MPAs) and reference (REF) areas. Data from Starr et al. (2015)

ness, (3) composition, (4) trophic level, and (5) individual specialization (IS). The Point Lobos reference area consisted of 2 locations situated north and south of the MPA (Fig. 2). The results of a preliminary analysis, using the methods described in the subsequent paragraphs, indicated that diets in the north and south reference areas did not differ significantly from each other in terms of the 5 metrics listed above ($p > 0.05$), except for prey taxon composition ($p < 0.05$). Therefore, these reference areas were pooled for subsequent comparison to the old MPA in all analyses except for prey taxon composition.

Diet richness, evenness, and composition were characterized by organizing prey into 18 taxonomic groups (Table 1). This classification strikes a balance between richness and ecological similarity by incorporating the lowest taxonomic groups to which prey were consistently identified and grouping taxa with highly similar morphologies and ecologies. These taxa exclude crabs and shrimp that could not be identified to the family level; sipunculans, urchins, and anemones, which were only encountered in 1 or 2 fish stomachs; and parasites or unidentified digested matter.

Richness and evenness. Prey accumulation as a function of number of samples was plotted to determine if sufficient samples were collected to characterize the diets of the MPA and reference areas (Ferry & Cailliet 1996, Bizzarro et al. 2007). The relationship between number of samples and number of prey taxa observed was plotted using the specaccum function in the vegan community ecology package of the software program R 2.10.1 (Bizzarro et al. 2007, Oksanen et al. 2010).

Table 1. Prey taxonomic groups used in dietary analysis

Prey taxon	Group(s) included
Amphipod	Amphipoda
Brittle star	Ophiuroidea
Cancer crab	<i>Cancer</i> spp.
Cephalopod	Cephalopoda
Crangonid shrimp	Crangonidae
Fish	Actinopterygii
Hermit crab	Paguridae
Hippolytid shrimp	Hippolytidae
Isopod	Isopoda
Kelp crab	Epialtidae
Mollusc	Mollusca (excluding Cephalopoda)
Mysids	Mysidacea
Other crab	Grapsidae, Lithodidae, Panopeidae, Parthenopidae, Xanthidae
Pandalid shrimp	Pandalidae
Pistol shrimp	Alpheidae
Polychaete	Polychaeta
Porcelain crab	Porcellanidae
Spider crab	Pisidae

Diet evenness was calculated using Pielou's evenness measure (J'):

$$J' = \frac{\sum p_j \log p_j}{\log n} \quad (1)$$

where p_j is the proportion of individuals that ate prey type j , and n is the total number of prey types, or richness (Krebs 1999).

Prey composition. The contribution of each prey type to the diet was determined using prey-specific abundance (Amundsen et al. 1996, Brown et al. 2012) and percent occurrence (Cortés 1997). Prey-specific abundances by number and weight (%PN_{*i*}, %PW_{*i*}) were calculated as:

$$\%PA_i = \frac{\sum_{j=1}^n \%A_{ij}}{n_i} \quad (2)$$

where A_{ij} is the abundance by number or weight for prey i in an individual stomach sample j , and n_i is the number of stomachs containing prey i . Percent occurrence (%O_{*i*}) was calculated as:

$$\%O_i = \frac{n_i}{n} \times 100 \quad (3)$$

The index of relative importance (IRI) is a compound index used to determine the importance of each prey type to the diet (Pinkas et al. 1971, Cortés 1997). A modified prey-specific version of the IRI (PSIRI) was calculated following Brown et al. (2012):

$$PSIRI_i = (\%PN_i + \%PW_i) \times \%O_i \quad (4)$$

The prey-specific calculation corrects for an inherent bias in the traditional calculation of IRI that

overemphasizes the contribution of %O (Brown et al. 2012). These PSIRI values were standardized as a percentage following Cortés (1997).

To reduce the effects of variation in diet biomass among fish of different sizes, differences in prey composition were investigated using standardized prey weights. These standardized weights were calculated for each stomach by dividing the raw weight of the prey taxon of interest by the weight of the fish to reduce the potential influence of fish size on prey quantity. Prey weight was used because it is an approximation of the energetic contribution of a prey type in an animal's diet, and it does not overemphasize the contribution of highly numerous prey items (Hyslop 1980). Prey composition was then determined at a population level by summing the standardized prey weights for an equal number of fish randomly drawn from the areas being compared.

To reduce the bias from unequal numbers of fish collected at each area, population totals for the old Point Lobos MPA and reference areas were calculated by randomly drawing 4 fish from each of 6 sampling grid cells in each area and summing the standardized prey weights of the 4 fish in each grid cell. These sample sizes included grid cells from both hook-and-line and trapping surveys and maximized the number of grid cells and number of fish per grid cell in each area.

A MANOVA (Quinn & Keough 2002) was used to determine if prey composition differed between the MPA and 2 reference areas. Because the number of prey categories was large relative to the number of samples and could introduce type I error, a principal components analysis (PCA, Quinn & Keough 2002) was first performed on total prey weights to reduce prey composition into 2 factors, which served as the dependent variables in the MANOVA. PCA and MANOVA were performed using the software package PASW Statistics 18.0.

Trophic level. The trophic level of each fish was calculated from stomach contents following Cortés (1999) and Ebert & Bizzarro (2007):

$$TL_k = 1 + \left(\sum_{j=1}^n P_j \times TL_j \right) \quad (5)$$

where TL_k is the trophic level of species k , P_j is the proportion of prey category j in the diet of species k , n is total number of prey categories, and TL_j is the trophic level of prey category j . Percent weight values were used for P_j , and prey groups were assigned trophic levels following the characterization of Ebert & Bizzarro (2007). An independent 2-sample t -test was used to detect differences in mean trophic level

between the MPA and pooled reference areas. A linear regression was used to test for a relationship between trophic level and fish total length.

Individual specialization. IS was calculated following Bolnick et al. (2002). This index incorporates Czekanowski's proportional similarity index (PS), calculated as the overlap between an individual and the population:

$$PS_i = \sum_j \min(p_{ij}, q_j) \quad (6)$$

where PS_i is the proportional overlap between individual i and its population, p_{ij} is the proportion of prey group j by number in the individual i 's diet, and q_j is the proportion of prey group j by number in the population as a whole.

The index of IS is then calculated as:

$$IS = \frac{1}{N} \sum_i PS_i \quad (7)$$

where N is the total number of individuals in the population. Resulting values range from 0 to 1, with 1 indicating complete overlap between individual diets and the population as a whole and lower values indicating greater specialization among individuals compared to the total population. An independent 2-sample t -test was used to detect differences in IS values between the MPA and the reference area.

Determining short-term effects of fishing exclusion at newly established MPAs

Baseline differences in gopher rockfish densities inside and outside new MPAs provided the basis for an analysis of the effects of conspecific density on gopher rockfish diets across the central California region (Fig. 3, Starr et al. 2010, 2015). Diets were compared inside and outside of 4 MPAs established in 2007 at Año Nuevo, Point Lobos, Piedras Blancas, and Point Buchon. Only data from 2008 and 2009 were included in comparisons of all locations because the Piedras Blancas location was not sampled in 2007. Analyses were essentially the same as the analysis of the old Point Lobos MPA; however, the scale of the measurements differed. In the Point Lobos analysis, fish were pooled within individual grid cells to serve as the sample units. In contrast, a population total for each metric was calculated for each of the new MPAs and reference areas by pooling the stomach contents of fish from multiple grid cells at each area, and these population totals served as the sample units.

Population total values were used because means based on averages of individual variation could

Table 2. Number of gopher rockfish stomachs analyzed by location, area, and year. MPA: marine protected area; REF: reference area

Location and area	2007	2008	2009	Total
Año Nuevo MPA	19	46	56	121
Año Nuevo REF	23	39	49	111
Point Lobos Old MPA	23	38	45	106
Point Lobos New MPA	20	15	41	76
Point Lobos REF	30	36	56	122
Piedras Blancas MPA	0	23	16	39
Piedras Blancas REF	0	14	30	44
Point Buchon MPA	11	18	22	51
Point Buchon REF	6	14	17	37
Total	132	243	332	707

obscure differences at the population level. These population totals were calculated for each dietary measure (i.e. richness, evenness, composition) after summing stomach contents for 31 fish randomly drawn from each MPA and reference area. This number represents the smallest number of fish collected at a given area from 2008 to 2009 (Point Buchon reference area, Table 2) and was chosen to equalize sample sizes among areas.

Richness, evenness, and prey composition were compared inside and outside of MPAs using a randomized block design. The independent variable in all analyses was whether an area was designated as an MPA or as a reference area. In prey composition analysis, the number of prey categories was large relative to the number of samples and could introduce type I error; therefore, a PCA (Quinn & Keough 2002) was performed on total prey weights prior to analysis to reduce prey composition into 2 factors, which served as the dependent variables. A reference area was paired geographically with each of the 4 MPAs, allowing geographic location to be used as a blocking factor in an RCB MANOVA (Quinn & Keough 2002).

Determining effects of other factors on diet

The remainder of the study explored factors other than fishing exclusion that could affect gopher rockfish diet. Therefore, the following analyses were conducted without taking the effects of MPAs and reference areas into account, and examined overall fish density in an area regardless of its protected status as well as environmental variables.

Relationship between diet and fish density. Linear regressions were used to investigate the relationship between gopher rockfish density and dietary vari-

ables. Mean prey taxon richness and evenness, trophic level, and IS were calculated for each sampling area as described above. Linear regressions were then used to test for relationships between these variables and the average gopher rockfish density in each area, expressed as catch per unit effort, which was calculated as the number of fish caught per angler hour spent fishing with standardized hook-and-line gear (Starr et al. 2010).

Relationship between diet and environmental variables. To investigate the potential influence of environmental variables on diet that could contribute to differences among geographic locations, a canonical correlation analysis (CCA, Quinn & Keough 2002) was conducted using environmental and dietary variables calculated for each sampling grid cell. Environmental variables included depth, temperature at depth, area of hard substrate, and latitude. Depth of collection for each fish was measured using the boat's depth finder and was averaged for all fish collected within a grid cell. Temperature at depth was collected throughout the study in each grid cell using a continuously recording sensor lowered to 3 m above the seafloor, and measurements were averaged for each grid cell. The proportion of hard substrate within each grid cell was calculated in the software program ArcGIS 9.2 using habitat layers from the Seafloor Mapping Lab at California State University Monterey Bay. The habitat layers classified substrate as rock or sediment based on rugosity. Latitude data were taken from the coordinates of each sampling grid cell center point. Diet variables were calculated as standardized prey weights averaged for all fish caught in a given grid cell. CCA was performed using the software package PASW Statistics 18.0.

Relationship between diet and depth. A linear regression was used to further examine the relationship between diet and depth. PCA Factor 1 from the PCA analysis described above was used to summarize dietary variation. A linear regression was used to test for a relationship between the mean PCA Factor 1 score and the mean depth of fish collection at each sampling area.

RESULTS

In total, 1018 gopher rockfish were collected across 4 locations and 3 yr, of which 311 had empty stomachs (30.6%). Diet composition was analyzed for the remaining 707 fish (Table 2). Fish total lengths ranged from 16.7 to 32.9 cm, with a mean of 26.4 cm. An RCB

ANOVA showed that length did not significantly differ inside and outside of MPAs ($F_{1,243} = 1.944$, $p = 0.164$); however, the block factor of geographic location was significant ($F_{3,243} = 21.045$, $p < 0.001$).

Overall diet description and trophic level

Gopher rockfish prey items represented 7 phyla and at least 60 distinct species (Table S1 in the Supplement at www.int-res.com/articles/suppl/m536p229_supp.pdf). Overall, decapod crustaceans dominated the diet (70.04% PSIRI) and consisted primarily of 20 different crab species (45.9% PSIRI), shrimps (14.5% PSIRI), and mysids (7.2% PSIRI). Echinoderms, predominantly brittle stars, were also important to the diet (18.26% PSIRI). The taxonomic group cephalopods consisted almost entirely of benthic *Octopus* sp. While most fishes had to be classified as unidentified due to their state of digestion, the majority of identified groups were benthic species (e.g. Cottidae, Gobiidae, Pleuronectiformes), although a few pelagic groups (e.g. Clupeidae, juvenile *Sebastes*) were also encountered. No significant relationship was observed between trophic level and total fish length ($p = 0.23$, $R^2 = 0.003$).

Determining long-term effects of fishing exclusion at Point Lobos

Richness and evenness. The number of stomachs used for dietary analyses at these sites was deemed sufficient. All cumulative prey curves reached an inflection point between 20 and 40 stomachs, and all curves reached an asymptote ($b < 0.05$), indicating sufficient sample size for prey taxon analysis.

There was no detectable difference in prey richness or evenness of gopher rockfish diet items between the old MPA and the pooled reference areas. The MANOVA revealed that diets from the old Point Lobos MPA and pooled reference areas did not differ significantly in mean prey taxon richness ($F_{1,210} = 1.84$, $p = 0.18$) or evenness ($F_{1,210} = 1.04$, $p = 0.31$). Overall prey diversity (the multivariate effect of richness and evenness) also did not differ between areas ($F_{2,209} = 1.02$, $p = 0.36$).

Prey composition. There were no detectable differences in prey taxon composition (as measured by Principal Components 1 and 2) between the old MPA and the reference areas.

Trophic level. More than 30 yr of fishing exclusion did not appear to alter the TL of the gopher rockfish

calculated from stomach contents. TL in the old Point Lobos MPA ranged from 3.16 to 4.24, with a mean of 3.59, as opposed to the pooled reference areas, which ranged from 3.10 to 4.24 with a mean of 3.56. The 2-tailed t -test showed that these differences were not significant ($t_{210} = 0.775$, $p = 0.439$).

Individual specialization. The extent of IS differed significantly between the old MPA and pooled reference areas. Mean IS, the overlap between individuals and their population, was 0.23 for the combined north and south reference areas, as opposed to a mean of 0.28 for the old MPA. The 2-tailed t -test showed that these differences were significant ($t_{201} = 2.57$, $p = 0.01$). Thus, in comparison to the old MPA, individuals in the reference area were on average 5% more specialized in relation to their population as a whole.

Determining short-term effects of fishing exclusion in newly established MPAs

Richness and evenness. The number of stomachs used for dietary analyses at these sites was deemed sufficient. All cumulative prey curves reached an inflection point between 20 and 40 stomachs. While some of the curve slopes for prey taxon analysis deviated from an asymptote, these deviations were likely caused by uncommon prey items and were thus not considered severe. Therefore, analyses were still performed using these prey taxonomic groups, while recognizing the potential underestimate of richness at these areas.

There were no detectable differences in prey taxon richness or evenness of gopher rockfish diet items between fish from new MPAs and fish from reference areas. The RCB MANOVA performed on population totals indicated that diets inside and outside of the new MPAs did not differ significantly in terms of taxon richness ($F_{1,3} = 0.60$, $p = 0.50$) or evenness ($F_{1,3} = 4.16$, $p = 0.13$). Overall diversity (multivariate effect of richness and evenness) also did not differ significantly inside and outside of MPAs ($F_{2,2} = 7.14$, $p = 0.12$). The block factor of geographic location was significant for taxon evenness ($F_{3,3} = 47.49$, $p = 0.01$) but not significant for total taxon richness ($F_{3,3} = 1.00$, $p = 0.50$) or diversity ($F_{6,6} = 1.22$, $p = 0.41$).

Prey composition. Prey taxon composition did not differ significantly inside and outside of MPAs; however, significant differences were observed among geographic locations in terms of Factor 1 (Fig. 4). The

first 2 principal components explained 33.9 and 22.1% of the variation, respectively.

Trophic level. Mean TLs were highly similar for all areas, ranging from 3.50 in the Point Buchon MPA to 3.61 in the Año Nuevo MPA. No significant differences in mean TL were observed inside versus outside new MPAs (ANOVA, $F_{1,3} = 0.99$, $p = 0.39$). The block factor of geographic location was also not significant ($F_{3,3} = 0.08$, $p = 0.97$).

Individual specialization. No significant differences in mean IS were observed inside versus outside new MPAs (ANOVA, $F_{1,3} = 0.66$, $p = 0.48$). The block factor of geographic location was also not significant ($F_{3,3} = 0.91$, $p = 0.53$). However, IS values were higher inside all MPAs except for the Año Nuevo MPA, suggesting a possible interaction between geographic location and MPA effect (Fig. 5).

Determining effects of other factors on diet

Relationship between diet and fish density.

Gopher rockfish density was not related to most dietary metrics (Table 3). Linear regression analyses did not find significant relationships ($p > 0.05$) be-

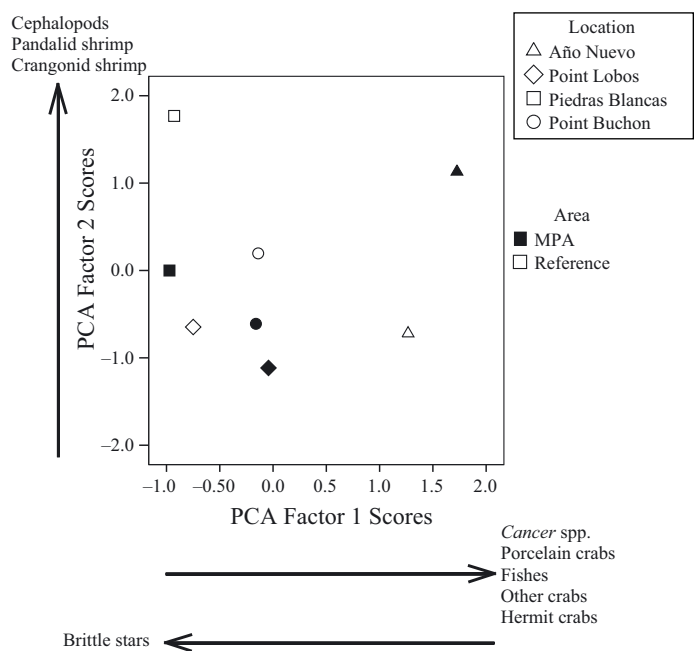


Fig. 4. Plot of principal components analysis (PCA) of prey taxa showing separation of Año Nuevo from other geographic areas along Factor 1. Black symbols indicate diet composition of specimens from marine protected areas (MPAs); white symbols represent reference areas. Arrows represent loadings greater than 0.70

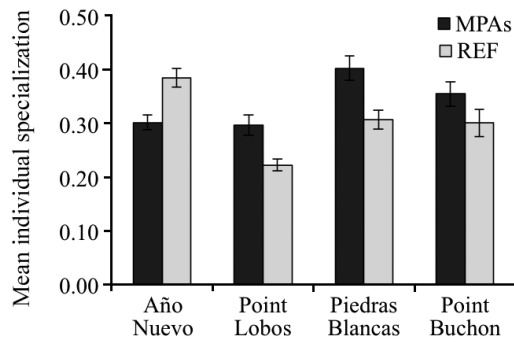


Fig. 5. Mean individual specialization (diet overlap between individuals and population) at new marine protected areas (MPAs) and reference (REF) areas showing no consistent difference among areas. Vertical bars represent standard error

Table 3. Relationship between diet metrics and gopher rockfish density

Metric	p	R ²	Direction
Taxon richness	0.38	0.13	None
Taxon evenness	0.04	0.55	Negative
Trophic level	0.31	0.17	None
Individual specialization	0.99	0.17	None

Table 4. Summary of canonical correlation analysis performed on prey taxa. Canonical loadings are for the one significant root (CV1)

Canonical variate/root	Canonical correlation	p-value
CV1	0.80	0.01
CV2	0.75	0.37
CV3	0.39	0.99
CV4	0.31	0.99
CV1 canonical loading		
Environmental variable	Depth	-0.86
	Latitude	0.78
	Proportion of rocky substrate	0.42
	Temperature at depth	0.05
Dietary variable	Amphipod	-0.22
	Brittle star	-0.53
	<i>Cancer</i> spp.	0.69
	Cephalopod	0.12
	Crangonid shrimp	-0.01
	Fish	-0.07
	Hermit crab	-0.03
	Hippolytid shrimp	0.44
	Isopod	-0.05
	Kelp crab	-0.12
	Mollusc	-0.02
	Mysids	0.06
	Other crab	0.16
	Pandalid shrimp	-0.02
	Pistol shrimp	0.00
	Polychaete	-0.24
	Porcelain crab	0.58
	Spider crab	0.04

tween gopher rockfish density and prey taxon richness, trophic level, or IS. However, there was a significant and moderately strong negative relationship ($p = 0.04$, $R^2 = 0.55$) between prey taxon evenness and gopher rockfish density.

Relationship between diet and environmental variables. CCA showed a strong relationship between environmental variables and prey taxonomic groups (Table 4). The first canonical root ($r = 0.80$) was significantly different from zero ($p = 0.01$), and the environmental variables explained 5.1% of the overall variance of the dietary variables. Deeper depths and lower latitudes were associated with more brittle stars and fewer porcelain and *Cancer* spp.

Relationship between diet and depth. Plotting the PCA Factor 1 scores of prey taxon composition against average depth of fish collection revealed a significant, moderately strong relationship between diet and depth (Fig. 6, $p = 0.02$, $R^2 = 0.61$). However, depth was confounded with geographic location. The average depth of fish collection ranged from 16.1 m at the Año Nuevo MPA to 28.8 m at the Point Buchon MPA.

DISCUSSION

The case study of the Point Lobos State Marine Reserve provides evidence that mid-level trophic changes in MPAs are not guaranteed. Despite greater fish density inside the MPA, gopher rockfish diets were not markedly different from nearby unprotected areas after 35 yr of fishing exclusion. The finding of greater IS outside the MPA is the opposite of what competition theory would predict, although a statistically significant difference in specialization of 5% may not be ecologically significant. While changes in fish abundance and biomass can occur rapidly once protected areas are established (Halpern & Warner 2002), associated changes in species composition and trophic structure may occur gradually and over timeframes of 10 to 15 yr (Micheli et al. 2004, Babcock et al. 2010). Thus, increased fish densities may not produce changes to trophic structure or prey species composition in the central California MPAs, or such changes may take even longer to occur.

Without a historical baseline at Point Lobos, it is not possible to say that gopher

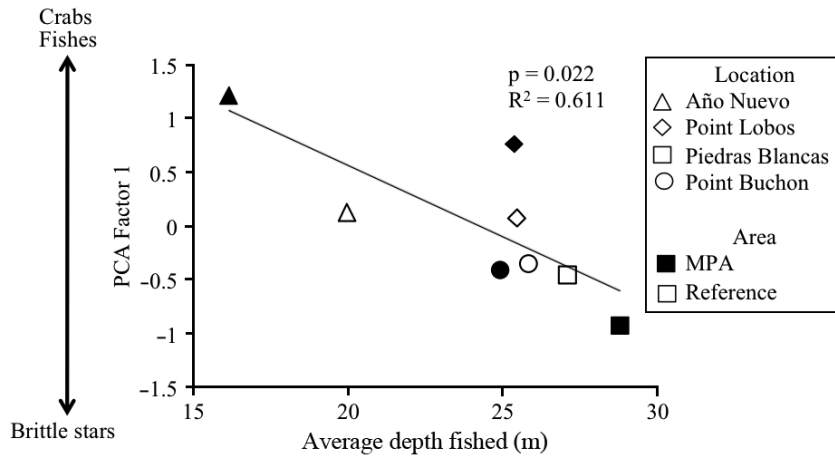


Fig. 6. Relationship between diet and depth showing that depth is confounded with geographic location. The y-axis represents the principal components analysis (PCA) Factor 1 scores for prey composition depicted in Fig. 4

rockfish feeding habits have not changed in 35 yr but only that diets did not differ compared to the fished reference areas. While recreational and commercial fishing with hook and line and traps do occur in the reference areas, this fishing pressure may not be extensive enough to produce drastic differences in feeding dynamics compared to the protected area. The old Point Lobos MPA is also a small reserve, and different trends may occur in larger protected areas. This underscores the importance of collecting site-specific baseline information and monitoring the performance of reserves individually as well as collectively.

Although controlled experimental work with sticklebacks suggests that IS and among-individual diet variability should increase with conspecific density (Svanbäck & Bolnick 2007), there was no consistent effect associated with increased gopher rockfish densities in the MPAs surveyed. Significantly greater IS compared to the reference area was measured in the Año Nuevo MPA, and while this result is consistent with competition theory, all other MPAs exhibited lower IS than their reference areas (or higher overlap between individuals and the overall population), which is the opposite of what competition theory predicts. The differing effect of the MPA at Año Nuevo suggests that there may be some interaction with geography that could affect MPA performance.

The lack of differences in diet inside and outside of all MPAs surveyed suggests that although the densities of gopher rockfish inside MPAs are statistically greater than in the reference areas, the magnitude of these differences may not be substantial enough to produce density-dependent changes in fish diets. Gopher rockfish densities in the central California

MPAs included in this study were observed to be 1.4 to 2.0 times greater than those of the corresponding reference areas (Fig. 3, Starr et al. 2010). In contrast, Svanbäck & Bolnick (2007) documented increased specialization in stickleback diets at a high-density treatment with 3 times the number of fish as low-density treatments. MPAs do show potential for increasing fish densities to substantially greater numbers than fished areas: fish densities in protected areas have been documented to be 8 (Babcock et al. 1999), 10 (Fanelli et al. 2010), and even 14 times greater than in fished areas (Willis et al. 2003). Diet evenness, another measure of specialization, did

decrease with increasing gopher rockfish density across areas in the present study, which exhibited a 3-fold difference in density. Thus, density-driven feeding changes may yet be observed if fish densities in the central California MPAs increase over time. The relationship between fish density and individual diets may also not be a linear function, and fish densities may need to cross a threshold before trophic changes occur.

While this study primarily focused on the effects of intraspecific density on diet, interspecific interactions may also influence gopher rockfish feeding habits. Co-occurring species that exploit similar prey resources include the black-and-yellow rockfish *Sebastes chrysomelas*, brown rockfish *S. auriculatus*, China rockfish *S. nebulosus*, copper rockfish *S. caurinus*, kelp rockfish *S. atrovirens*, grass rockfish *S. rastrelliger*, treefish *S. serriceps*, and cabezon *Scorpaenichthys marmoratus* (Hallacher & Roberts 1985, Lea et al. 1999, Love et al. 2002). Monitoring of the central coast MPAs revealed that densities of these species tended to be higher inside the MPAs than outside, although these differences were not significant (Starr et al. 2010). Greater densities of interspecific as well as intraspecific competitors would presumably amplify the effects of competition inside the MPAs. However, no evidence of competitive effects, such as decreased richness or increased specialization, was observed in MPAs, suggesting that any differences in the density of other fish competitors are not substantial enough to impact gopher rockfish feeding interactions.

Competition theory lays the groundwork for increased specialization and resource use diversification by positing that individuals switch or restrict

their resource use as resources become scarce (Svanbäck & Bolnick 2007). However, prey resources may not be limiting at the areas sampled in this study. The central California coast is a highly productive system that may be able to support rockfish populations at densities greater than those observed. The finding of no significant difference in prey richness inside and outside of the MPAs suggests that a similar suite of prey types is available to gopher rockfish at nearby locations irrespective of protected status, and indicates that the greater numbers of fish inside the MPAs have not depleted any major prey groups. Moreover, increased fish densities also do not necessarily guarantee changes in their feeding ecology (Badalamenti et al. 2008). Previous findings of significant diet differences inside and outside of protected areas are likely due to habitat modification and changes in prey availability caused by trawling (Fanelli et al. 2009, 2010). However, because small invertebrate species were found to be the primary prey, the fishing practices of hook-and-line and trapping gear used in this study location were unlikely to directly affect the availability of gopher rockfish prey.

Differences in depth among the geographic locations appear to account for some of the differences in prey composition observed at the new MPAs. Fish from Año Nuevo, which were collected at shallower depths than other locations, ate more *Cancer* and porcelain crabs, which may be due to the low intertidal and shallow subtidal distribution of these species (Morris et al. 1980). Brittle stars, such as *Ophiothrix spiculata*, were important prey in fish collected at deeper depths in Point Lobos and Piedras Blancas, and indeed this species has a depth distribution that extends to over 2000 m (Morris et al. 1980). However, *Cancer* and porcelain crabs do also occur at deeper depths (90 to 100 m), and brittle stars can likewise inhabit the shallow regions of the low intertidal (Morris et al. 1980, Carroll & Winn 1989). Thus, depth alone probably does not explain the differences in prey composition among geographic locations, and other habitat features are likely important. The patterns in prey composition observed mirror those of groundfish species composition at these MPAs, where the greatest differences in species composition occurred among locations rather than inside and outside of MPAs (Starr et al. 2010). These results suggest that nearshore kelp forest and rocky reef communities are not uniform along the central California coast.

An investigation into the abundance and distribution of various prey species at each area was beyond

the scope of this study, as many of the species eaten by the gopher rockfish are small and cryptic and are not included in subtidal invertebrate surveys. Subtidal surveys conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans in the general geographic regions included in this study documented larger organisms like bat stars and anemones but not most species consumed by the gopher rockfish. Based on the assumption that a generalist predator will show little selectivity in feeding, the stomach contents of generalist feeders can be used as a means to sample the marine environment (Frid & Hall 1999, Link 2004). The large number of prey types encountered in this study supports the assumption that gopher rockfish are not highly discriminate feeders. Thus, these results provide a partial characterization of the cryptic invertebrate communities of these MPAs and reference areas, as sampled by the gopher rockfish.

The present study provides several contributions to the management of marine resources and the understanding of MPAs. This study did not document trophic changes after 35 yr of protection in the Point Lobos MPA, which suggests that trophic changes should not necessarily be expected to occur once MPAs are implemented. Furthermore, no consistent differences in feeding ecology were observed in new MPAs, despite greater densities of gopher rockfish inside 3 of the 4 MPAs surveyed. This may indicate that the food web is relatively stable at these locations, and increased densities may not necessarily be detrimental to gopher rockfish inside MPAs.

The differences in diet among geographic locations revealed in this study suggest that food web changes associated with MPAs may be location specific. This underscores the importance of considering site-specific differences when assessing the collective performance of many MPAs. California's network of MPAs, spanning the entire coastline, is now being monitored in regions; however, the differences observed among MPAs in the central California region in this study suggest it may be necessary to group MPAs at a finer geographic scale to assess their overall effects. MPAs are intended to protect the entire ecosystem within their borders, often with the added hope of increasing fish abundances. To understand the full ecological implications of establishing MPAs, it is important to know how the effects of fish abundance could influence the food web. The central California MPAs show the potential to increase the size and density of some fish species within their borders, which may eventually lead to shifts in fish feeding ecology. Accounting for location-specific differences

like those observed in this study is important to understand how each MPA performs over time and should be considered when investigating general MPA effectiveness.

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