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Dietary niche expansion of a kelp forest predator recovering from intense commercial exploitation

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Abstract. Marine ecosystems are increasingly at risk from overexploitation and fisheries collapse. As managers implement recovery plans, shifts in species interactions may occur broadly with potential consequences for ecosystem structure and function. In kelp forests off San Nicolas Island, California, USA, we describe striking changes in size structure and life history traits (e.g., size at maturation and sex change) of a heavily fished, ecologically important predator, the California sheephead (*Semicossyphus pulcher*). These changes occurred in two phases: (1) after intense commercial fishery exploitation in the late 1990s and (2) following recovery in the late 2000s, nearly a decade after management intervention. Using gut contents and stable-isotope values of sheephead and their prey, we found evidence for a dietary niche expansion upon recovery of population size structure to include increased consumption of sea urchins and other mobile invertebrate grazers by larger sized fish. By examining historical diet data and a time series of benthic community composition, we conclude that changes in dietary niche breadth are more likely due to the recovery of size structure from fishing than major shifts in prey availability. Size-dependent predator–prey interactions may have ecosystem consequences and management measures that preserve or restore size structure, and therefore historical trophic roles of key predators, could be vital for maintaining kelp forest ecosystem health.

Key words: California sheephead; fishery; niche breadth; predatory–prey interactions; San Nicolas Island, USA; sea urchin; Semicossyphus pulcher; *stable isotopes; trophic ecology.*

Introduction

In the last 15 years, studies have raised the alarm about severe overexploitation of marine resources, warning of systematic collapse of fisheries, and the ecosystem-wide consequences of overfishing (e.g., Jackson et al. 2001, Myers and Worm 2003, Frank et al. 2005). Recent research has argued that the prevailing "doom and gloom" view of a complete failure of fisheries management is unsubstantiated (Worm et al. 2009), yet recovery of fisheries has occurred infrequently, despite strong management intervention (Hutchings 2000, Worm et al. 2009). Recent syntheses highlight how the exploitation and recovery of top predators can alter food webs and ecosystem function through direct and indirect pathways (Estes et al. 2011), and these findings are beginning to inform ecosystem-based approaches to fisheries management.

Fishing is a unique type of exploitation because it is often size selective and targets the largest individuals. In addition to reducing abundance, fishing can reduce a population's size structure (e.g., Hamilton et al. 2007, Worm et al. 2009). In response to fishing, researchers have observed declines in predatory-fish body size and shifts in trophic structure (even in the absence of changes in predator biomass), highlighting the importance of size-structured interactions (Shackell et al. 2010). With recovery from overfishing or protection inside no-take marine reserves, both abundance and size structure of fished species predictably increase (Lester et al. 2009). Typically, researchers have examined how increasing predator abundance inside marine protected areas can result in increased levels of prey mortality, with cascading effects on lower trophic levels (e.g., Shears and Babcock 2002, Behrens and Lafferty 2004). What is often overlooked is that management actions resulting in changes in size structure (independent of changes in abundance) may also have profound impacts on prey populations if predator–prey interactions are size dependent (Pederson and Johnson 2006, Ling et al. 2009).

For generalist predators, dietary niche breadth (or trophic niche width) may shift following changes to size structure, if specific prey types are consumed by different predator size classes. Ontogenetic niche shifts are a common feature of many aquatic systems, and diets of generalist fish predators are often size dependent (Werner and Gilliam 1984). We hypothesized that dietary niches would expand following recovery from intense size-selective fishing, as large individuals begin to

add prey types to their diet that were previously unavailable to small-bodied gape-limited individuals. Evidence for these patterns exists in aquatic stream communities where ontogenetic shifts in diet occur for many predators, yet dietary breadth and the number of trophic links in the food web increase as a function of predator size (Woodward and Hildrew 2002). Changes in dietary niche breadth have also been shown to occur seasonally in response to shifts in prey resources (Zaret and Rand 1971) and in response to habitat fragmentation (Layman et al. 2007b), but it is less well known how population recovery from overfishing can modify size-dependent trophic relationships between predator and prey.

When combined with historical data from Cowen (1983, 1986, 1990), our studies (Hamilton et al. 2007, 2011a, b) on a California sheephead (*Semicossyphus pulcher*) population at San Nicolas Island (SNI), off southern California, USA, allowed us to address the ecological consequences of three decades of exploitation and recovery through comparison of changes in size structure, life history traits, and trophic relationships. Throughout southern California, sheephead are commonly caught in recreational and commercial fisheries. Recreational catches peaked in the 1980s and remain high in some areas, while commercial catches peaked in the late 1990s following the rapid expansion of a live-fish fishery (Alonzo et al. 2004). Given mounting concerns about overexploitation, the California Department of Fish and Game (CDFG) instituted a series of regulations in the late 1990s and early 2000s that resulted in reduced take, primarily in the commercial fishery. Commercial fishing predominated on SNI and we were thus able to observe this population through periods of different management strategies and fishing pressure.

Materials and Methods

Collections, surveys, and fishery landings

The study occurred at San Nicolas Island, located ~100 km west of Los Angeles (33°13′07″ N, 119°30′12″ W). California sheephead were collected at SNI using spears in depths of 8–20 m. Data from 1980–1982 were presented in Cowen (1990), and we followed similar collection protocols in 1998, and again in 2007, to catch representative samples of the size structure present at each site. We measured the size and mass of each individual and used Kolmogorov-Smirnov two-sample tests to compare shifts in size structure through time. Sheephead are protogynous hermaphrodites, capable of changing sex from female to male (Warner 1975). We identified sexual class by visually inspecting the gonads and with histology. Logistic regression was used to calculate the size at maturation and sex change (Caselle et al. 2011). Dorsal spines were used for aging and stable-isotope analysis. We estimated the percentage of volume of prey taxa from gut contents in 2007, according to Cowen (1983) and Hamilton et al. (2011a). To examine ontogenetic shifts in diet, we conducted a principal components analysis on the top 10 prey categories and used PC1 in a linear regression vs. fish length. Finally, we calculated dietary overlap between the 1980–1982 and 2007 gut content data following Zaret and Rand (1971).

Densities (individuals/m^2) of kelps and macroinvertebrates, and percent cover of macroalgae and sessile invertebrates were recorded on fixed transects during biannual community surveys (U.S. Geological Survey). We used these surveys to ascertain whether shifts in kelp communities could explain changes in trophic ecology, independent of shifts in sheephead size structure. Species were grouped into broad taxonomic and functional categories, and we calculated average density or percent cover from the three sites (out of seven) nearest our sheephead collections (West and East Dutch Harbor, and Daytona Beach). We report time series of changes in abundance of key taxa (urchins, sessile invertebrates, kelp, foliose red algae, and coralline algae) and a time series of PC1 (representing their combined abundance). One-way ANOVA was used to examine differences in prey abundance among the three sheephead collection periods, using benthic data for the five surveys (2.5 yr) surrounding our collections.

Commercial and recreational sheephead fishery landings data for 10 × 10 nautical miles (1 nautical mile equals 1.85 km) fishing blocks were provided by the CDFG. Because recreational landings at SNI are minimal, we focused on commercial landings in Block 813, which encompasses all collection sites.

Stable-isotope analysis

Stable isotopes are a common technique used to study dietary niches, and they provide a time- and space-integrated representation of trophic interactions. Ratios of ^{15}N to ^{14}N (i.e., δ^{15}N) are enriched with trophic transfer and can be used to estimate trophic position, while ratios of ^{13}C to ^{12}C (i.e., δ^{13}C) vary among primary producers and can be used to determine sources of dietary carbon. Sheephead dorsal spines were available for stable-isotope analysis from 1998 ($n = 55$) and 2007 ($n = 68$). Spine collagen likely integrates diet information over a period of one or more years (Koch 2007). Spines were demineralized in 0.5 mol/L HCl for ~12–15 h at 5°C, rinsed with 2:1 chloroform : methanol to remove lipids, rinsed with deionized water, lyophilized, and the resulting collagen was weighed (~0.5 mg) into tin capsules. Putative prey samples were collected in 2004 at SNI and 2008 at nearby Santa Cruz Island. Based on functional and isotopic similarities, putative prey items were classified into 11 prey types (Table 1). We rinsed and removed inedible portions of prey, and homogenized tissue in a Wiley mill following lyophilization. For reasons described in Newsome et al. (2010), we did not lipid-extract prey. [C]/[N] ratios of most prey are <4.0 and contain minimal amounts of ^{13}C-depleted lipids (Table 1; Sweeting et al. 2006).

TABLE 1. (A) Sample size, mean standard length (SL), median age, and $\delta^{13}C$ and $\delta^{15}N$ values of dorsal spine collagen for California sheephead collected in 1998 and 2007, and (B) sample size, $\delta^{13}C$, and $\delta^{15}N$ of soft tissue of common invertebrate prey of California sheephead.

Group and age class	n	Mean SL (mm)	Median age (yr)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	[C]/[N]	Gut volume with sea urchin (%)
A) Sheephead							
1998, immature	12	170	3	−12.9 (0.3)	14.7 (0.5)	2.7 (0.1)	⋯
1998, female	34	253	5	−12.7 (0.4)	14.7 (0.4)	2.8 (0.2)	⋯
1998, male	9	318	6	−12.5 (0.6)	14.6 (0.5)	2.8 (0.3)	⋯
2007, immature	3	265	3.5	−12.7 (0.6)	15.1 (0.1)	2.8 (0.1)	5.9
2007, female	35	345	7	−12.5 (0.8)	15.0 (0.5)	2.7 (0.1)	14.0
2007, male	30	453	10	−11.9 (1.0)	15.2 (0.7)	2.7 (0.2)	32.6
B) Invertebrates							
Red sea urchins, *Stronglyocentrotus franciscanus*	22			−14.4 (0.8)	11.4 (1.0)	5.9 (2.3)	
Purple sea urchins, *Strongylocentrotus purpuratus*	24			−13.0 (0.9)	11.1 (0.6)	3.9 (0.9)	
Brittle stars, *Ophiothrix* spp.	20			−12.8 (0.6)	12.1 (0.6)	5.1 (0.5)	
Cancer crabs, *C. antennarius/productus*	14			−15.2	13.0 (0.3)	4.0 (0.3)	
Kelp crabs, *Pugettia producta*	5			−14.5 (0.8)	11.3 (0.9)	4.2 (0.2)	
Brachyuran crabs, *Scyra acutifrons*	11			−17.1 (1.0)	10.4	4.4 (0.4)	
Barnacles, *Balanus* spp.	20			−19.8 (0.6)	11.8 (0.4)	3.9 (0.3)	
Chlorostoma snails, *C. eiseni/funebralis/regina*	25			−14.4 (0.7)	11.5 (0.8)	3.7 (0.2)	
California mussels, *Mytilus californicus*	22			−18.6 (1.5)	9.8 (0.8)	3.3 (0.2)	
Giant rock scallop, *Crassedoma gigantea*	12			−16.9 (0.5	10.5 (0.3)	3.2 (0.1)	
Bryozoans, *Membranipora* spp.	10			−19.3 (1.6)	7.5 (0.4)	4.4 (0.5)	

Notes: Sheephead were divided into different sexual classes to illustrate changes in diet on San Nicolas Island as a function of size and sex. Values in parentheses are SD. Included is the percentage of the gut volume composed of sea urchins from gut content analyses performed on 2007 samples (no gut contents were available from 1998 [shown with ellipses]). Mean SL and median age were not recorded for invertebrates.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were determined using a Carlo-Erba (Milan, Italy) or Costech (Valencia, California, USA) elemental analyzer (NC 2500) coupled to a Finnegan Delta Plus XL mass spectrometer (Thermo Fisher Scientific, Whaltham, Massachusetts, USA) at the Carnegie Institution of Washington (Washington, D.C., USA). Isotopic results are expressed as δ values, $\delta^{13}C$ or $\delta^{15}N = 1000 \times [(R_{sam}/R_{stan}) - 1]$, where R_{sam} and R_{stan} are the $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$ ratios in parts per thousand, or per mil (‰), of the sample (R_{sam}) and the standard (R_{stan}). The standards are Vienna-Pee Dee Belemnite (V-PDB) for carbon and atmospheric N_2 for nitrogen. The within-run standard deviation of acetanilide and alanine standards was ≤0.2‰ for $\delta^{13}C$ and $\delta^{15}N$.

To make direct isotopic comparisons among sheephead and their prey, we corrected spine collagen values for trophic discrimination and diet collagen fractionation by subtracting 3.5‰ from measured $\delta^{13}C$ and $\delta^{15}N$ values (Sholto-Douglas et al. 1991, Post 2002, Koch 2007) and present isotope values in bivariate $\delta^{13}C$ vs. $\delta^{15}N$ space. Variation in vertebrate trophic discrimination factors (SD = ~0.5‰) from laboratory- and field-based studies (Vanderklift and Ponsard 2003, Newsome et al. 2010) are small in comparison to the magnitude of isotopic variation in sheephead among our collection periods (see *Results*), and thus do not compromise our conclusions regarding niche expansion over time.

Spatial metrics

To estimate dietary niche variation at the population level, we calculated a series of spatial metrics for sheephead spines collected in 1998 and 2007. Convex hull (CH), nearest neighbor distance (NND), and distance to centroid (DC) are useful for calculating the degree of isotopic dispersion in two-dimensional bivariate space (e.g., $\delta^{13}C$ vs. $\delta^{15}N$); see Layman et al. (2007*a*) for details on how these metrics are calculated. Briefly, we used a R-based bootstrap program that incorporated the analytical precision (0.2‰) of spine collagen $\delta^{13}C$ and $\delta^{15}N$ to calculate the convex hull (or total area) and associated standard deviation for each population. Mean NND (±SD) is the mean Euclidean distance to each sheephead's nearest neighbor in bivariate space, and thus, is a measure of the overall density of consumers. Mean DC (±SD) is the mean Euclidean distance of each sheephead to the centroid of the population. We also calculated standard ellipse areas for each sheephead population using the statistical package Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011) and present mean ellipse areas (±SD).

The application of spatial metrics to isotopic data requires that the isotopic variance among putative prey sources is similar among populations, localities, or time periods (Layman et al. 2007*a*, Hoeinghaus and Zeug 2008). Our analysis of sheephead isotopic variation minimizes this potential pitfall, because, while the isotopic composition of prey could vary among years

in response to environmental conditions, the overall pattern we observe remains robust because it is driven by differences in prey ecological function (e.g., macroalgae consumer vs. filter feeder) that is manifested at the taxonomic level. Similar isotopic differences among functional groups have been observed for invertebrates collected from kelp forests in other southern and central California localities (Page et al. 2008, Newsome et al. 2009, 2010, Hamilton et al. 2011a).

RESULTS

Rapid expansion of an unregulated commercial livefish fishery in the early 1990s (Fig. 1A), to supply demand for the Asian seafood market (Alonzo et al. 2004), resulted in a striking decrease in the size distribution (K-S test, D-crit = 0.69, $P < 0.0001$) and size of maturation (291 mm standard length [SL] in 1980; 202 mm SL in 1998) and sex change (479 mm SL in 1980; 311 mm SL in 1998) of sheephead, compared to 1980 levels when fishing pressure was lower (Fig. 1B). In the late 1990s, fisheries regulations were implemented to address concerns about overexploitation. As a result of these regulations, and other factors such as escalating fuel prices and periodic military activity in the waters surrounding SNI, commercial fishery landings declined precipitously (Fig. 1A). In response, by the year 2007, sheephead exhibited a rapid recovery of size structure (K-S test, D-crit = 0.74, $P < 0.0001$) and the size at maturation (202 mm SL in 1998; 283 mm SL in 2007) and sex change (311 mm SL in 1998; 408 mm SL in 2007) to near those levels seen in the early 1980s (Fig. 1B).

Stable-isotope analysis of sheephead and putative prey sources demonstrated an expansion of the dietary niche to alternative prey types following recovery (Table 1, Fig. 2A). This expansion occurred because some fish exhibited a higher reliance on consumption of mobile invertebrates that commonly graze kelp, such as sea urchins, larger crabs, and gastropods. In contrast, fish in 1998 fed almost exclusively on small brachyuran crabs and filter/suspension feeding invertebrates. As a result, dietary niche breadth estimates were significantly larger in 2007 vs. 1998 for all spatial metrics (for CH, $F_{1,19\,998} = 123\,068.4$, $P < 0.0001$; DC, $F_{1,121} = 21.15$, $P < 0.0001$; NND, $F_{1,121} = 7.18$, $P = 0.0084$; SIBER, $F_{1,19\,998} = 147\,439.4$, $P < 0.0001$; Fig. 2A), indicating a broader population-level diet upon recovery of size structure. Primarily, this dietary expansion occurred along the δ^{13}C axis (Fig. 2A), which reflects the source of primary production contributing to the diet, and the shift was most pronounced for large males (Table 1).

For sheephead collected in 2007, we found that size-based shifts in diet measured from gut contents and stable isotopes corroborate the inferred changes in trophic ecology through time. We found a significant positive relationship between fish length and δ^{13}C, such that larger sheephead are enriched in ^{13}C ($F_{1,42} = 10.4$, $r^2 = 0.31$, $P < 0.0001$; Fig. 2B), reflecting the isotopic
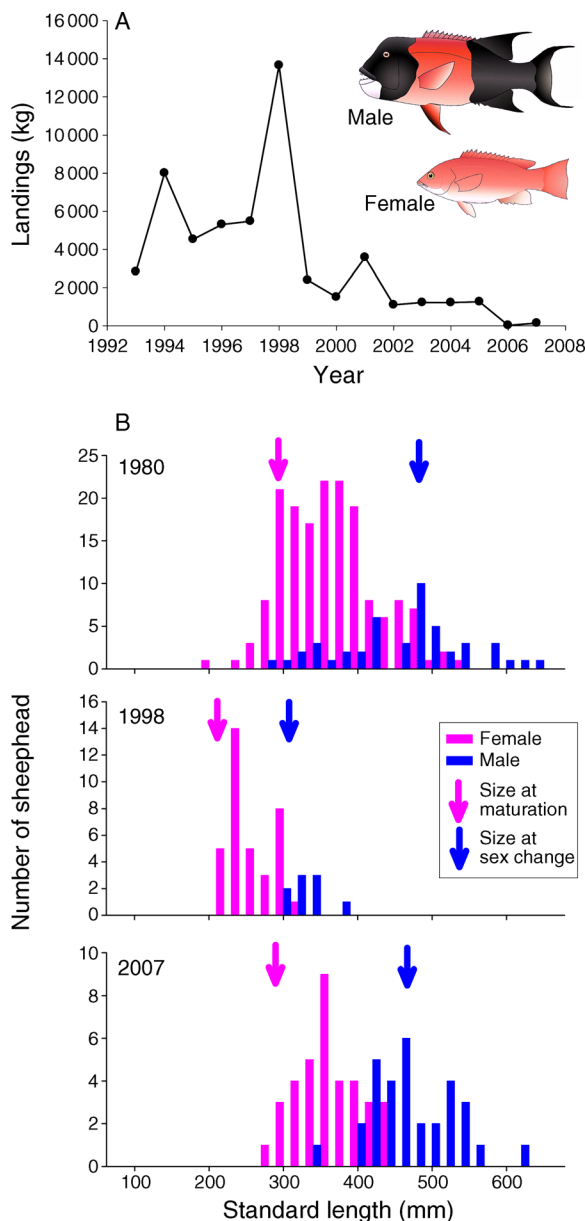

FIG. 1. Exploitation and recovery of California sheephead (*Semicossyphus pulcher*) at San Nicolas Island, California, USA. (A) Commercial fisheries landings from 1993 to 2007 from the study area, illustrating rapid exploitation and subsequent decline following management intervention. Sheephead images by Larry G. Allen. (B) Shifts in size structure of males and females, and changes in the timing of maturation and sex change of sheephead across three decades.

composition of mobile herbivores, such as sea urchins, over sessile filter feeders. In addition, a significant negative relationship was observed between sheephead length and PC1 from gut contents ($F_{1,52} = 25.2$, $r^2 = 0.33$, $P < 0.0001$; Fig. 2C). Larger sheephead consumed more sea urchins, while smaller sheephead consumed more bivalves, barnacles, and shrimp (PC1 loadings: urchins [−0.71], barnacles [0.64], bivalves [0.78], and shrimp

[0.63]). Males, which are larger in size, had a higher percentage of volume of sea urchins in their gut contents than females or immatures (Table 1). We did not find an association between fish length and PC2 from gut contents ($F_{1,52} = 1.3$, $r^2 = 0.02$, $P = 0.25$), indicating that sheephead of many size classes consumed small crabs, snails, and mesograzer crustaceans in 2007 (PC2 loadings: crabs [−0.69], gastropods [−0.43], ophiuroids [0.58], and isopods/amphipods [0.80]). Gut content data did not exist for 1998 samples; however, a comparison of data from the early 1980s and 2007, both periods when large sheephead were present, indicated a roughly similar diet diversity and composition (Appendix A), with dietary overlap equaling 0.85 (values above 0.6 indicate significant overlap; Zaret and Rand 1971).

Niche expansion could be explained by increases in the number of large sheephead capable of handling larger prey items following recovery or by changes in prey availability. Using the most comprehensive data set available on benthic community composition over three decades at our study locations, we found some evidence for gradual shifts in kelp forest assemblages over the 30-year time series (e.g., urchin density and invertebrate cover), but less evidence of major shifts in community structure during the three sheephead collection periods (Fig. 3; Appendix B). In the time windows surrounding our collections, we did not find significant differences in total sea urchin density (although red urchin density was higher in the late 2000s), kelp density, the density of other macroinvertebrates, and foliose red algal cover, but did observe declines in the cover of sessile suspension/filter feeders and increases in crustose coralline algal cover during the late 1990s (Appendix B). These trends were reflected in the time series of PC1 of key benthic taxa (PC1 loadings: urchins [−0.67], coralline algae [−0.29], kelp [0.69], red algae [0.55], sessile inverts [0.42]; Fig. 3F). Shifts in sessile invertebrates were primarily driven by declines in the sea cucumber *Pachythyone rubra* and increases in tube-dwelling polychaetes (Appendix B).

DISCUSSION

We attribute the reduction in sheephead size structure and subsequent alteration of life history traits to fishing, because similar life history shifts occurred at other heavily fished southern California locations during the study period (Hamilton et al. 2007). In contrast, size structure and the timing of maturation and sex change were not observed to change at a lightly fished location in Baja California. Sheephead size structure recovered at SNI after fishing pressure was reduced in 1998, and age data from 2007 indicated most individuals were <10 years old (Table 1), and thus recruited to the population as commercial harvest abated. This rapid recovery of size structure (~140 mm increase in mean length) in <10 years time was likely facilitated by the rich prey resource base and high productivity at SNI (Cowen 1986), which lies within the California Current. Sheephead grow

faster at SNI than all other locations previously studied (Cowen 1990, Caselle et al. 2011, Hamilton et al. 2011b). Shifts in the timing of sex change also occurred within a generation (from 311 to 408 mm SL), returning to near the historic value of 479 mm SL. These results highlight the potential for rapid and plastic responses of life history traits to fishing, such as the timing of sex change. Sheephead have relatively small home ranges (Topping et al. 2005) and sex change is thought to be under social control, similar to many wrasses (Robertson 1972). The timing of sex change is thus determined by the structure of local mating groups, which likely contributes to the observed plasticity in this trait.

We conclude that the expansion of dietary niche breadth occurred primarily in response to size-selective fishing rather than large-scale changes in prey availability. Crabs and sea urchins were prevalent in sheephead diets in 1980–1982 (Cowen 1983, 1986; Appendix A). Cowen (1986) showed that sheephead predation had little impact on an abundant crab standing stock at SNI; however, experimental removals of sheephead from a large reef on SNI demonstrated that sheephead predation could control urchin population abundance and sheltering behavior (Cowen 1983). In the early 1980s, urchin densities were relatively low on SNI (Fig. 3; Appendix B) and few urchins remained exposed to large sheephead predators outside cracks and crevices (Cowen 1983). Similar observations of the importance of sheephead predation in controlling purple and red urchin populations have been reported from other southern California locations (Tegner and Dayton 1981). In 1998, during the peak of the sheephead fishery, isotopic data indicated a dietary reliance on small brachyuran crabs (similar to the 1980s) and suspension/filter feeding invertebrates. Interestingly, there was a notable lack of urchins or other mobile grazers in the diet (Fig. 2A), despite survey evidence indicating the prevalence of these prey types in the environment (Fig. 3). The isotopic spatial metrics confirmed that there was little variation in the diet following a contraction in sheephead size structure. Subsequently, a dietary niche expansion occurred from 1998 to 2007 following a reduction in fishing pressure, and it was not accompanied by large-scale changes to the kelp forest prey base. Increases in $\delta^{13}C$ values in 2007 (Fig. 2A), along with higher values of all spatial metrics, showed that sheephead expanded their dietary niche to include larger mobile grazers. With large fish reappearing at SNI by 2007, sheephead diets more closely reflected those reported by Cowen (1983, 1986) from pre-fishing time periods (Appendix A). The results highlight the utility of using recently developed spatial metrics to characterize changes in dietary niche breadth with isotopic data (Layman et al. 2007a, b, Jackson et al. 2011).

The broad shifts in sheephead diets we observed reflect size-specific differences in trophic interactions. At SNI and eight other locations throughout southern California, urchins were consistently found in a greater
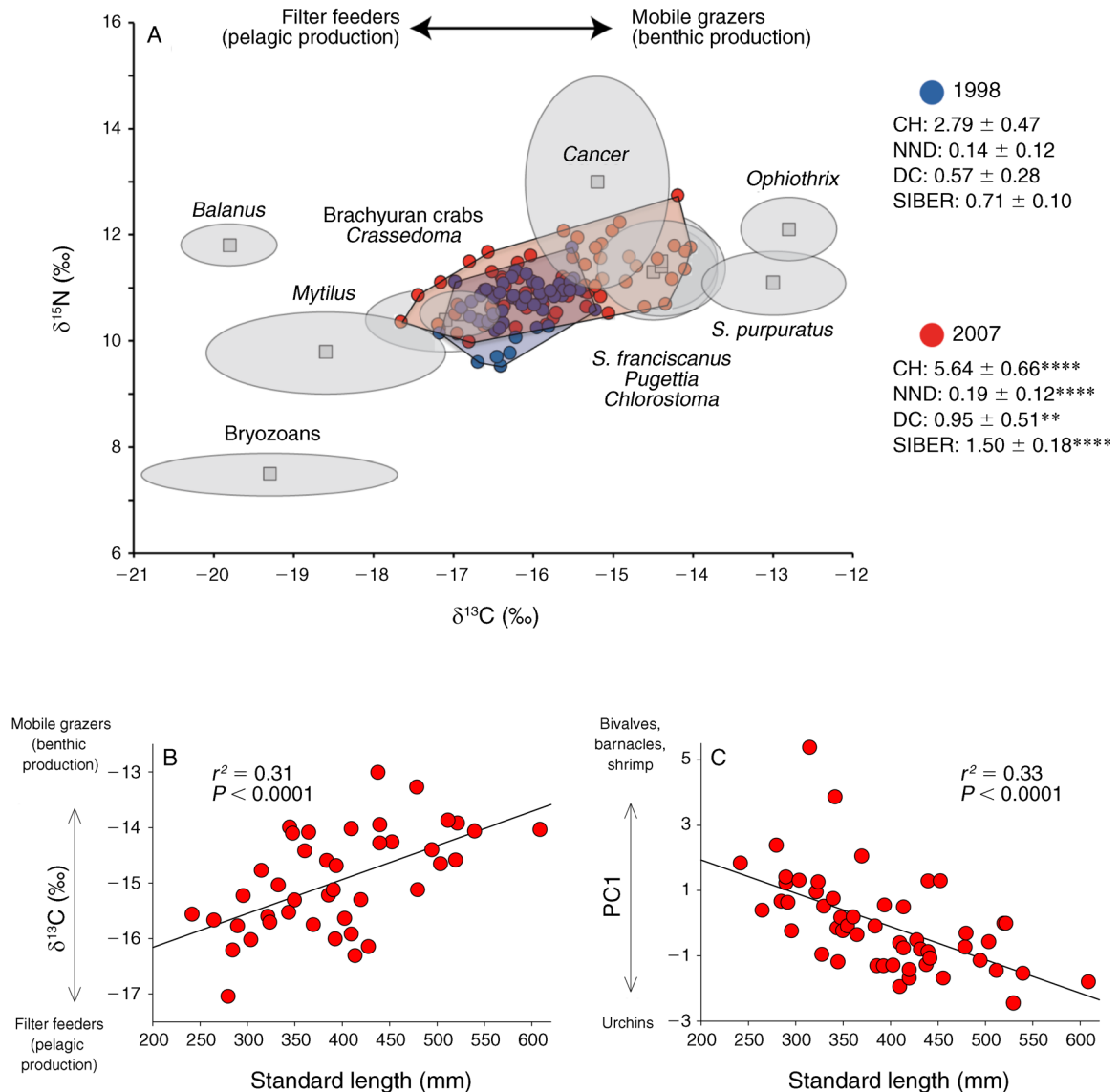
Fig. 2. Dietary niche expansion and size-based shifts in trophic ecology. (A) Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of putative prey items and sheephead spine collagen from 1998 and 2007. Sheephead isotope values were corrected for trophic discrimination and diet-collagen fractionation and are presented in prey space, such that overlap indicates likely prey sources contributing to sheephead diets. Spatial metrics ($\pm$SD) for sheephead: convex hull (CH), nearest neighbor distance (NND), distance to centroid (DC), and standard ellipse area (SIBER). A significant increase in spatial metrics from 1998 to 2007 is indicative of a dietary niche expansion. See Table 1 for common and full scientific names. (B) Relationship between fish length and $\delta^{13}C$ from stable isotopes in 2007 indicates that larger sheephead are enriched in ^{13}C, consistent with an ontogenetic diet shift toward consumption of larger mobile invertebrates that consume kelp over filter/suspension-feeding invertebrates and small brachyuran crabs. (C) Relationship between fish length and principal component 1 (PC1) from gut contents in 2007 indicate that dietary shifts occur from sessile filter feeders (e.g., bivalves) and small crustaceans (e.g., barnacles and shrimp) to larger mobile invertebrates (e.g., sea urchins) with increases in sheephead size.

     ** $P < 0.01$; **** $P < 0.0001$.

proportion of the gut contents of larger fish, while sessile suspension/filter feeders dominated the diet of smaller fish, and prey such as brachyuran crabs were eaten by all size classes (Fig. 2C; Hamilton et al. 2011a). Tegner and Dayton (1981) described predation by sheephead on sea urchins in the Pt. Loma kelp forest, observing that large males were capable of consuming all sea urchin size

classes, while smaller females exhibited increased handling times and only consumed smaller urchins, which are typically unavailable and remain hidden under the spine canopy of large adults. In contrast, Cowen (1986) reported that sheephead populations in Baja California did prey on sea urchins, despite being relatively small bodied; unfortunately, size-specific diet analyses were
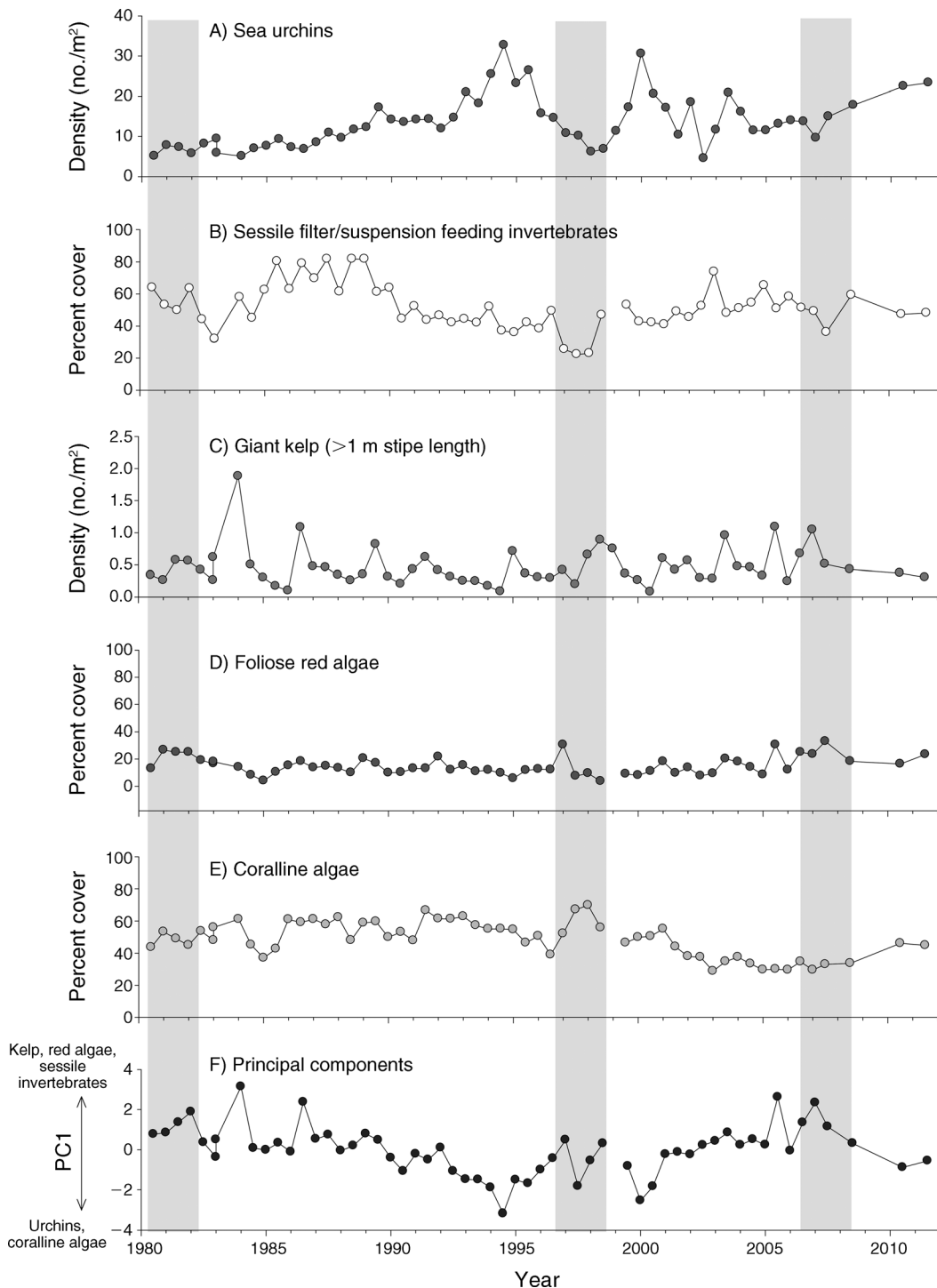
FIG. 3. Time series of density and percent cover of benthic taxa at San Nicolas Island from 1980 to 2011: (A) sea urchins, (B) sessile invertebrate filter/suspension feeders, (C) giant kelp, (D) foliose red algae, (E) coralline algae, and (F) principal component scores of the above taxonomic categories. Gray-shaded bars indicate the five survey periods that overlap with the three sheephead collections at San Nicolas Island. See Appendix B for statistical analysis comparing density or percent cover among these time periods.

not reported. Interestingly, the primary species of urchin preyed upon by sheephead in Baja California (*Centrostephanus coronatus*) forages more actively, which may make it more susceptible to sheephead predation than the *Stronglyocentrotus* species consumed at SNI and other southern California locations (Cowen 1986). Although the result of increasing dietary niche breadth following the recovery of sheephead is not surprising given our understanding of ontogenetic diet shifts in size-structured populations (Werner and Gilliam 1984), to our knowledge, this is one of the few records documenting niche expansion in response to the reduction of fishing pressure.

Because many predatory fish are gape limited and population recovery often includes an increase in size structure, dietary niche shifts may be common and may have far-reaching consequences for ecosystem structure and function. For rock lobsters that consume hard-shelled prey similar to sheephead, consumptive capabilities are also often size dependent, affecting the propensity for phase shifts from kelp beds to urchin barrens (Pederson and Johnson 2006, Ling et al. 2009). It has been argued that overexploitation of sea urchin predators such as sheephead and spiny lobster (*Panulirus interruptus*) in southern California has increased the susceptibility of kelp beds to deforestation through overgrazing (Tegner and Dayton 2000, Jackson et al. 2001, Behrens and Lafferty 2004; but see Foster and Schiel 2010 for an alternative perspective). At our study locations on SNI, sea urchin density did not vary among our three collection periods, but the time series (Fig. 3) indicated sea urchins were generally more abundant (and more variable) through much of the 1990s and early 2000s after the commercial sheephead fishery expanded. In addition, crustose coralline algal cover peaked in the mid-1990s, and then declined as sheephead recovered. Similar declines in crustose coralline algal cover have been reported with urchin predator recovery inside New Zealand MPAs (Shears and Babcock 2002). At SNI, these changes could reflect community responses to variation in the abundance and size structure of sheephead; however, those effects are difficult to disentangle from environmental forcing (e.g., El Niño Southern Oscillation and Pacific Decadal Oscillation) and foraging effects of other urchin predators, such as sea otters (Tinker et al. 2008, Newsome et al. 2010), which were introduced to SNI in the late 1980s. Ultimately, large-scale recovery of predator abundance and size structure through sound fisheries management (e.g., increased size limits) and conservation measures (e.g., no-take marine reserves) may serve to increase top-down control on prey with cascading effects on community structure, thereby enhancing ecosystem resilience and the services they provide to society.

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SUPPLEMENTAL MATERIAL

Appendix A

A table comparing the gut contents of California sheephead in 1980–1982 and 2007 (*Ecological Archives* E095-015-A1).

Appendix B

A comparison of density and percent cover of key benthic taxa from the five survey periods overlapping the California sheephead collections (*Ecological Archives* E095-015-A2).