

Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System

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ABSTRACT

Diets of top predators may be useful indicators to the availability of forage fish in marine ecosystems. Juvenile rockfish (young-of-the-year *Sebastes* spp.) compose a significant part of the diet for many predators in the central California Current, including chinook salmon (*Oncorhynchus tshawytscha*), and several species of marine birds and mammals. Herein, we develop annual indices of juvenile rockfish relative abundance by collating time series data sets on: (i) the proportion of rockfish in the diet of three species of seabirds breeding on Southeast Farallon Island (1975–2002); (ii) the number of rockfish in chinook salmon stomachs (1980–99); and (iii) the abundance of rockfish captured in scientific mid-water trawl net surveys (1983–2002). We used Principal Component Analysis (PCA) to combine indices, and refer to these as ‘Multivariate Rockfish Indices’ (MRI). Combining time series verifies the patterns shown by each alone and provides a synoptic perspective on juvenile rockfish relative abundance. The diets of predators with the largest foraging ranges (Common Murre, *Uria aalge*) and chinook salmon co-varied strongly with the net samples, and appear to be the best indicators. The salmon also sampled species of *Sebastes* not caught in the nets. The MRI reveals interannual variability in juvenile rockfish abundance, a substantial decline in abundance in the 1990s, and a partial recovery in the early 2000s. Predator-based sampling is a cost-effective enhancement of scientific net sampling.

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INTRODUCTION

Rockfish (*Sebastes* spp.) are important ecologic and economic components of North Pacific large marine ecosystems. In the California Current, juvenile rockfish form critical prey resources for predatory fish (Merkel, 1957; Lenarz, 1980; Brodeur, 1991; Hunt *et al.*, 1999), marine birds (Ainley *et al.*, 1995; Sydeman *et al.*, 2001; Miller and Sydeman, 2004), and mammals (Pike, 1958; Lowry *et al.*, 1991). As adults, many of the 70+ species are commercially and recreationally harvested. Because of delayed maturation and extreme longevity, many rockfish species are vulnerable to overexploitation. Populations appear to be structured by cohort strength, with highly variable annual reproductive success (and presumably recruitment; Woodbury and Ralston, 1991; Ralston and Howard, 1995; Sakuma and Ralston, 1995; Yoklavich *et al.*, 1996). As a result of exploitation and temporal environmental variability, many rockfish stocks in the California Current have declined and are now considered ‘over-fished’ (<http://www.pcouncil.org>).

Fisheries-independent data are available for stock assessment. Since the mid-1980s, mid-water trawl net surveys have been used to assess interannual variability in rockfish abundance off north-central California (Ralston and Howard, 1995; Field *et al.*, in press). In the dynamic central California Current, where Ekman transport can be substantial (Schwing *et al.*, 2000), advection of larval forms may reduce net-based abundance estimates (Ainley *et al.*, 1993; Sakuma and Ralston, 1995; Yoklavich *et al.*, 1996). Therefore, supplementary indices are desirable.

Food habits of top predators may complement the traditional net sampling approach. Variation in seabird diets, and life history parameters, may reflect prey availability in the environment (Furness and

Camphuysen, 1997; Furness and Tasker, 2000). Diet composition may provide direct information on prey availability. Indeed, interannual changes in the proportions of different prey items in marine bird diets indicate variation in forage fish abundance (e.g. Hatch and Sanger, 1992; Montevicchi and Myers, 1995, 1996; Barrett, 2002; Miller and Sydeman, 2004). However, much of the previous research has inferred, rather than demonstrated, links between forage fish abundance and diet composition (Anderson *et al.*, 1980, 1982; Cairns, 1987, 1992; Barrett and Krasnov, 1996).

Predatory fish may also serve as indicators of forage fish abundance (Fahrig *et al.*, 1993; Roseneau and Byrd, 1997; Frid and Hall, 1999). In the northwestern Atlantic, long-term studies of cod (*Gadus morhua*) diet have shown declines of euphausiids and increases in herring in the Gulf of St Lawrence (Hansen and Chouinard, 2002), corresponding with changes in the abundance of these prey in the environment. Communities of predatory fish have also been examined to infer long-term temporal and spatial variability in benthic community dynamics (Link, 2004). In the California Current, several species of salmon are predators of young-of-the-year rockfish, and could provide additional indices of abundance. Young-of-the-year rockfish were present in half of the adult chinook salmon diet samples collected in the vicinity of San Francisco, California in June and July 1955 (Merkel, 1957), and elsewhere in the California Current more recently (Brodeur and Percy, 1992; Hunt *et al.*, 1999).

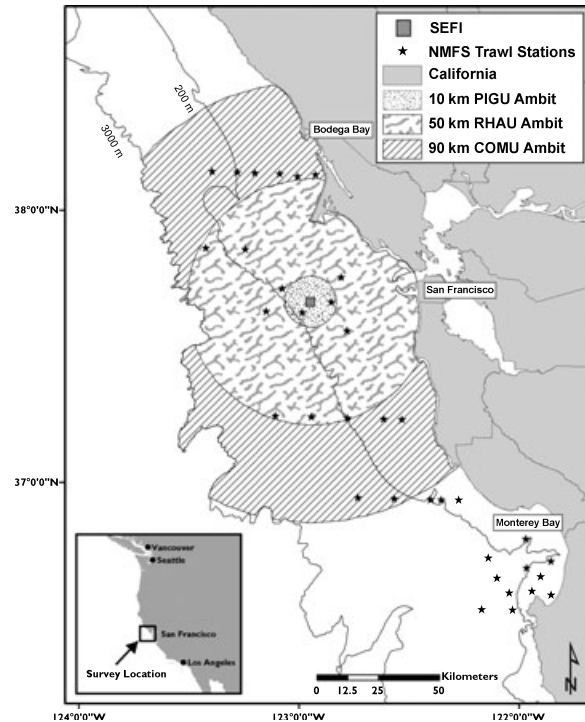
Herein, we test the hypothesis that the diets of marine birds and chinook salmon provide indices to the relative abundance of pelagic juvenile rockfish. We consider two primary questions: (i) what are the functional relationships between the take of juvenile rockfish by seabirds and salmon relative to abundance as measured by mid-water trawl net surveys, and (ii) does combining predator diets and mid-water trawl net surveys confer any benefits to understanding interannual and longer-term variability in rockfish reproductive success in this region of the California Current?

METHODS

Study area

We conducted this research in the northern-central California Current System (CCS), bounded in the south by Monterey Bay and extending northwards to Bodega Bay (Fig. 1). The study area included the wide continental shelf of the Gulf of the Farallones and

Figure 1. Map of central California and the Gulf of the Farallones showing the location of National Marine Fisheries Service trawl net sampling stations, and the estimated foraging grounds of Common Murre (COMU), Pigeon Guillemot (PIGU), and Rhinoceros Auklet (RHAU). SEFI, Southeast Farallon Island.



adjacent waters. Seabirds were sampled at the Farallon Islands, the largest seabird colony in the continental U.S. Salmon were sampled in the Gulf of the Farallones.

Time series

Seabird diet

PRBO Conservation Science (Stinson Beach, California) has conducted studies of seabird food habits on Southeast Farallon Island, 42 km west of San Francisco (37°42'N, 123°00'W) each year since 1972 (Ainley *et al.*, 1990). Common Murres (*Uria aalge*) and Pigeon Guillemots (*Cephus columba*) provision young with single prey items brought to the colony; we identified forage fish by stationing observers 10–30 m from feeding parents. Because it is difficult to identify juvenile rockfish to the species level when not in the hand, we have limited information on which rockfish species comprise the diet of murre and guillemot offspring, although most are likely *S. jordani*, *S. entomelas*, and *S. flavidus* (Table 1). Since 1987, we have also collected fish from Rhinoceros Auklets (RHAU;

Table 1. List of rockfish species (*Sebastes* spp.) found by different sampling methods: Rhinoceros Auklet (RHAU), salmon, and trawl net surveys.

Common name	Scientific name	Sampling methods
Brown rockfish	<i>S. auriculatus</i>	RHAU, salmon, trawls
Aurora rockfish	<i>S. aurora</i>	Salmon
Copper rockfish	<i>S. caurinus</i>	RHAU, salmon, trawls
Dark-blotched rockfish	<i>S. crameri</i>	Salmon, trawls
Greenstriped rockfish	<i>S. elongatus</i>	Salmon
Widow rockfish	<i>S. entomelas</i>	RHAU, salmon, trawls
Yellowtail rockfish	<i>S. flavidus</i>	RHAU, salmon, trawls
Chilipepper	<i>S. goodei</i>	Salmon, trawls
Squarespot rockfish	<i>S. hopkinsi</i>	RHAU, salmon, trawls
Shortbelly rockfish	<i>S. jordani</i>	RHAU, salmon, trawls
Black rockfish	<i>S. melanops</i>	RHAU, salmon, trawls
Blue rockfish	<i>S. mystinus</i>	RHAU, salmon, trawls
Speckled rockfish	<i>S. ovalis</i>	RHAU, salmon
Bocaccio	<i>S. paucispinis</i>	RHAU, salmon, trawls
Canary rockfish	<i>S. pinniger</i>	Salmon, trawls
Redstripe rockfish	<i>S. proriger</i>	Salmon
Rosy rockfish	<i>S. rosaceus</i>	Salmon
Yelloweye rockfish	<i>S. ruberrimus</i>	Salmon
Bank rockfish	<i>S. rufus</i>	RHAU, trawls
Stripetail rockfish	<i>S. saxicola</i>	RHAU, salmon, trawls
Halfbanded rockfish	<i>S. semicinctus</i>	RHAU, trawls
Pygmy rockfish	<i>S. wilsoni</i>	Salmon, trawls
Sharpchin rockfish	<i>S. zacentrus</i>	Salmon

Cerorhinca monocerata) provisioning offspring, and have identified these prey items to species. Rhinoceros Auklets carry multiple fish (and often multiple species) in each 'bill load'. The percentage of the diet composed of juvenile rockfish was estimated by dividing the number of rockfish observed/collected by the total number of forage fish identified in the diet for each species each year. We calculated the long-term mean take of juvenile rockfish for each species, and expressed the annual data as an anomaly (annual – long-term mean) statistic (Fig. 2).

Salmon diet

Fisheries biologists from the U.S. National Marine Fisheries Service (NMFS), Santa Cruz Laboratory (P. Adams, T. Laidig, and K. Silberberg) identified whole fish in stomachs of adult chinook salmon captured by four Commercial Passenger Fishing Vessels (CPFV) in the vicinity of the Farallon Islands from 1980 through 1999 (Fig. 2). The total number of stomachs, number of empty stomachs, number of stomachs containing at least one juvenile rockfish, and the number of stomachs with other prey items (no rockfish) were recorded (Table 2). Juvenile rockfish found in the stomachs were removed and placed in alcohol for subsequent identification. This 20-yr time series is expressed as the mean number of juvenile rockfish counted per salmon stomach containing juvenile

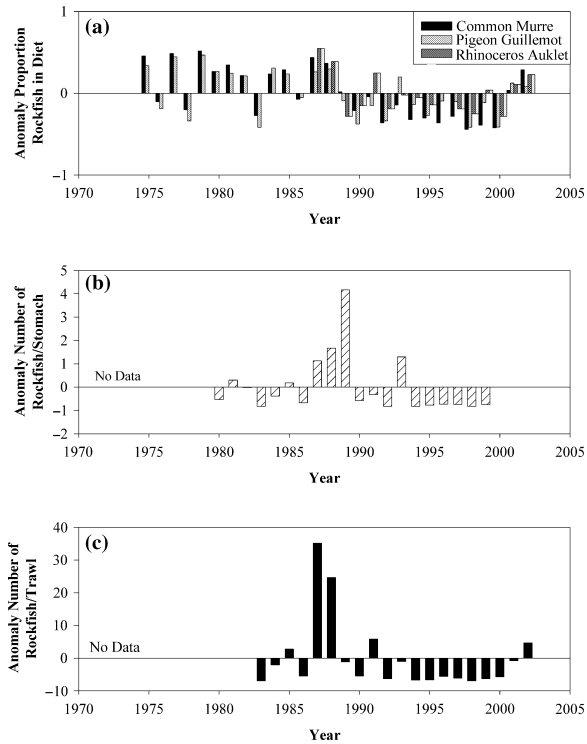
rockfish per year. A total of 6484 salmon stomachs were sampled and 21 rockfish species identified (Table 1).

Trawl net sampling

Since 1983 NMFS, Santa Cruz has conducted standardized mid-water trawl net surveys for pelagic juvenile *Sebastes* (Field *et al.*, in press). From 1986 to 2002, NMFS conducted three sequential 'sweeps' through the study area, sampling young-of-the-year class abundance at stations (Fig. 1). Only fish larger than 20 mm standard length (SL) are included in catch rate calculations due to selective properties of the cod-end liner (0.95 cm stretched mesh). This size also generally coincides with transformation from the late larval to pelagic juvenile stage (Moser *et al.*, 1977). Sampling was completed in approximately 30 days at sea, and typically began in mid-May and lasted through early mid-June. The target depth for the trawl net surveys was 30 m, although a few tows were made at 10 and 100 m (NMFS unpublished data).

Pelagic juvenile rockfish catches were adjusted to account for variability in the length and age composition of the catch. To accomplish this, individual fish ages were predicted from SL by using linear inverse growth curves (i.e. age = $f[SL]$) that were estimated for each species in each year. Specifically, the predicted age of species s in year y at standard length l is $\hat{\tau}_{syl} = a_{sy} + b_{sy}l$, where a_{sy} and b_{sy}

Figure 2. Anomalies of: (a) the proportion of juvenile rockfish in seabird offspring diet (1975–2002); (b) the number of rockfish per salmon stomach with rockfish (1980–99); and (c) the standardized number of juvenile rockfish caught in trawl net surveys (1983–2002). In each case, anomalies represent deviations from the long-term mean for each time series.



were estimated by least-squares regressions of age-length data gathered from microscopic examination of otolith daily increments (see Laidig *et al.*, 1991; Woodbury and Ralston, 1991). For each haul and each species sampled (subscripts not included), abundances of fish of different ages were adjusted to a common age by using an exponential model with constant mortality rate Z , i.e.

$$N_l^* = N_l \exp[-Z(\tau^* - \hat{\tau}_{syl})],$$

where N_l^* is the adjusted number of individuals of length l , N_l is the unadjusted number, and τ^* is the common age to which abundances were adjusted. In all calculations τ^* was set equal to 100 days, which is generally representative of the pelagic juvenile stage during May–June (Woodbury and Ralston, 1991) and Z was fixed at 0.04 day^{-1} . This latter figure was obtained by interpolation of larval and settled juvenile mortality rates (Adams and Howard, 1996; Ralston *et al.*, 2003). The N_l^* were then summed over all lengths occurring within a haul, yielding the haul-

Table 2. Number of salmon stomachs sampled between 1980 and 1999, number of stomachs that contained at least one rockfish, and number of empty stomachs.

Year	Total number	With Rockfish	Empty
1980	144	34	110
1981	406	266	140
1982	374	186	188
1983	0	0	0
1984	456	133	323
1985	506	169	337
1986	141	33	108
1987	883	392	491
1988	993	453	540
1989	517	287	230
1990	153	15	138
1991	637	210	427
1992	0	0	0
1993	457	127	420
1994	0	0	0
1995	250	5	245
1996	60	5	55
1997	457	48	409
1998	0	0	0
1999	50	2	48

specific catch of each species sampled, adjusted for variability in length/age composition. Finally, the 35 trawl net stations were divided amongst seven spatial strata and the stratified mean and variance calculated (Cochran, 1977).

Abundance estimates were derived by taking the largest of three stratified mean values (i.e. per sweep estimate) obtained each year from 1986 to 2002 (Ralston and Howard, 1995). In 1983–85, only a single sweep through the study area was conducted (no replication), and the value obtained for that survey was used (Fig. 2). Twenty-seven rockfish species have been identified from these net samples, with 16 frequently captured (Table 1).

Statistical analyses

We transformed (natural log) the salmon diet and trawl net counts of juvenile rockfish. For the seabird data, we used raw proportions as transformations did not serve to improve normality (PRBO unpublished data). We used univariate regression analysis to model the co-variance between the five indices (three seabirds, salmon, and trawl nets). We fit linear and curvilinear functions. To derive combined indices of juvenile rockfish abundance we used Principal Component Analysis (PCA). The resulting Principal Component (PC 1 in all cases) represents a linear

combination of the original set of variables, with eigenvalues representing the amount of variance in the original data set explained by each PC (Affi and Clark, 1996). Initially, we derived four combined indices for different time periods; we refer to these as 'Multivariate Rockfish Indices' (MRI). *MRI 1* reflects 20 yr (1980–99), and includes murre, guillemot, and salmon diet (excludes auklet diet and trawl net estimates due to the shorter duration of these time series). *MRI 2* reflects 17 yr (1983–99), and includes murre, guillemot, salmon, and trawl net surveys. *MRI 3* reflects 16 yr (1987–2002) and diet data from murre, guillemots, auklets, and trawl net surveys. *MRI 4* reflects 13 yr (1987–99), and includes data from all sources. We fit polynomial regressions to illustrate temporal trends in these MRI (including year and year² as independent variables). Subsequently, to examine the contribution of each original index to *MRI 4*, we created five more MRI by sequentially removing each original index from analysis. *MRI 5* excludes murre, *MRI 6* excludes guillemots, *MRI 7* excludes auklets, *MRI 8* excludes salmon, and *MRI 9* excludes trawl net surveys. As above, for *MRI 5*–*MRI 9*, we fit polynomial regressions to illustrate temporal trends, and evaluated the relative fit of each model using the coefficient of determination (R^2). All statistical tests were performed using STATA v. 7.0 (Stata Corporation, 2002); P -values of ≤ 0.05 were assumed to be significant.

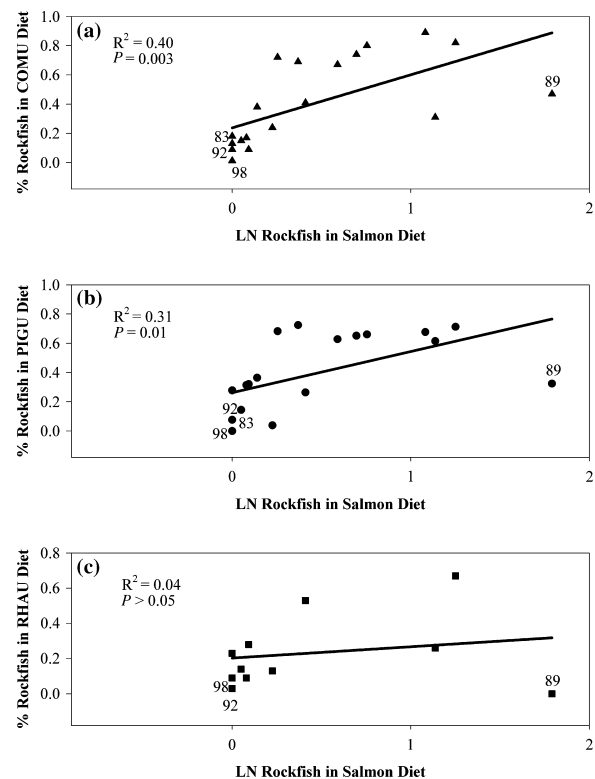
RESULTS

A total of 23 species of *Sebastes* were identified in bird, salmon, and trawl net samples; 13 species were identified in the auklet diet. Six species found in the salmon stomachs were not sampled by trawl nets or birds (Table 1). Relative rockfish abundance in the study area, as reflected by the seabird diet, salmon diet, and rockfish trawl net surveys, was highly variable from year to year, with long-term trends evident as well. In general, rockfish abundance in seabird diets was high before 1989, declined in the 1990s, and increased again, although in the early 2000s it remained at a lower level than in the 1980s (Fig. 2a). Prior to the late 1980s, rockfish abundance in the seabird diets was also low in 1976, 1978, and 1983 (1976 and 1983 were El Niño years). In trawl net surveys and salmon diet, relative rockfish abundance was generally high between 1985 and 1989, declined in the 1990s, and increased again in the early 2000s (Fig. 2b,c). In the salmon and trawl net surveys rockfish abundance was also reduced in 1983, a strong El Niño year.

Co-variation between predators

There was substantial co-variation in the proportion of rockfish in the seabird diets (murre/guillemot: $R^2 = 0.76$, $P < 0.001$, $N = 30$ yr; murre/auklet: $R^2 = 0.67$, $P < 0.001$, $N = 16$; guillemot/auklet: $R^2 = 0.61$, $P < 0.001$, $N = 16$). There were 4 yr (1983, 1992, 1994, and 1998), three of them strong El Niño events (1983, 1992, and 1998; <http://www.cpc.ncep.noaa.gov>), in which the salmon stomachs contained no juvenile rockfish (Table 2). In 1989, the salmon take of juvenile rockfish was considerably higher than that by the seabirds. Therefore, we tested for co-variation between salmon and seabirds both including and excluding 1989. When 1989 was excluded, the salmon time series positively co-varied with seabirds (murre/salmon: $R^2 = 0.57$, $P < 0.001$, $N = 20$; guillemot/salmon: $R^2 = 0.57$, $P < 0.001$, $N = 20$; auklet/salmon: $R^2 = 0.46$, $P = 0.005$, $N = 13$). Including 1989, the relationships were not as strong (murre/salmon: $R^2 = 0.40$, $P = 0.003$, $N = 21$; guillemot/

Figure 3. Relationship between juvenile rockfish ingested by salmon and seabirds: (a) Common Murre (COMU), (b) Pigeon Guillemot (PIGU), and (c) Rhinoceros Auklet (RHAU). El Niño years (1983, 1992, and 1998; <http://www.cpc.ncep.noaa.gov>) are highlighted, as is 1989, an apparent outlier.



salmon: $R^2 = 0.31$, $P = 0.01$, $N = 21$; auklet/salmon: $R^2 = 0.04$, $P > 0.05$, $N = 14$; Fig. 3a–c).

Co-variation between predators and trawl net surveys

There were positive relationships between juvenile rockfish in the seabird and salmon diets and estimates of abundance based on the mid-water trawl net survey (Fig. 4a–d). For murre, the best fit was linear ($y = 0.037 + 0.227x$, $R^2 = 0.81$, $P < 0.001$). For guillemots and auklets, the best fits were curvilinear ($y = 0.053 + 0.274x - 0.030x^2$, $R^2 = 0.63$, $P < 0.001$; $y = 0.146 - 0.053x + 0.062x^2$, $R^2 = 0.78$, $P < 0.001$, respectively). The best relationship between rockfish in salmon stomachs and trawl net surveys was also curvilinear ($y = 0.053 + 0.274x - 0.030x^2$, $R^2 = 0.62$, $P < 0.001$).

Time-varying Multivariate Rockfish Indices

The first four MRIs (MRI 1–MRI 4) showed relatively similar eigenvalues and factor loadings on the original time series (range: 0.40–0.61; Table 3). MRI 3 (1987–2002) accounted for 87% of the variance in the original data, but the others were also quite similar (range: 0.79–0.82). When plotted through time, these

MRI demonstrate a decline in relative abundance from 1987 to 2000 (Fig. 5), and an increase in 2001 and 2002 (MRI 3, Fig. 5c). MRI 3, with a period of 16 yr and an obvious concave trend ($R^2 = 0.63$, $P = 0.002$) and MRI 4, with a period of 13 yr and a declining trend ($R^2 = 0.70$, $P = 0.002$; Fig. 5d), showed the best fit to the data.

Time-invariant Multivariate Rockfish Indices

Controlling for period (1987–99) and removing each index sequentially did not alter patterns of decreasing pelagic juvenile *Sebastes* abundance though the 1990s (Fig. 6). The original indices had very similar factor loadings (range: 0.44–0.55) on MRI 5–MRI 9 (Table 4). Notably, the eigenvalues (and corresponding variances explained) by MRI 5 (excluding murre) and MRI 9 (excluding trawl net surveys) were lower than the MRI developed including these indices. By excluding guillemots, and especially auklets and salmon, the proportion of the variance explained by the MRI increased noticeably (by 4–9%). In regressing these against time (year), MRI 5 (no murre) had an $R^2 = 0.50$ ($P = 0.007$); MRI 6 (no guillemots), $R^2 = 0.64$ ($P = 0.001$); MRI 7 (no auklets), $R^2 = 0.59$,

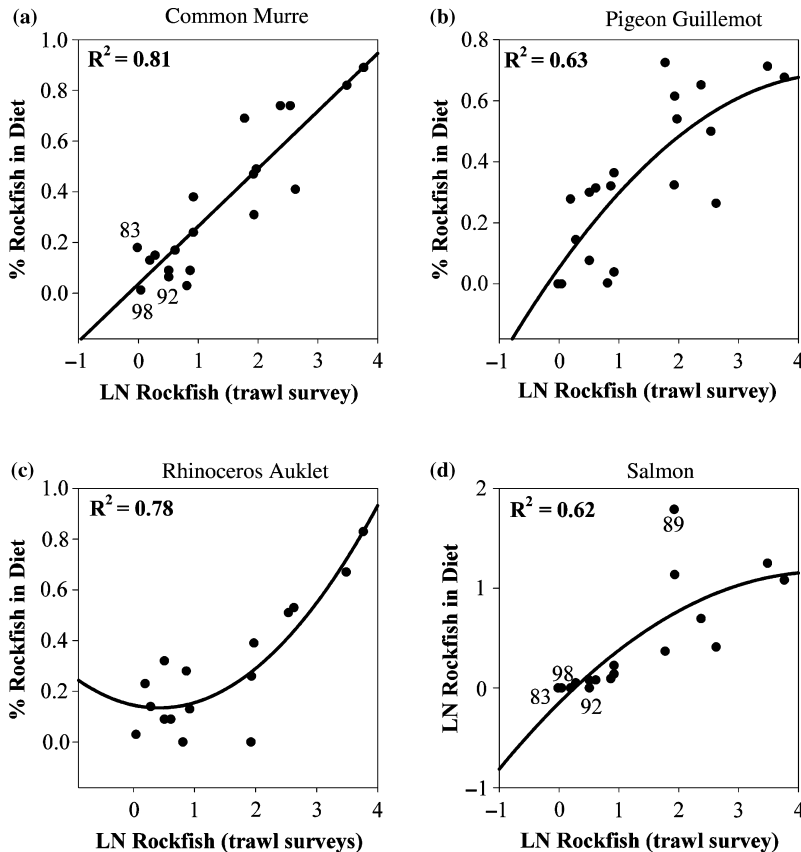


Figure 4. Relationship between juvenile rockfish abundance in the environment (based on National Marine Fisheries Service trawl net surveys) and take by seabirds (a–c) and salmon (d).

Table 3. Principal Component Analysis including (eigenvalue, variance explained, and factor loadings for PC 1) that includes the diet of murre, guillemots, and salmon (1980–99; MRI 1); the diet of murre, guillemots, salmon, and trawl net surveys (1983–99; MRI 2); the diet of murre, guillemots, auklets, and trawl net surveys (1987–2002; MRI 3); all indices (1987–99; MRI 4).

	1980–99 (MRI 1)	1983–99 (MRI 2)	1987–2002 (MRI 3)	1987–99 (MRI 4)
Eigenvalue	2.37	3.29	3.48	3.99
Proportion of variance	0.79	0.82	0.87	0.80
Common Murre	0.61	0.52	0.51	0.48
Pigeon Guillemot	0.60	0.49	0.48	0.45
Rhinoceros Auklet	ND	ND	0.49	0.41
Salmon	0.52	0.46	ND	0.40
Trawl Net Surveys	ND	0.53	0.51	0.49

ND, no data.

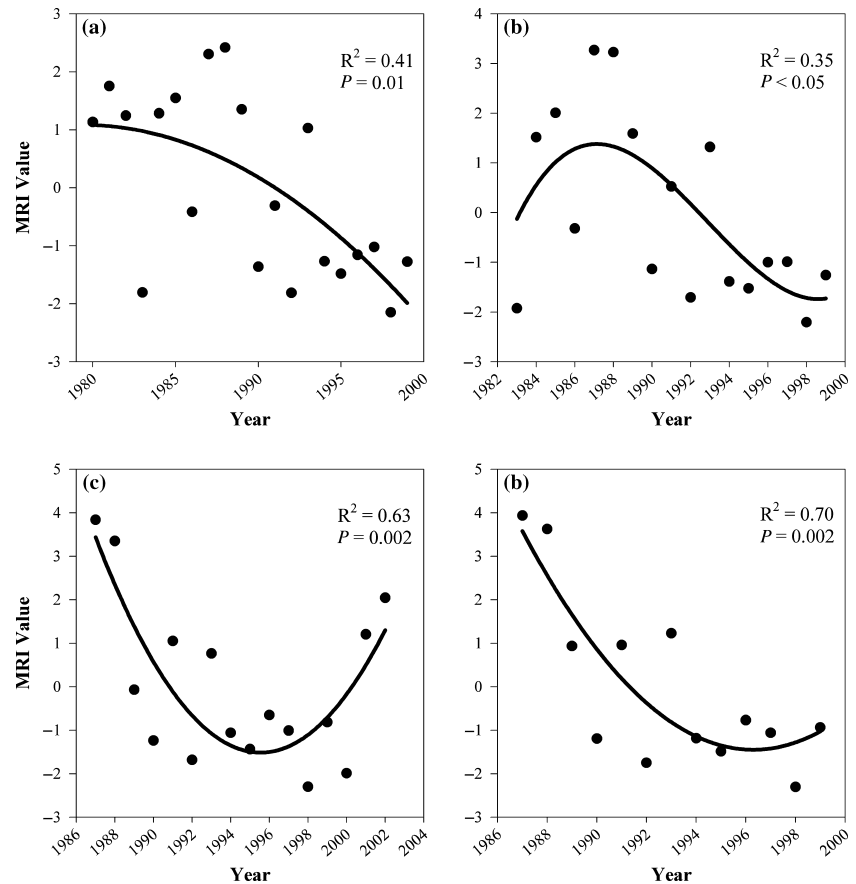


Figure 5. Trends in time-varying Multivariate Rockfish Indices (MRI): (a) MRI excludes auklets and trawl net surveys; (b) MRI 2 excludes auklets; (c) MRI 3 excludes salmon; (d) MRI 4 includes all indices.

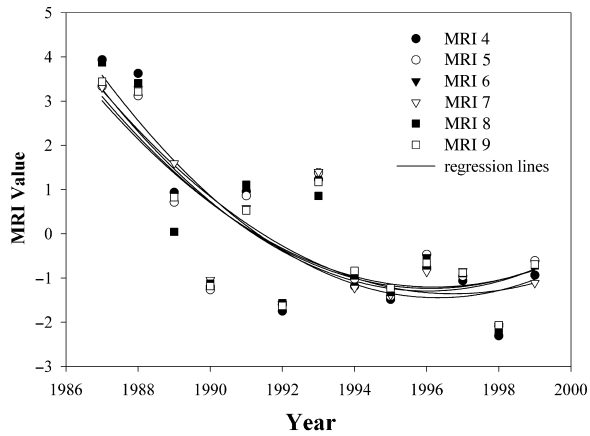
($P = 0.002$); MRI 8 (no salmon), $R^2 = 0.51$ ($P = 0.006$), and MRI 9 (no trawl net surveys), $R^2 = 0.52$, $P = 0.005$. The original indices, which appear to be contributing most, are murre, salmon, and trawl net surveys.

DISCUSSION

We have contrasted and combined four predator-based and one vessel-based sampling method of pelagic

juvenile rockfish abundance in the northern-central CCS. The original indices include the offspring diet for three species of seabird of the family Alcidae (murre, guillemots, and auklets) and diet of adult chinook salmon. We compared these indices against mid-water (30 m) net samples to better understand the importance and validity of each. This study reflects a unique collaboration between seabird ecologists, fisheries scientists, and recreational fishers working to understand long-term forage fish dynamics in this

Figure 6. Trends in time constant MRI for the period 1987–99. MRI 4, all indices (repeat of Fig. 5d); MRI 5 excludes murre; MRI 6 excludes guillemots; MRI 7 excludes auklets; MRI 8 excludes salmon; MRI 9 excludes trawl net surveys.



ecosystem. We demonstrated significant co-variation in the take of an assemblage of juvenile rockfishes, primarily represented by *S. jordani*, *S. entomelas*, and *S. flavidus*. In general, we found that predator diets, while indirect, provide interpretable indices to inter-annual and longer-term variation in pelagic juvenile rockfish abundance. To our knowledge, this study represents the first attempt to combine indices obtained by seabirds, predatory fish, and vessel-based net samples. In doing so, we have provided verification of each sampling method, as well as a synoptic perspective often not revealed by using single indices. To our knowledge, this study is the first to compare seabird and salmon diets, albeit for a single genus of prey.

In combining these time series, as we have undertaken in creating the MRI, a couple of caveats deserve mention. First, the MRI provides information on both abundance and availability (to predators), but we cannot distinguish between them. Secondly, the MRI provides information on multiple spatial scales, from the local to the mesoscale. We cannot, however,

determine the spatial scales of sampling by the predators, even though this has been roughly estimated for the seabirds (Fig. 1). This figure shows the presumed maximal foraging extent for the birds, but does not reflect the actual ‘sampling’ of the environment. Therefore, it is of considerable interest that the patterns shown by each index were similar (Fig. 2). The guillemots have the most restricted foraging range (approximately 10 km), while murre can travel up to 90 km in a single foraging bout (Ainley *et al.*, 1993). It is unknown how far adult chinook salmon may travel during feeding, but presumably over substantial areas. Irrespective of foraging ambit, the sampling devices (birds, fish, and nets) all showed similar interannual variability and trends. In 1983, 1992, and 1998, rockfish abundance was substantially reduced, and in the 1990s, abundance was generally low. Thus, the MRI, as synoptic measurements of juvenile rockfish abundance and availability, provide a comprehensive picture of juvenile rockfish dynamics from a local to a regional scale.

Predator diets and fish monitoring

The suggestion that predator diets can provide information on forage fish abundance, availability, and even body condition and age-structure is not new (e.g. Sunada *et al.*, 1981; Fahrig *et al.*, 1993; Roseneau and Byrd, 1997; Link, 2004). Indeed, predator diets are being used as indicators to fish and zooplankton abundance in other regions of the world (e.g. <http://www.ccamlr.org>). By sampling spatially and temporally patchy prey, predators provide information on fish abundance and availability that augments, and may enhance, information obtained from net surveys. In some cases, predators may provide the only information on species or communities that are difficult to sample, or have limited commercial value and hence are generally not targeted by fisheries research programs (Link, 2004). Such is the case here for salmon, which ingested six species of *Sebastes* that were not found in mid-water trawl net surveys or seabird diet.

	MRI 4	MRI 5	MRI 6	MRI 7	MRI 8	MRI 9
Eigenvalue	4.00	3.09	3.24	3.38	3.44	3.06
Proportion of variance	0.80	0.77	0.81	0.85	0.86	0.77
Common Murre	0.48	ND	0.54	0.52	0.51	0.55
Pigeon Guillemot	0.45	0.52	ND	0.48	0.48	0.53
Rhinoceros Auklet	0.41	0.47	0.46	ND	0.49	0.47
Salmon	0.40	0.45	0.44	0.47	ND	0.46
Trawl Net Surveys	0.49	0.55	0.55	0.52	0.52	ND

ND, no data.

Table 4. Principal Component Analysis (PC 1) for the period 1987–99, including MRI 4 (all indices) and sequentially dropping each of the others; MRI 5 excludes murre; MRI 6 excludes guillemots; MRI 7 excludes auklets; MRI 8 excludes salmon; MRI 9 excludes trawl net surveys.

There are several potential difficulties with using predators as 'sampling devices'. These include: (i) active prey selection by the predator (i.e. a diet that does not reflect the abundance of forage fish species in the environment; Van Pelt *et al.*, 1997; Link and Garrison, 2002; Link, 2004), (ii) age- or size-specific prey choice (Hill *et al.*, 1996; Reid *et al.*, 1996; Hansen and Chouinard, 2002; Link and Garrison, 2002), (iii) difficulties in calibrating changes in diet with variability of prey in the environment (Hunt *et al.*, 1991), and (iv) non-linear responses which complicate interpretations and limit utility. Despite these concerns, the predators examined herein showed remarkable co-variation in diet composition, as well as strong relationships with the net-based abundance estimates. There are a number of reasons why these indices of relative rockfish abundance appear to work independently and in combination. First, diet of each of the seabird species reflects food returned to dependent offspring at a single colony, Southeast Farallon Island; thus, we have standardized the age class of the predators to adult seabirds, and age of the prey to young-of-the-year *Sebastes*. Secondly, there appears to be spatial and temporal matching in the 'sampling' between the birds (primarily murre), salmon, and the vessel-based surveys. Of the three marine bird species considered, the foraging range of the murre is the largest (Ainley *et al.*, 1993). Murre foraging habitats are diverse, with birds feeding on the shelf, along the shelf break and slope, and out to the 1000-m isobath (Briggs *et al.*, 1987; Oedekoven *et al.*, 2001; Yen *et al.*, 2004). Therefore, the area 'sampled' by the murre is approximately rectangular in shape and resembled that of the ship-based surveys (Fig. 1). The murre showed the highest co-variation (highest R^2) with the salmon and trawl net surveys. Therefore, predator-based indices may be best when using a wide-ranging predator, even if that predator is constrained to forage to/from a central point, as in a seabird colony. Thirdly, for the birds, there appears to be a preference for juvenile rockfish when they are available in the environment. Ainley *et al.* (1995) showed that reproductive success increases when there is a greater proportion of rockfish in the diets. The exception may be the auklet, which apparently prefers juvenile rockfish early in the chick-rearing period, but switches to northern anchovy (*Engraulis mordax*) later when their offspring are large (Thayer and Sydeman, in press).

Multivariate Rockfish Indices

Infrequently have predatory fish and seabird diets been compared with independent measures of prey abun-

dance in the environment. By combining information from the predators and trawl nets, we have developed indices that may be more representative than each index alone. As noted above, the seabirds, salmon, and trawl nets all differ in how they 'sample' *Sebastes* in the environment. As coastal advection may force juvenile *Sebastes* out of their preferred habitats (Ainley *et al.*, 1993), it is important to have an 'adaptive' sampling plan. Predators naturally provide this, by their static, station-based net-sampling method. Therefore, by combining predator and net sampling we have enhanced the sampling protocol in space and time. Murre are known to forage to 200 m depths (Piatt and Nettleship, 1985), which in this case enhances sampling depth as well.

Annual variability in MRI was high in all models, and the overall trend was one of decreasing pelagic juvenile rockfish abundance/availability. There was a marked increase in rockfish abundance in the MRI containing the years 2001 and 2002. During the mid- to late-1980s, juvenile rockfish were, in general, abundant, but declined and remained low in the 1990s. Miller and Sydeman (2004) attributed this to changes in intense upwelling. Therefore, the MRI is apparently useful as integrated measures of interannual to inter-decadal variability in juvenile rockfish abundance.

CONCLUSIONS: IMPLICATIONS FOR FISHERIES MANAGEMENT

Information provided by seabird and fish predators in assessing pelagic juvenile rockfish abundance complements traditional ship-based net sampling procedures. As some dietary time series are of substantial duration, so-called predator-based sampling (PBS) may facilitate hind-casting and retrospective modeling of forage fish abundance. Moreover, information on predator-prey relationships and prey consumption is needed for managing fisheries from an ecosystem perspective. Diet provides important information on natural mortality rates for the fish, which could be included in stock assessments. Diet also provides a fundamental parameter for prey consumption models that estimate the quantity required by ecologically dependent species (May *et al.*, 1979). Prey consumption models could be included in fishery management plans to minimize the effects of fishing on upper-trophic-level predators. In conclusion, determining predator food habits is critical to implementing ecosystem-based fisheries management. Predators as sampling devices also provide a novel means to deepen understanding of temporal and spatial patterns in forage fish abundance.

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