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Shearwaters as ecosystem indicators: Towards fishery-independent metrics of fish abundance in the California Current

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ABSTRACT

Shearwaters are ideal for monitoring ocean conditions in the California Current because these predators are abundant, conspicuous, and responsive to oceanographic variability. Herein we evaluated black-vented (*Puffinus opisthomelas*), Buller's (*P. bulleri*), flesh-footed (*P. carneipes*), pink-footed (*P. creatopus*), short-tailed (*P. tenuirostris*), and sooty (*P. griseus*) shearwaters as fishery-independent indicators of predatory or prey fish availability. We analyzed four years (1996, 2001, 2005, 2008) of monthly (August–November) National Oceanic and Atmospheric Administration seabird surveys, and United States Geological Survey Pacific Coast Fisheries Database catch, from the California coast to 200 nm offshore. An ordination of shearwater abundance and fish catch revealed that the shearwaters and 11 fish/squid species were significantly correlated with one or more of three principal components, which explained 86% of the variation and revealed distinct species assemblages. We evaluated multiple linear regression models for 19 fisheries using five shearwater metrics: density, aggregation, and behavior (traveling, stationary, feeding), three oceanographic indices, and latitude. Eight of these models had a shearwater metric as the primary predictor. In particular, feeding black-vented shearwater abundance explained 75% of dolphinfish (*Coryphaena hippurus*) longline catch. This research illustrates the utility of shearwaters as ecosystem indicators, with direct application for predicting fishery catch of commercial importance.

1. Introduction

Upper-trophic level predators provide a promising tool for synthesizing complicated patterns by integrating multiple drivers of oceanographic variability and ecosystem response (Ballance et al., 1997; Croll et al., 1998; Wells et al., 2008; Zador, 2013). Seabirds are particularly useful indicators of ecosystem structure and productivity because they are responsive to environmental variability over multiple spatial (10s–1000s km) and temporal (days to years) scales (Briggs et al., 1987; Hyrenbach and Veit, 2003; Springer and van Vliet, 2014; Veit et al., 1997). Because seabirds are not directly constrained by their physiological temperature tolerance, and are completely reliant on the sea for food, their at-sea distributions are assumed to be driven by ocean productivity and prey availability (Ballance, 2007; Piatt et al., 2007). Seabirds are increasingly being used in ecological studies to reflect changing prey distribution and abundance in marine ecosystems (Springer and van Vliet, 2014; Zador et al., 2013).

Shearwaters are an ideal focal taxa for monitoring ocean conditions in the California Current System (CCS), because each species occupies a distinct habitat, so their community composition should reflect changes in environmental conditions and prey availability (Burger, 2001; Gould and Piatt, 1993; Hyrenbach and Veit, 2003). Six *Puffinus* shearwaters regularly occur in the CCS: black-vented (*Puffinus opisthomelas*), Buller's (*Puffinus bulleri*), flesh-footed (*Puffinus carneipes*), pink-footed (*Puffinus creatopus*), short-tailed (*Puffinus tenuirostris*), and sooty (*Puffinus griseus*) (Ainley, 1976) (Table 1). After the breeding season, shearwaters migrate from nesting locations outside of the CCS to the productive CCS, to become the most abundant seabirds in this ecosystem during the boreal spring–summer (April–September) despite substantial year-to-year variability in abundances (Ainley, 1976; Ainley and Hyrenbach, 2010; Briggs et al., 1987). In contrast to locally breeding seabird species, whereby foraging distribution is constrained by distance from a breeding colony (Ballance et al., 1997; Oedekoven et al., 2001; Shaffer et al., 2009; Yen et al., 2004), these non-breeding shearwaters are able to move unconstrained to exploit often ephemeral prey patches. For instance, migrating sooty shearwaters travel over 1000 km d^{-1} and range from southern California to British Columbia during their "wintering" season in the CCS (Adams et al., 2012; Shaffer et al., 2006). Therefore, the distribution and abundance of these wide-ranging predators provides a valuable tool for assessing changes in the productivity of the marine ecosystem in response to seasonal, interannual, and longer-term oceanographic variability.

Previous research has demonstrated the potential for developing predictive models built upon the covariation of seabirds and both

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Table 1
Six shearwater species examined listed in order of decreasing abundance in this study. Mean, median, and maximum density (number per 100 km^2) were calculated for the 86 sampling units (see Materials and methods section). Biogeographic domain from Ainley, 1976; Briggs et al., 1987; Hyrenbach and Veit, 2003.

Shearwater	Code	Scientific name	Domain	Mean ± SD	Median	Max
Sooty	SOSH	*Puffinus griseus*	Subarctic	50.55 ± 162.8	2.5	1192.7
Pink-footed	PFSH	*Puffinus creatopus*	Subtropical	18.81 ± 122.2	1.0	1133.4
Buller's	BUSH	*Puffinus bulleri*	Transition	6.09 ± 11.2	1.1	51.8
Black-vented	BVSH	*Puffinus opisthomelas*	Subtropical	3.19 ± 14.9	0.0	108.8
Short-tailed	STSH	*Puffinus tenuirostris*	Subarctic	0.04 ± 0.3	0.0	3.2
Flesh-footed	FFSH	*Puffinus carneipes*	Transition	0.04 ± 0.2	0.0	0.8

their prey (forage species) and other upper-trophic level predators (predatory fish). Changes in prey availability to seabirds, measured by consumption, have been used to infer changes in prey distribution and abundance (Ainley et al., 1995; Velarde et al., 1994). In particular, seabird diet, reproductive success, and phenology have been used as proxies for commercial fish species distribution and abundance (Mills et al., 2007; Roth et al., 2007; Sydeman et al., 2008) and to predict commercial fish catch (Velarde et al., 2004). Trophic equivalency studies, whereby the shared food webs supporting seabirds and predatory fish are characterized, have demonstrated that seabirds can be proxies for predatory fish, either by shared reliance on changing prey abundances (Roth et al., 2007), or by covariation in response to environmental fluctuations (Sydeman et al., 2008). These studies demonstrate the utility of seabirds as fishery-independent biological indicators for commercially valuable and other stocks.

Fisheries management relies on a variety of data, with fishery-independent metrics of fish abundance and biomass often complementing fishery-dependent catch metrics (Hoggarth, 2006). Additionally, environmental metrics of ocean conditions are often correlated with fish abundance and catches (Mantua et al., 1997). For instance, the California sardine (*Sardinops sagax*) fishery incorporates an environmental variable into its management plan, yet the recent decoupling of the sea surface temperature and sardine recruitment relationship underscores the limitations of developing predictive models relying on empirical covariation (McClatchie et al., 2010). Therefore, using the abundance and behavior of upper-trophic predators, including seabirds, to develop more mechanistic fishery-independent metrics of ecosystem productivity and stock abundance is a promising avenue for enhancing EBM in marine systems (Zador, 2013).

Building upon previous studies, we tested the hypothesis that the at-sea distribution and abundance of shearwaters indicate commercial fishery catches in the CCS. Our approach differs from the aforementioned studies, which used nesting seabirds, because we examined the at-sea dispersion and behavior of non-breeding seabirds, with no constraints other than prey availability (see also Ainley et al., 2009). Furthermore, we provide a broad description of the dynamic CCS ecosystem, by examining a wide range of fishery species, including lower-trophic prey and upper-trophic predators (Field et al., 2006; Mantua et al., 1997).

In this paper we quantified the covariation between the shearwater community and the commercial catch of 13 predatory and prey fish/squid species in California over four study years (1996, 2001, 2005, 2008) in the summer–fall (August–November). Our objectives were to: 1) quantify the associations between shearwaters, fish, and environmental parameters; 2) develop regression models for each commercial fish species while considering specific fishery gear types; and 3) test metrics of at-sea shearwater density, aggregation, and behavior to determine their predictive potential.

2. Materials and methods

2.1. Shearwater data

Seabirds were surveyed during NOAA Southwest Fisheries Science Center (SWFSC) ecosystem assessment surveys of the CCS. A subset of these data was extracted to include observations within the United States Exclusive Economic Zone (EEZ) off California (Fig. 1). SWFSC cruises surveyed the study area throughout the summer–winter (July–December) in four years (1996, 2001, 2005, 2008). However, we only included in the analysis 15 survey months with sufficient effort (>15 survey days): August, September and October for all four survey-years, and November for every year except 1996.

Seabirds were surveyed by trained observers using standardized continuous strip transect methods (Tasker et al., 1984). Densities calculated were not corrected for flux (Spear et al., 1992) and thus constitute a measure of relative abundance (birds km^{-2}). Seabirds were surveyed while the vessel was underway during daylight hours, weather permitting, within a 300-meter strip extending from the bow in a 90° arc to one side of the vessel with the best visibility (Philbrick et al., 2003; Tasker et al., 1984). The following sighting data were collected: time, latitude, longitude, species, number of individuals, radial distance from the ship, and behavior. Seabird behaviors were recorded using the following categories: sitting on the water, flying, ship following, feeding, piracy or other.

Survey data collected during “fair” to “excellent” observation conditions were considered, thus ensuring shearwaters were detectable within the 300-meter survey strip (Philbrick et al., 2003). While shearwaters not identified to species were not included in this analysis, the higher taxonomic grouping of sooty/short-tailed shearwater was used whenever observers could not distinguish between these two species. To account for potential misidentifications, a “dark shearwater” category was defined as including three shearwater codes: sooty, short-tailed, and sooty/short-tailed. Previous studies have used this taxonomic grouping, due to the difficulty of distinguishing these shearwaters at-sea (Briggs et al., 1987; Sydeman et al., 2009; Yen et al., 2006).

2.2. Fish catch data

Commercial fish catch data were obtained from the USGS Pacific Coast Fisheries GIS Resource Database, which summarizes California commercial landing receipts collected by the California Department of Fish and Wildlife (CDFW) (Perry et al., 2010). Catch data (weight in pounds) were extracted for the survey months and years of the SWFSC cruises for 13 commercially important species. Three of these species are potential prey of shearwaters: northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and market squid (*Loligo opalescens*) (Table 2). The remaining ten species represent trophic equivalents of shearwaters and may have acted as foraging facilitators or competitors: bonito (*Sarda chiliensis*), dolphinfish (mahi) (*Coryphaena hippurus*), jack mackerel (*Trachurus symmetricus*), opah (*Lampris guttatus*), jumbo squid (*Dosidicus gigas*), albacore tuna (*Thunnus alalunga*), bluefin tuna (*Thunnus orientalis*), skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and Pacific whiting (hake) (*Merluccius productus*) (Table 2). The catch data included multiple gear types, with 10 of the 13 fish/squid species being caught with more than one type of fishing gear (Table 3). To eliminate incidental catch records, only those gears that contributed 95% of the catch by weight of a given target species were included in the analysis, resulting in 26 fish/gear combinations, henceforth referred to as fisheries (Table 3).

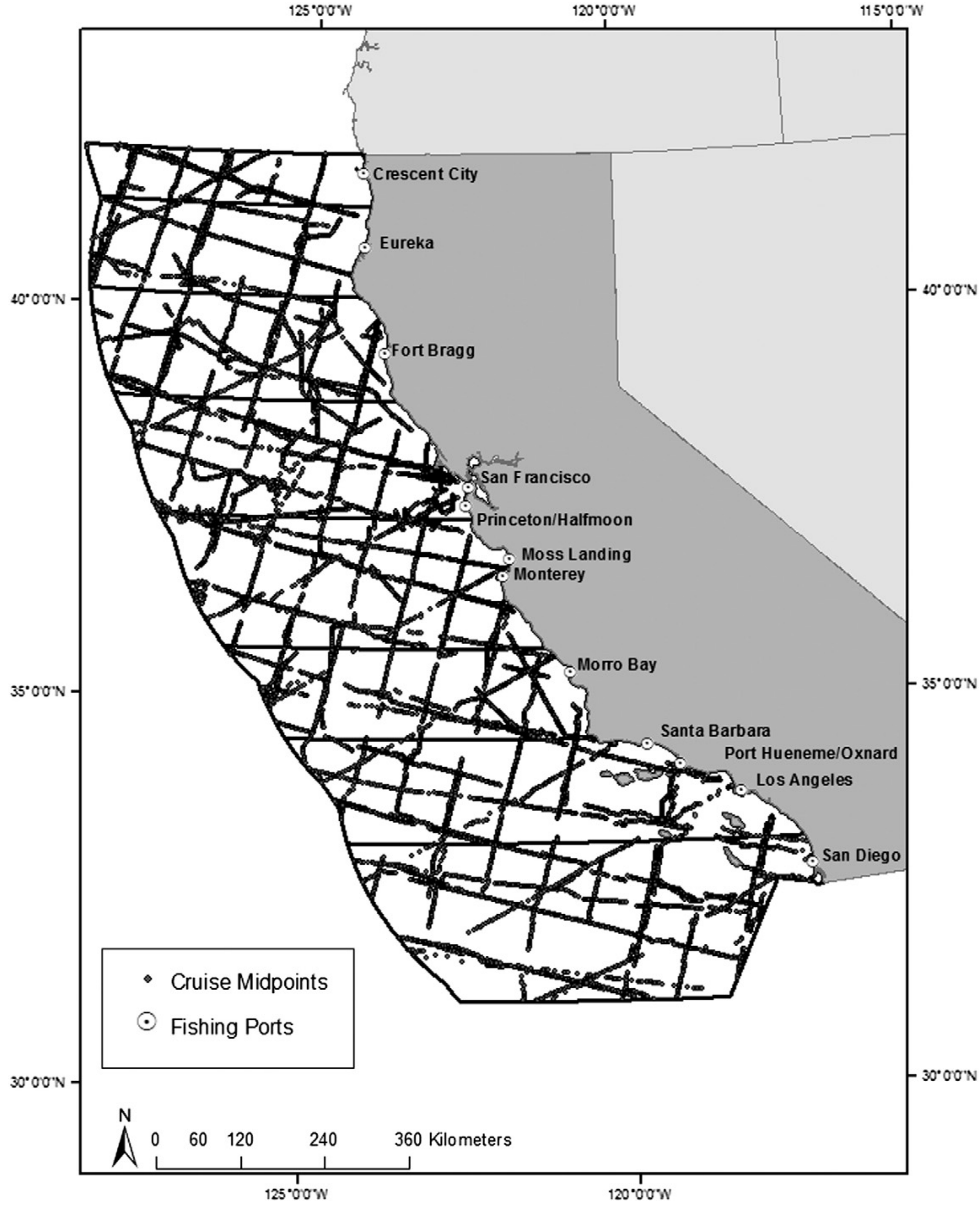

Fig. 1. Map of eight geographic regions examined and the major fishing ports in California. SWFSC survey effort during the four survey years (1996, 2001, 2005, 2008) is depicted for the 15 survey months with transect midpoints.

It is important to note that the fish catch data are fishery-dependent, and therefore subject to inherent biases and limitations. However, the underlying assumption of this study is that commercial catch is a proxy for fish availability to specific fisheries (defined by distinct gear types), and indicates the status of fishery species over space and time (Hoggarth, 2006).

2.3. Spatial and temporal resolution

Commercial fish catch is recorded within CDFW fishing blocks. While the majority are 10 × 10 min of latitude/longitude, some blocks are much larger, extending from the shore out to the U.S. 200-mile EEZ (Perry et al., 2010). Because of this disparity, small blocks were aggregated into larger blocks to facilitate the analysis of the data at a similar spatial scale. This aggregation resulted in the loss of onshore-offshore resolution, but retained latitudinal resolution (Fig. 1). The 8 resulting regions × 15 survey months resulted in 120 time/area sampling units for analysis, of which 94 were sampled by the SWFSC cruises. Eight sampling units having minimal survey effort (<10 km^2) were excluded from the analysis, resulting in a matrix of 86 sampling units.

Shearwater sightings were aggregated within a given survey month to match the temporal scale of the fish catch data. Shearwater densities were calculated per square kilometer of survey effort (survey track length × 0.3 km strip width) (Table 1) and the catch (in tons) for the thirteen commercial fish/squid species (Table 3) were calculated for each of these time/area sampling units.

Table 2
Thirteen commercially-important fish/squid species examined. Biogeographic domain from FishBase, www.fishbase.org; accessed 10 August 2011. Trophic level data (if available) from Brodeur and Pearcy, 1992; Field et al., 2006; Dambacher et al., 2010.

Species (Code)	Domain	Trophic link	Level	Oceanographic indicator	References
Northern Anchovy (ANCH) *Engraulis mordax*	Transition	Prey	3.3	Decadal fluctuations Major fishery in CCS	Checkley et al. (2000); Chavez et al. (2003)
Bonito (BONI) *Sarda chiliensis*	Transition	Equivalents	–	Climate induced variability	Pearcy et al. (1985)
Dolphinfish (DOLP) *Coryphaena hippurus*	Subtropical	Equivalents	4.4	Climate induced variability	Norton (1999)
Jack Mackerel (MACK) *Trachurus symmetricus*	Transition	Equivalents	3.5	Climate induced variability	Pearcy et al. (1985); Brodeur and Ware (1995)
Opah (OPAH) *Lampris guttatus*	Subtropical	Equivalents	4.2	Climate induced variability	Brodeur et al. (2006); Polovina et al. (2008)
Pacific Sardine (SARD) *Sardinops sagax*	Transition	Prey	2.8	Decadal fluctuations Largest fishery in CA	Emmett et al. (2005); Chavez et al. (2003)
Jumbo Squid (SQJU) *Dosidicus gigas*	Subtropical	Equivalents	4.0	Climate induced variability	Nigmatullin et al. (2001); Field et al. (2007)
Market Squid (SQMA) *Loligo opalescens*	Transition	Prey	3.7	Climate induced variability Major fishery in CCS	Jackson and Domeier (2003); Zeidberg et al. (2006)
Albacore Tuna (TUAL) *Thunnus alalunga*	Transition	Equivalents	4.3	Major fishery in CCS	Laurs et al. (1977); Laurs (1983)
Bluefin Tuna (TUBF) *Thunnus orientalis*	Transition	Equivalents	4.2	Climate induced variability	Marcinek et al. (2001)
Skipjack Tuna (TUSJ) *Katsuwonus pelamis*	Subtropical	Equivalents	4.4	Climate induced variability	Barkley et al. (1978)
Yellowfin Tuna (TUYF) *Thunnus albacares*	Subtropical	Equivalents	4.3	Climate induced variability	Block et al. (1997); Marcinek et al. (2001)
Pacific Whiting (WHIT) *Merluccius productus*	Transition	Equivalents	3.5	Climate induced variability Largest fishery in CCS	Bailey et al. (1982); Field et al. (2006)

2.4. Environmental indices

Four environmental indices were considered. The latitude of the northern boundary of each of the eight regions was used to quantify north–south gradients. Three basin-wide indices were used to indicate monthly variability in ocean conditions: Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and Multivariate ENSO Index (El Niño Southern Oscillation, MEI). The PDO is derived using the first empirical orthogonal function (EOF) of sea surface temperature and sea surface height (www.jisao.washington.edu/pdo/), and the NPGO is based on the second EOF while deriving the PDO (www.o3d.org/npgo/). A positive PDO is characterized by anomalously warm SST in the CCS (Mantua and Hare, 2002). A positive NPGO results in upwelling favorable winds south of 38°N and a decrease in SST (Di Lorenzo et al., 2008). PDO and NPGO indices were obtained corresponding to the survey months.

Table 3
Summary of catch data for the thirteen fish/squid species examined. See Table 2 for key to species codes. Weight in tons, gear types included, gear codes, and the percent of catch within the 86 sampling units (see Materials and methods section) are shown.

Species	Tons	Gear types (code) (% of catch)	# Types
ANCH	7875.6	Purse Seine (PS) (68.5), Drum Seine (DS) (27.8)	2
BONI	244.8	Purse Seine (PS) (94.3), Drum Seine (DS) (4.7)	2
DOLP	1.3	Set Longline (SL) (58.5), Hook & Line (HL) (34.5), Troll (TR) (3.4)	3
MACK	1545.1	Purse Seine (PS) (94.2), Drum Seine (DS) (5.6)	2
OPAH	94.6	Drift Gillnet (DG) (93.4), Set Gillnet (SG) (4.9)	2
SARD	51974.7	Purse Seine (PS) (79.2), Drum Seine (DS) (20.5)	2
SQJU	36.3	Hook & Line (HL) (91.2), Large Trawl Footrope (TF) (7.2)	2
SQMA	60710.0	Purse Seine (PS) (80.2), Drum Seine (DS) (18.4)	2
TUAL	5027.3	Jig/Bait (JB) (57.8), Troll (TR) (34.1), Purse Seine (PS) (3), Hook & Line (HL) (2)	4
TUBF	1631.1	Purse Seine (PS) (97.7)	1
TUSJ	1298.9	Purse Seine (PS) (99.6)	1
TUYF	453.9	Purse Seine (PS) (97.1)	1
WHIT	92.5	Midwater Trawl (MT) (94.4), Bottom Trawl (BT) (4.8)	2
		Total	26

ENSO events are quantified by NOAA's Earth System Research Laboratory using the MEI, by selecting the principal component of six ocean–atmosphere parameters in the tropical Pacific (www.esrl.noaa.gov/psd). In the CCS, positive MEI values (El Niño) indicate positive anomalies of SST and sea level height along the coast (Bograd et al., 2000; Rasmusson and Wallace, 1983; Wolter and Timlin, 1998). The MEI is calculated for bi-monthly periods; indices were obtained for the bi-monthly period preceding the survey month (e.g., July/Aug was used for the August survey).

2.5. Statistical methods

2.5.1. Principal Components Analysis

The catch of the 13 fish/squid species and the density of the seven shearwater taxa were analyzed using Principal Components Analysis (PCA), with PC-ORD software 5.10 (MjM Software 2006). PCA is an ordination method that describes the covariation among variables using a reduced number of synthetic variables (McCune et al., 2002). Although this method assumes normal distributions, which usually does not apply to community data, several studies have used PCA to analyze seabird communities and habitat associations (e.g. Ainley et al., 2005; Ballance et al., 1997; Weichler et al., 2004). To cope with non-normality, the shearwater density and fish catch data were log transformed $y' = \log(y + 1)$ and relativized to ensure equal weights in the ordination, which was performed with 999 randomizations. Because the oceanographic indices (PDO, NPGO, MEI) were already standardized, latitude was the only log transformed $(y' = \log(y))$ environmental variable. To interpret the ordination, Pearson correlations were calculated between the species and the principal components, and between the ordination axes and the four environmental indices.

2.5.2. Stepwise linear regression models

Multiple linear regressions were used to examine the relationships between 13 dependent variables (fish/squid species catch) and 39 explanatory variables within the 86 sampling units: five metrics for each of the seven shearwater taxa (density, aggregation, and the incidence of three behaviors), and four environmental indices (latitude, PDO, NPGO, MEI). Due to the cross-correlations of the explanatory variables, we performed stepwise regressions using SPSS Statistics 20 (IBM, 2011). Stepwise regression selects the explanatory variable that has the highest correlation with the dependent variable, and subsequent predictors are considered based on their contribution to the explained variance, until no significant predictors are left. Each time a predictor is added to the model, a removal test is performed in order to determine if any redundant predictors can be eliminated. Additionally, the Durbin–Watson statistic was used to assess the model's assumption that the errors in the regression were independent (Field, 2009).

The log transformed shearwater and fish catch data were used to meet the assumptions of normality. However, because the residuals from the regressions did not always meet normality assumptions, a more stringent significance level of 0.025 was used to add predictors to the model (e.g., Ainley et al., 2005).

Five at-sea shearwater metrics were calculated for the 86 sampling units: 1) density, 2) aggregation, and the incidence of three behaviors: 3) feeding, 4) traveling, and 5) sitting. The density of each species was calculated for each sampling unit, by dividing the number of shearwaters sighted by the total area (square kilometers) surveyed. The degree of aggregation of each species was quantified using the number of birds sighted as individuals divided by the number of birds sighted as groups (more than 1 bird) (Spear and Ainley, 2005). Finally, because seabird behavior is indicative of prey availability, with sitting and turning (non-directional flight) behaviors increasing in the presence of prey (Veit, 1999; Veit et al., 1997), three distinct behaviors were considered: feeding, traveling, and sitting (Spear and Ainley, 2005). Traveling, a non-stationary behavior, included both directional and non-directional flight, as the distinction between the two was not defined in 1996. Feeding and sitting, both considered stationary behaviors, were determined using the original classification as such in the field. This resulted in five predictors for each shearwater species: shearwater density (shearwaters km^{-2}), proportion of shearwaters sighted as individuals, and proportion of shearwaters feeding, traveling, and sitting (Table 4). However, feeding behavior was never recorded for short-tailed and flesh-footed shearwaters.

To determine if fishing gear influenced the regression models, two analyses were conducted relating the catch of each fish/squid species to their respective gear types: 1) pair-wise cross-correlations, and 2) paired t-tests (2 gear types) or repeated measures ANOVA (>2 gear types) (Appendix). First, significant Pearson correlation coefficients ($p < 0.05$) indicated that the catch by different gears was correlated in time and space. In other words, different gear types targeted a particular species within the same sampling units. Second, if the catch of the different gear types was significantly different, then the gear type influenced the quantity of the catch. Because gear type significantly affected the catch for several species, this categorical variable was added as a predictor in the stepwise regression models. In those instances when the gear type had a significant influence on the dependent variable, separate gear-specific models were created for each gear type (Appendix). This approach resulted in 19 fishery models, 12 gear-specific and 7 non-specific.

Table 4
Five shearwater predictors used for each species in the regression models, with shearwater species (SPSH) as an example. Seven shearwater taxa were considered: sooty (SOSH), pink-footed (PFSH), Buller's (BUSH), black-vented (BVSH), short-tailed (STSH), flesh-footed (FFSH), and dark (DASH).

Variable	Description
SHSPDens	Shearwaters km^{-2}
SHSPSing	Proportion of shearwaters sighted as single individuals
SHSPFeed	Proportion feeding
SHSPTrav	Proportion directional flight and non-directional flight
SHSPSitt	Proportion sitting

3. Results

3.1. Principal Components Analysis

The PCA quantified the association between the shearwaters, fish/squid catch, and environmental indices. The PCA yielded three meaningful axes, as determined using two criteria: the observed eigenvalue compared to the average eigenvalue generated using randomizations, and the observed eigenvalue compared to the broken-stick eigenvalue (McCune et al., 2002). The three orthogonal axes explained 85.5% of the variation (Axis 1: $r^2 = 56.7$; Axis 2: $r^2 = 26.8$; Axis 3: $r^2 = 2.0$). The randomization tests resulted in two marginally significant axes, Axis 1 ($p = 0.058$) and Axis 2 ($p = 0.064$), and a significant Axis 3 ($p = 0.003$). Three predatory fish species (jumbo squid, albacore tuna, and Pacific whiting) and one environmental index (MEI) were not significantly correlated with any of the ordination axes.

Principal Component (PC) 1 captured a faunal gradient, driven by the abundance of three species negatively correlated with this axis ($p < 0.001$) (Table 5): short-tailed shearwater, flesh-footed shearwater, and bluefin tuna (Fig. 2). This axis was not significantly correlated with any of the environmental indices examined, and therefore may capture more of a seasonal signal rather than environmental variability.

PC 2 reflected a north–south gradient in species distributions, and the disparity between distinct warm and cold-water assemblages. This axis was significantly correlated with low latitude and a positive PDO index, and marginally correlated with a negative NPGO index (Fig. 2). Overall, 15 species (five shearwaters and nine fish/squid) were significantly correlated with this axis (Table 5). PC 2 had the highest number of significant species loadings, including five shearwaters (pink-footed, black-vented, flesh-footed, sooty, and dark), seven predator fish species (yellowfin, skipjack, and bluefin tunas, bonito, dolphinfish, jack mackerel, opah), and two prey fish species (market squid and sardine) (Table 5).

PC 3 characterized differences within the shearwater community, as none of the fisheries were significantly correlated with this axis. The third PC was significantly loaded on by all shearwaters except for the short-tailed, and was positively correlated with black-vented densities, and negatively with the other shearwater species (Table 5). Axis 3 was significantly ($p < 0.05$) loaded on by negative PDO indices, suggesting a signal of higher productivity.

Table 5
Loadings of the thirteen fish/squid species and seven shearwater taxa on the three principal component axes. Bold font indicates the results of the Pearson cross correlations between the species and the axes were significant at the $p < 0.001$ level, and italic font indicates significance at the $p < 0.05$ level. See Tables 1 and 2 for keys to species codes.

	PC 1	PC 2	PC 3
ANCH	0.013	*0.037*	0.032
BONI	−0.005	**0.180**	0.048
DOLP	−0.001	**0.175**	0.017
MACK	0.000	**0.148**	0.052
OPAH	−0.011	**0.048**	0.012
SARD	−0.032	**0.065**	0.016
SQJU	0.021	−0.064	−0.025
SQMA	−0.022	**0.075**	0.032
TUAL	−0.001	0.001	−0.010
TUBF	**−0.113**	**0.128**	−0.059
TUSJ	−0.011	**0.207**	−0.027
TUYF	−0.007	**0.197**	−0.002
WHIT	0.025	−0.088	−0.029
SOSH	−0.023	*0.051*	−0.076
PFSH	−0.050	**0.272**	**−0.185**
BUSH	−0.017	0.014	**−0.053**
BVSH	0.016	**0.240**	**0.370**
STSH	**−0.817**	−0.106	*0.097*
FFSH	**−0.277**	**0.173**	**−0.198**
DASH	−0.024	*0.051*	*−0.076*

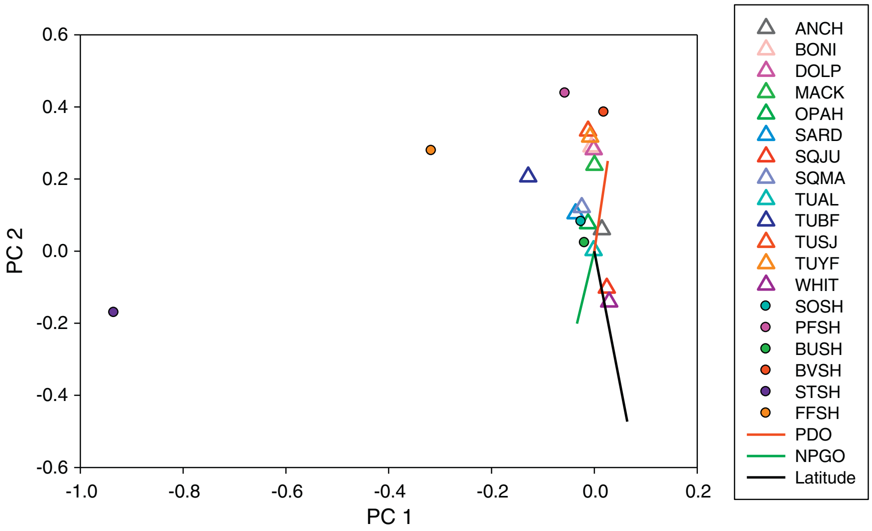

Fig. 2. Results of Principal Components Analysis showing ordination of shearwater and fish/squid species on Axes 1 and 2. Shearwaters are depicted as circles, fish/squid species as triangles, and significant environmental parameters ($p < 0.05$) as lines. Subtropical species are shown in warm colors and subarctic species are shown in cool colors. See Tables 1 and 2 for keys to species codes.

3.2. Stepwise linear regression models

We used multiple linear regressions to create models for each commercial fishery using five metrics of shearwater density, aggregation, and behavior.

3.2.1. Non-gear-specific models

Because gear type had no influence on the linear regressions for anchovy, bonito, mackerel, sardine, jumbo squid, market squid, and whiting, the models for these species combined multiple gear types. The variance explained by the non-gear-specific models varied from 3.7% for whiting to 35% for market squid (Table 6). The resulting best-fit models of fishery catches ranged from 1 to 5 predictors (Table 7).

Latitude was the environmental index chosen most frequently in the models; bonito, mackerel, sardine and market squid were related to low latitudes, while high latitudes were associated with whiting (Table 6). Two fisheries, whiting and jumbo squid, were only significantly related to one environmental variable, latitude and MEI, respectively. The other five fisheries exhibited significant relationships with shearwater metrics. In particular, all included black-vented shearwaters as a predictor; metrics for this species were chosen most often in the non-gear-specific models (Table 6).

3.2.2. Gear-specific models

Gear-specific models were created for three fisheries where gear type had a significant influence on the regression models (dolphinfish, opah, and albacore tuna), and for three tuna species caught with one gear type (bluefin, skipjack, and yellowtail). Three of the gear-specific models resulted in no variance explained: dolphinfish caught by troll, albacore caught by purse seine, and albacore caught by hook-and-line (Table 8). The variance explained for the remaining nine fisheries varied from 14 to 75% (Table 8), incorporating from one to six variables as predictors (Table 9).

Similarly to the non-gear-specific models, latitude was the environmental index most commonly related to the fishery catches; troll-caught albacore was associated with high latitudes, and five other fisheries were associated with low latitudes (opah caught using two different gear types, dolphinfish caught with hook-and-line, and skipjack and yellowfin tunas) (Table 8). Skipjack and yellowfin tuna caught by purse seine were also associated with positive PDO indices, indicating warm-water conditions in the California Current. In contrast, cooler water conditions, indicated by positive NPGO and negative MEI values, were correlated with albacore caught by jig, and opah caught with drift gillnet. The gear-specific models were most often associated with pink-footed shearwaters (Table 8).

Comparisons of the gear-specific models for the same target species revealed that the results for each gear type differed (Table 8). For example, dolphinfish caught with hook-and-line was predicted by latitude and pink-footed shearwaters, dolphinfish caught with set longline was predicted by black-vented shearwaters, and none of the variables

Table 6
Results of the non-gear specific multiple linear regression models showing the percent variance explained by the model and the predictors for each model. For each shearwater, five metrics were tested (Table 5), but only those predictors chosen in the models are shown. Predictors are indicated by order of high to low significance, and whether the predictor has a positive or negative relationship with the dependent variable. Bold font indicates significance at the $p < 0.001$ level and italic font indicates significance at the $p < 0.05$ level. See Table 2 for key to species codes.

	ANCH	BONI	MACK	SARD	SQJU	SQMA	WHIT
% variance	14.2	16.1	21.3	20.4	6.2	35.0	3.7
PDO							
NPGO							
MEI					*Neg (1)*		
Latitude		*Neg (4)*	*Neg (2)*	*Neg (1)*		**Neg (3)**	*Pos (1)*
SOSHDens	**Pos (1)**						
PFSHDens		*Pos (2)*		*Pos (3)*			
PFSHTrav						*Neg (4)*	
BUSHDens	*Neg (2)*						
BUSHSitt				*Pos (2)*			
BVSHDens		**Pos (1)**		*Pos (4)*		**Pos (2)**	
BVSHProp						*Pos (5)*	
BVSHFeed	*Pos (3)*	*Neg (3)*	**Pos (1)**				
DASHDens						**Pos (1)**	

Table 7
Summary of the non-gear specific multiple regression models. See Table 2 for key to species codes.

Fishery	# Predictors	Adjusted r^2	F	df	p-value	Durbin–Watson
ANCH	3	0.13	9.301	168	<0.001	1.537
BONI	4	0.14	7.984	167	<0.001	2.238
MACK	2	0.20	22.830	169	<0.001	1.929
SARD	4	0.19	10.685	167	<0.001	1.514
SQJU	1	0.06	11.245	170	0.001	1.479
SQMA	5	0.33	17.874	166	<0.001	1.541
WHIT	1	0.03	6.600	170	0.011	2.111

Table 8
Results of the gear-specific multiple linear regression models showing the variance explained by the model and the predictors for each model. For each shearwater, five metrics were tested (Table 5), but only those predictors chosen in the models are shown. Predictors are indicated by order of high to low significance, and whether the predictor has a positive or negative relationship with the dependent variable. Bold font indicates significance at the $p < 0.001$ level and italic font indicates significance at the $p < 0.05$ level. See Table 2 for key to species codes and Table 3 for key to gear codes.

	DOLP_HL	DOLP_SL	OPAH_DG	OPAH_SG	TUAL_JA	TUAL_TR	TUBF_PS	TUSJ_PS	TUYF_PS
% variance	33.3	75	68	30.8	13.5	22.9	28.7	44.2	50.7
PDO								**Pos (3)**	*Pos (5)*
NPGO					*Pos (2)*				
MEI			*Neg (3)*						
Latitude	**Neg (1)**		**Neg (1)**	**Neg (2)**		**Pos (1)**		**Neg (1)**	**Neg (1)**
SOSHProp					*Pos (1)*				
PFSHDens	*Pos (2)*						**Pos (1)**	**Pos (2)**	**Pos (2)**
PFSHTrav								*Pos (5)*	**Pos (3)**
BUSHProp							Neg (3)		
BVSHFeed		**Pos (1)**							
BVSHTrav				**Pos (1)**					*Neg (6)*
FFSHDens				*Neg (3)*					
FFSHSitt							**Pos (2)**		
DASHDens			*Pos (2)*					*Neg (4)*	*Neg (4)*

examined explained dolphinfish caught with troll. Interestingly, the two subtropical tuna species caught by purse seine had five of six identical predictors, illustrating that certain gear types shared more explanatory variables than individual target species (Table 8).

3.2.3. Shearwaters as predictors

Sooty or dark shearwater density was positively correlated with anchovy, market squid, and opah caught with drift gill-net, and negatively correlated with skipjack and yellowfin tuna caught with purse seine (Fig. 3). Additionally, non-aggregating (single) sooty shearwaters were associated with albacore tuna caught with jig. Pink-footed shearwater density was a predictor for sardine, bonito, dolphinfish caught by hook-and-line, and bluefin, skipjack and yellowfin tunas (Fig. 4). Pink-foot traveling behavior was positively correlated with skipjack and yellowfin tunas, yet negatively correlated with market squid. Buller's shearwater density was negatively correlated with anchovy, stationary Buller's were correlated with sardine, and aggregating Buller's were correlated with bluefin tuna (Fig. 5). Black-vented shearwater metrics were predictors for the highest number of fisheries (Fig. 6). Feeding behavior was a predictor for anchovy, mackerel, and dolphinfish caught with set longline, whereas non-feeding behavior was a predictor for bonito. Black-vented density was a predictor of bonito, sardine, and market squid, and non-aggregating birds were correlated with market squid. Traveling black-vents were predictors of opah caught with set-gillnet, yet stationary birds were predictors of yellowfin tuna (Fig. 6). Flesh-footed shearwater density was negatively correlated with opah caught with set gillnet, and stationary behavior was a predictor for bluefin tuna (Fig. 7). Short-tailed shearwaters were not selected as a predictor for any of the fisheries examined.

Table 9
Summary of the gear-specific multiple regression models. See Table 2 for key to species codes and Table 3 for key to gear codes.

Fishery	# Predictors	Adjusted r^2	F	df	p-value	Durbin–Watson
DOLP_HL	2	0.317	20.71	83	<0.001	1.548
DOLP_SL	1	0.747	252.57	84	<0.001	2.024
DOLP_TR	0	n/a	n/a	n/a	n/a	n/a
OPAH_DG	3	0.668	57.995	82	<0.001	1.569
OPAH_SG	3	0.282	12.152	82	<0.001	1.692
TUAL_JA	2	0.114	6.477	83	0.002	1.147
TUAL_TR	1	0.22	24.973	84	<0.001	1.374
TUAL_PS	0	n/a	n/a	n/a	n/a	n/a
TUAL_HL	0	n/a	n/a	n/a	n/a	n/a
TUBF_PS	3	0.261	10.981	82	<0.001	1.729
TUSJ_PS	5	0.407	12.669	80	<0.001	1.321
TUYF_PS	6	0.469	13.537	79	<0.001	1.447

4. Discussion

Our results illustrate the value of shearwaters as fishery-independent predictors of the prevalence of forage fish and predatory fish, two important ecosystem-wide indicators of ocean productivity and ecosystem structure in the CCS. More specifically, we quantified the associations between the shearwater community and commercial fish and squid catch in the CCS. Considering that latitude, which is not considered a predictor for temporal variability, was the most commonly selected environmental index, shearwaters outperformed the oceanographic indices in their ability to indicate temporal changes in fish availability. Furthermore, one of the most notable contributions of this study was to illustrate the utility in the use of a variety of shearwater behavior and aggregation metrics, in addition to their at-sea distribution and abundance, to gauge fishery status.

The species-specific biogeographic affinities of the shearwater community may be indicative of the types of fish species expected in a region. In such cases, the presence of a shearwater species along with the absence of a fishery species could be suggestive of a fishing effect on either lower- or upper-trophic fish species or the avoidance of shearwater and predatory fish competition. Therefore, shearwaters have the

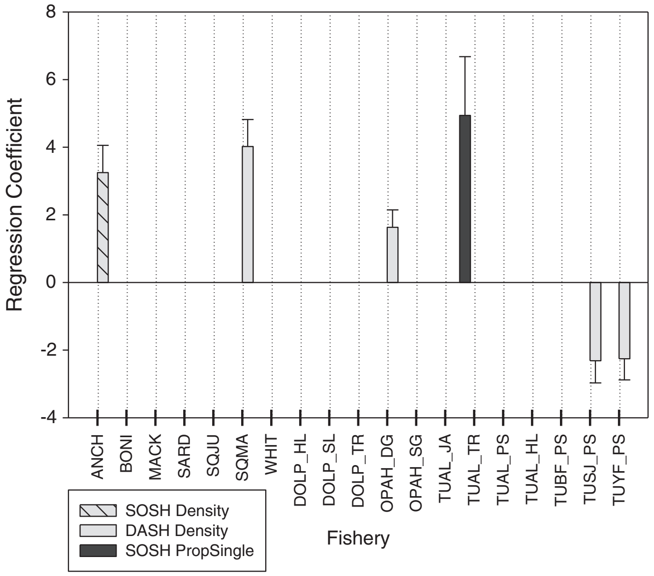

Fig. 3. Graph depicting the fisheries that sooty or dark shearwaters were chosen as predictors for, and the regression coefficients and standard error of the predictors. See Table 2 for key to species codes and Table 3 for key to gear codes.

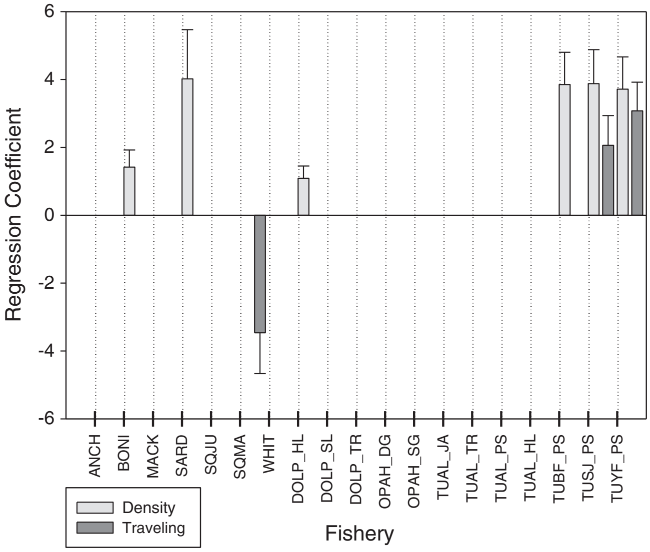

Fig. 4. Graph depicting the fisheries that pink-footed shearwaters were chosen as predictors for, and the regression coefficients and standard error of the predictors. See Table 2 for key to species codes and Table 3 for key to gear codes.

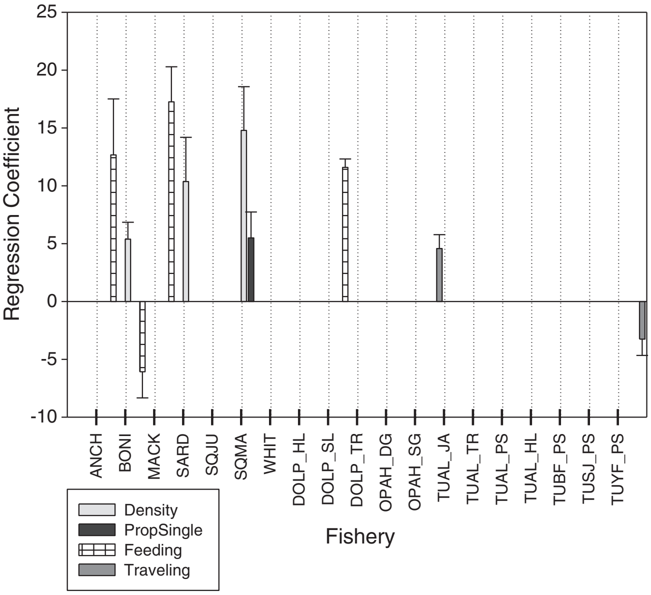

Fig. 6. Graph depicting the fisheries that black-vented shearwaters were chosen as predictors for, and the regression coefficients and standard error of the predictors. See Table 2 for key to species codes and Table 3 for key to gear codes.

potential to indicate both density and distribution of forage and/or predatory fish.

4.1. Species associations

Three faunal assemblages were identified by the covariation of the seven shearwater taxa and the 13 fish/squid species: fall, subtropical, and temperate. The fall species assemblage (short-tailed shearwater, flesh-footed shearwater, and bluefin tuna), identified by their negative loadings on PC 1, could potentially represent a shared seasonal signature, since these species visit the study area in the fall/winter. The short-tailed shearwater is a late fall migrant, whose abundance in the California Current peaks during winter (Ainley, 1976; Briggs et al., 1987). Similarly, bluefin tuna are primarily caught in the eastern Pacific during quarters 4 and 1 (Okamoto and Bayliff, 2003), and migrate to the western Pacific to spawn (Polovina, 1996). Flesh-footed shearwaters migrate south during the fall towards their breeding grounds in Australia and New Zealand (Ainley, 1976; Tuck and Wilcox, 2010).

Furthermore, the PC 1 pattern may also have been influenced by shared inter-annual patterns of abundance, since none of these species were sighted or caught during 2008. However, it is likely that these species responded differently to oceanographic conditions in the study area. Although 2008 was a cold year in the CCS, identified by strong upwelling and La Niña conditions, the lowest productivity was observed in waters off southern California (McClatchie et al., 2009). Thus, one possible explanation is that the two shearwaters, which are associated with higher latitudes, remained in the northern CCS where productivity was high, and the subtropical tuna maintained a southerly distribution off the coast of Baja California, where primary production was anomalously high. However, PC 1 should be interpreted with caution because

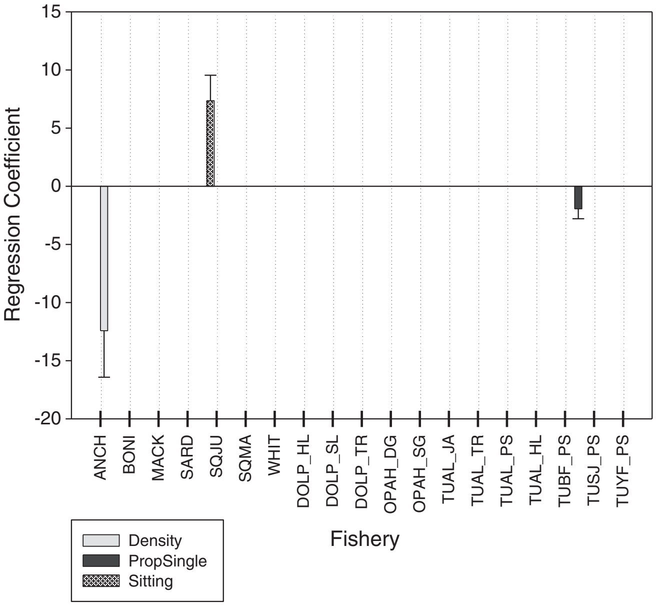

Fig. 5. Graph depicting the fisheries that Buller's shearwaters were chosen as predictors for, and the regression coefficients and standard error of the predictors. See Table 2 for key to species codes and Table 3 for key to gear codes.

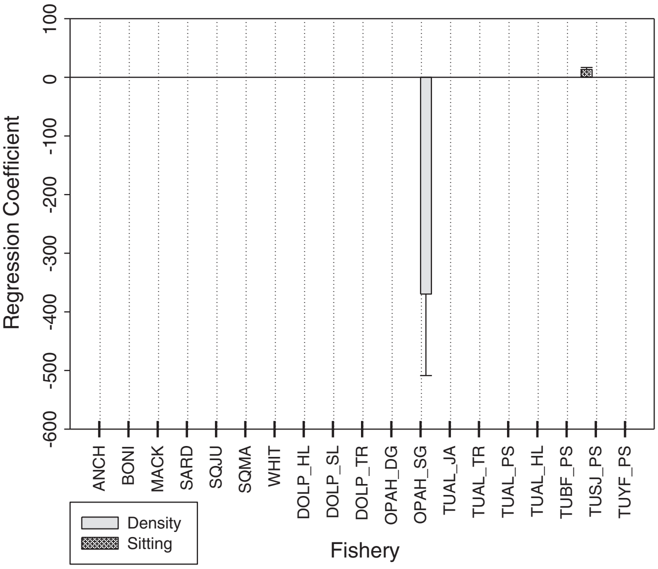

Fig. 7. Graph depicting the fisheries that flesh-footed shearwaters were chosen as predictors for, and the regression coefficients and standard error of the predictors. See Table 2 for key to species codes and Table 3 for key to gear codes.

the causes underlying the shared variability of these three species are unclear. Furthermore, this axis is highly influenced by the strong loading of the short-tailed shearwater (Fig. 2), which is a numerically rare species in the study area.

The subtropical and temperate species assemblages corresponded to known biogeographic affinities associated with latitudinal and temperature gradients. PC 2 quantified these shared patterns of shearwater and fish/squid species distributions and identified two species groupings (Fig. 2). A subtropical assemblage involved three shearwaters (pink-footed, black-vented, and flesh-footed) and four fish (bonito, dolphinfish, skipjack and yellowfin tuna). A temperate assemblage involved two shearwaters (sooty and dark), market squid, and five fishes (mackerel, bluefin tuna, opah, sardine, and anchovy).

Additionally, the ordination revealed habitat differences among the shearwater species. The short-tailed and black-vented differed from the other shearwater species, as evidenced by their negative PC 1 loading and their positive PC 3 loading, respectively (Table 5). These species represent the two opposite biogeographic "poles" of the shearwater community in the CCS: the subpolar short-tailed shearwaters have the northern-most distribution and the subtropical black-vented shearwaters have the southern-most distribution (Gould and Piatt, 1993).

4.2. Shearwaters as fishery predictors

The ability of shearwaters to explain fish availability is underscored by their wide applicability: 8 of the 19 fishery models had a shearwater metric as the primary predictor (selected first in the step-wise analysis). In fact, all of the shearwater metrics were chosen as predictors in the models, highlighting the utility of shearwater abundance, aggregation, and behavior. Finally, by creating different models for specific gears, we provided more accurate predictions that were gear sensitive. While it is a concern that multiple testing using many different shearwater variables could inflate the type I error rate, all models resulted in significance levels of $p < 0.01$.

In this study, the subtropical black-vented shearwater exhibited the most predictive power for the fishery species examined. Black-vented parameters were chosen as the first predictor for bonito, mackerel, dolphinfish caught with set longline, and opah caught with set gillnet. These fish species could be facilitators of prey capture by the shearwater. In particular, dolphinfish caught by set longline was the model with the best performance, 75% of the variance was explained by feeding black-vented shearwaters. The dominant shearwater in the system, the sooty shearwater, explained the most variance in the catches of three abundant fishery species: northern anchovy, market squid, and albacore tuna. Although pink-footed metrics were chosen as predictors in six fisheries, this species was only the strongest relative predictor for the bluefin tuna. Finally, because short-tailed and flesh-footed shearwaters are rare in the study area, their use as predictors proved rather limited.

The absence of covariation of jumbo squid and Pacific whiting with the shearwater community could be the result of the deep diurnal habits of these fish species, which migrate to the surface at night (Bailey et al., 1982; Gilly et al., 2006), whereas shearwaters forage during the day (Shaffer et al., 2009). Furthermore, jumbo squid catch is episodic (Field et al., 2007), and Pacific whiting have shifted their distribution north and offshore in the California Current since 1995 (Cooke et al., 2006).

4.3. Shearwater predictions

4.3.1. Sooty shearwater

The broad dark shearwater category was created to facilitate the use of the models for non-expert bird surveyors. However, since 99% of the dark shearwaters consisted of sooty shearwaters, these patterns reflect the most abundant shearwater in the system during the summer–fall (Ainley, 1976; Briggs et al., 1987). Therefore, the results of this species complex and of the numerically dominant sooty shearwater will be discussed together.

Sooty and dark shearwaters were positively associated with fish/squid species that occur in cold-water and coastal upwelling habitats, and negatively correlated with subtropical and offshore species (Fig. 3). In particular, these shearwaters were associated with their known prey, coinciding with previous research showing an increase in sooty shearwater density in the presence of higher densities of forage fish (Ainley et al., 2009). For instance, their density was positively correlated with anchovies and market squid, two important sooty prey items in California waters in the late summer/fall (Baltz and Morejohn, 1977; Chu, 1984).

These subarctic shearwaters were also associated with predatory fish. While the positive relationship with drift gillnet-caught opah is not clear, opah were associated with cold-water conditions, as evidenced by the predictive power of negative MEI indices for this fishery (Table 8). Similarly, sooty shearwater abundances increase after anomalously cool near-surface water temperatures off southern California (Hyrenbach and Veit, 2003). Conversely, dark shearwaters were negatively correlated with subtropical skipjack and yellowfin tunas, whose distribution is limited to warm surface waters (SST > 17°°C) (Barkley et al., 1978; Block et al., 1997). Additionally, commuting, rather than aggregating shearwaters, were associated with albacore tuna caught with jig. While sooty shearwaters are found inshore of the 2000-m isobath in association with cool upwelling plumes (Briggs et al., 1987; Yen et al., 2006), albacore tuna are associated with the North Pacific transition zone, and concentrate on the offshore (clear and warm) side of fronts delineating coastal upwelling centers (Laurs, 1983; Laurs et al., 1977).

4.3.2. Pink-footed shearwater

Since pink-footed shearwater metrics were significant predictors for fishery species with warm-water affinities (Fig. 4), they are useful indicators for conditions favorable for subtropical fish. For example, bonito and dolphinfish expand their range northward when sea surface temperatures increase, such as during El Niño (Norton, 1999; Pearcy et al., 1985; Schoener, 1985). In contrast to sooty shearwaters, pink-foots were positively associated with the two subtropical tunas (skipjack and yellowfin), and the bluefin tuna. Although bluefin can inhabit cooler waters than skipjack and yellowfin, they are most often found in subtropical surface waters (>17 °C) in the eastern Pacific (IATTC, 2001). However, pink-footed shearwaters have also been positively associated with higher densities of temperate predatory fish such as salmon (Ainley et al., 2009). Finally, pink-footed density was a predictor for sardines, which are more abundant and range over larger expanses during warm water conditions in the California Current (Chavez et al., 2003; Emmett et al., 2005).

Furthermore, pink-footed shearwaters exhibited different behavioral associations with predatory and forage fisheries. Traveling pink-foots were associated with predatory tunas (skipjack and yellowfin) that are highly migratory, whereas stationary shearwaters were correlated with a prey species (market squid). This disparity underscores the value of recording seabird behavioral metrics during at-sea surveys.

4.3.3. Buller's shearwater

Buller's shearwaters were indicative of oceanic fish species seaward of the shelf (Fig. 5). This result is to be expected for this species, which exhibits the most offshore distribution of the shearwater community, and inhabits deep, warm, and clear oceanic waters (Briggs et al., 1987). While Buller's densities were negatively related to anchovy catch, a high proportion of stationary behavior was positively correlated with sardines, suggesting that they are a more important prey source than anchovies for these shearwaters. Anchovies spawn closer to the coast within upwelling centers, whereas sardines spawn in transitional waters offshore (Checkley et al., 2000). Additionally, aggregations of Buller's were significant predictors of bluefin tuna catches. Both Buller's and bluefin migrate west through the study area on trans-Pacific migrations: the shearwaters return to New Zealand (Ainley, 1976; Everett and Pitman, 1993), and the tuna migrate towards the western Pacific (Okamoto and Bayliff, 2003; Polovina, 1996).

4.3.4. Black-vented shearwater

As expected, black-vented shearwater metrics were associated with fish/squid species with onshore and southern distributions, and with fisheries that expand during warm water periods (Fig. 6). During this study, black-vents were only sighted south of Monterey and onshore of the 2000-meter isobath, reinforcing previous descriptions of their coastal and southern distribution in the CCS (Ainley, 1976; Briggs et al., 1987). Moreover, this subtropical shearwater increases in abundance during warm-water seasons (fall) and years (El Niño) off California (Hyrenbach and Veit, 2003).

For example, high densities of black-vents were associated with bonito, although the shearwaters were engaged in non-feeding behavior. While this covariation was caused by the low latitude associations of these species, as demonstrated by the PCA, these southern waters might represent where the shearwaters are migrating into the CCS, yet not actively foraging. Moreover, black-vented shearwaters were observed traveling (transient behavior) through the cold-water conditions associated with set gillnet-caught opah, yet using (stationary behavior) areas occupied by the subtropical yellowfin tuna.

The importance of the foraging metric was illustrated by the relationship of feeding black-vented shearwaters with three fisheries: dolphinfish, jack mackerel, and anchovy (Fig. 6). The correlation with the two predatory fish could be due to shared expansion into the study area during warm water conditions. Dolphinfish and jack mackerel abundance increase off California during warm-water conditions. For example, during the 1983–1984 El Niño, mackerel became the most abundant fish species caught in purse seines, replacing market squid (Pearcy et al., 1985). Another possibility is that the predatory fish facilitated prey capture by the black-vented shearwaters.

The different behaviors associated with the three prey species examined reinforce the utility of evaluating multiple at-sea metrics. Black-vented shearwaters appear to be feeding on anchovies close to the coast, yet are indicators of warm-water conditions favorable to sardines, as suggested by their feeding behavior being a predictor of anchovies, and their density being positively correlated to sardine catches. Interestingly, although market squid catch was correlated with black-vented shearwater density, it was positively correlated with non-aggregating birds, defined by a higher proportion of solitary birds.

4.3.5. Flesh-footed shearwater

The contrasting relationship of flesh-footed shearwaters with opah and bluefin tuna (Fig. 7) suggests a correlation based on SST affinities. Their density was negatively correlated with set gillnet-caught opah, which was correlated with cooler water conditions, whereas flesh-foots are not sighted in the CCS during periods of cold water anomalies (Ainley, 1976). Stationary flesh-foots were positively correlated with bluefin tuna caught with purse seine. Yet, it is not known whether these shearwaters attend purse seine vessels at sea, or both species are responding to warm-water conditions and onshore incursions of clear, offshore water. However, due to the infrequent sightings of flesh-footed shearwaters, these results should be interpreted with caution.

4.3.6. Short-tailed shearwater

Short-tailed shearwater metrics were not a significant predictor of any of the fisheries examined, reinforcing the lack of clear associations with the fish/squid species demonstrated by the PCA (Fig. 2). However, this result could also be influenced by the seasonal coverage of the SWFSC cruises. Because these shearwaters arrive late in the season, late summer–early fall cruises may not fully capture the distribution patterns and habitat associations of this species.

5. Conclusions

Shearwaters can serve as bio-indicators of ecosystem responses to changing oceanographic conditions, and may be more insightful than environmental indices for ecosystem models. More specifically, because shearwater abundance, aggregation and behavior indicate the availability of their prey (forage fish and squid) and upper-trophic level fish to fisheries, they can enhance EBM of the California Current. This information can inform the Pacific Fisheries Management Council's development of fishery-independent ecosystem indicators for inclusion into stock assessments (PFMC, 2013). Seabird parameters have a demonstrated use in fisheries management, such as the use of black-legged kittiwake (*Rissa tridactyla*) breeding success data towards the management of the sandeel (*Ammodytes marinus*) fishery in the North Sea (Einoder, 2009). Additionally, quantifying and monitoring the covariation between seabirds and commercial fish can help to discriminate natural versus human-induced drivers of fisheries (Aebischer et al., 1990).

Resolving the spatial/temporal mismatch between shearwater surveys and fishing effort in order to generate predictions remains challenging. The SWFSC surveys are unique in their extensive spatial coverage of the CCS, however, there are disadvantages inherent to the large-scale sampling design and lack of space–time replication of these cruises. Additionally, the onshore–offshore separation of the catch data was inhibited by the inherent CDFW sampling grid, with overlap between the designated large blocks (extending from shore out to the U.S. EEZ), and the small coastal blocks.

Predictions at a smaller spatial scale would improve the utility of these models by increasing their temporal resolution and facilitating the spatial delineation of oceanographic features known to enhance fish catch. For example, focused fine-scale vessel surveys in the Southern California Bight in the fall could tease apart the mechanisms behind the covariation of black-vented shearwaters and dolphinfish (e.g. Hyrenbach and Veit, 2003; Yen et al., 2006). Furthermore, such disjunct surveys, focused on specific geographic areas and time periods, could be integrated with data from tagging studies, to develop regional and CCS-wide metrics of shearwater distribution, abundance, and behavior (Adams et al., 2012).

In conclusion, this research underscores the potential for using shearwaters as fishery-independent predictors of commercially important target species. More specifically, this study builds upon past research by examining multiple fishery species that have commercial importance and have been found to exhibit climate induced variability in the CCS. Yet, rather than using breeding seabirds, we have used at-sea density, aggregation, and behavior metrics of non-breeding shearwaters, which are free from central-place foraging constraints. The six species that we examined are effective indicators of fisheries perhaps because all are heavy-body, high wing loading shearwaters (Spear and Ainley, 1997), and while they can travel rapidly to exploit feeding opportunities, they also have a higher energetic cost of flight and are constrained to areas where prey availability or foraging opportunities are abundant. Furthermore, the metrics we developed are easily quantified using observations being routinely collected by at-sea survey programs, and are more practical than other variables traditionally used in the past (such as density), which require substantial post-cruise processing. Thus, we advocate the operationalization and wide use of these metrics in the CCS.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jmarsys.2014.08.010.

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Appendix.

Results of 1) pair-wise cross-correlations and 2) paired t-tests (2 gear types) or repeated measures ANOVA (> 2 gear types). For species with more than 2 gear types (indicated by *), only the most significant results are shown. Results are also shown for whether gear type was chosen as a predictor in the regression models. Based on these results, the final regression models for each species are listed. See Table 2 for key to species codes and Table 3 for key to gear codes.

	Correlation		**T-test/ANOVA**			**Regression**	
Species	**r^2**	**p-value**	**t**	**F**	**p-value**	**Gear chosen**	**Final models**
ANCH	0.57	<0.001	2.47		0.02	no	ANCH
BONI	0.00	0.79	1.87		0.07	no	BONI
DOLP*	0.24	<0.001		5.81	0.01	yes	DOLP _ HL, DOLP_SL, DOLP_TR
MACK	0.23	<0.001	1.96		0.05	no	MACK
OPAH	0.25	<0.001	6.52		0.00	yes	OPAH_DG, OPAH_SG
SARD	0.54	<0.001	1.70		0.09	no	SARD
SQJU	0.42	<0.001	0.52		0.61	no	SQJU
SQMA	0.56	<0.001	3.49		0.00	no	SQMA
TUAL*	0.21	<0.001		30.97	0.01	yes	TUAL_HL, TUAL_JA, TUAL_PS, TUAL_TR
TUBF	n/a	n/a	n/a		n/a	n/a	TUBF_PS
TUSJ	n/a	n/a	n/a		n/a	n/a	TUSJ_PS
TUYF	n/a	n/a	n/a		n/a	n/a	TUYF_PS
WHIT	0.00	0.79	0.13		0.89	no	WHIT