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Applied Fisheries Oceanography

Ecosystem Indicators of Ocean Conditions Inform Fisheries Management in the California Current

By William T. Peterson, Jennifer L. Fisher, Jay O. Peterson, Cheryl A. Morgan, Brian J. Burke, and Kurt L. Fresh

ABSTRACT. Fisheries oceanography is the study of ecological relationships between fishes and the dynamics of their marine environments and aims to characterize the physical, chemical, and biological factors that affect the recruitment and abundance of harvested species. A recent push within the fisheries management community is toward ecosystem-based management. Here, we show how physical and biological oceanography data can be used to generate indicators of ocean conditions in an ecosystem context, and how these indicators relate to the recruitment of salmonids, sablefish, sardines, and rockfish in the California Current.

INTRODUCTION

Fisheries oceanography includes at least three classes of studies: (1) determination and estimation of the parameters that define the habitats of different life-history stages of fishes, (2) integrated assessment of the "health" of the ecosystems supporting fished species, and (3) assessment of the effects of climate variability and future climate change on growth, survival, and the abundance of fish entering a targeted population (recruitment). Armed with information on fish ecology, ecosystem structure, habitat suitability, and climate variability, fisheries managers should be able to better understand recruitment variability. Moreover, by understanding the drivers of recruitment variability, this information could be of sufficient detail to provide outlooks for the recruitment of target species in advance of harvest.

The central and southern California Current has been a focal point for fisheries oceanographic studies for decades, primarily as a result of the collapse of the Pacific sardine (Sardinops sagax) population in the 1940s and subsequent replacement of sardines by northern anchovy (Engraulis mordax). The dramatic collapse of the sardine fishery became the impetus for the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program, initiated in 1949 (McClatchie, 2014). Research by CalCOFI scientists has focused, and continues to focus, on relationships between environmental variability and recruitment of sardine, anchovy, mackerel, rockfish, and squids, with emphasis on the relative roles of local upwelling vs. large basin-scale climate cycles such as the El Niño-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO).

Much less attention has focused on the recruitment variability of fished stocks

assessed by the National Oceanic and Atmospheric Administration/National Marine Fisheries Service (NOAA/NMFS) in the northern California Current, such as Pacific hake (Merluccius productus), rockfish (Sebastes spp.), and salmonids (Oncorhynchus spp.). One notable exception is the rockfish recruitment assessment surveys that are conducted in the central California Current (Ralston et al., 2013). To better understand the biophysical drivers of recruitment variability in the northern California Current, we initiated a seagoing sampling program off Newport, Oregon, at 44.7°N in 1996. This intensive sampling program tracks variations in physical and biological oceanographic conditions on a fortnightly basis throughout the year. Variables measured include vertical profiles of temperature and salinity; water sampling for nutrients and phytoplankton biomass and species composition; and plankton net tows for determination of biomass and species composition of copepods, krill, fish eggs, fish larvae, and crustacean larvae. The long-term goal of this program is to gather a time series of both biological and physical variables that would be useful for explaining variability in recruitment of commercially fished species, with an emphasis on variables associated



with the structure of the food chain upon which fishes feed either as larvae or juveniles (Figure 1). The year 2015 will mark the twentieth year of this rich and growing sampling program, which investigates correlations between various measures of physical and biological oceanographic conditions and the recruitment variability of fished species in the California Current. Here, we describe our efforts to explain recruitment variability of Pacific salmon and how similar approaches may be applied to sablefish, sardines, and rockfish.

With respect to salmonids from waters of the Pacific Northwest, previous studies have documented significant correlations between adult salmon returns with single environmental indicators such as the PDO (Mantua et al., 1997; Rupp et al., 2012), the biomass of cold-water "northern" copepods (Peterson and Schwing, 2003), and the biomass and species composition of ichthyoplankton species (Daly et al., 2013). Based on work by Pearcy (1992) and Hare and Francis (1995), in most years, the first few weeks (or at most, the first summer) that young salmon spend at sea appears to be when yearclass strength is set. Thus, we reasoned that by using physical and biological indicators of ocean conditions measured

at multiple scales during this critical survival period for salmon, we could garner a better understanding of conditions favorable and unfavorable for the survival of juvenile salmon, and provide an outlook on the number of adults returning to the Columbia River to spawn in future years. Our goal was to offer information that was easily adaptable to other species and easily interpretable and available to fisheries oceanographers, managers, and the public (http://www.nwfsc.noaa.gov/ oceanconditions).

The use of physical and biological ecosystem indicators at multiple scales is a rather unique approach to fisheries management (e.g., Burke et al., 2013). To characterize the oceanic environment influencing different life-history stages, we use basin-scale drivers (e.g., PDO, ENSO) as indices of transport in the California Current (CC), and we employ regional and local in situ data collected from our high-frequency, long-term sampling off Newport, Oregon, to characterize seasonal, interannual, and decadal changes in coastal upwelling and food chain structure (species composition of copepods and the ichthyoplankton taxa) that supports the larvae, juveniles, and adults of many fished species (Figure 1). Using such a broad variety of data across multiple spatial scales (basin-scale to local), and incorporating data from direct and frequent observations, allows us to take an ecosystem approach to characterizing ocean conditions. By measuring biophysical conditions at fortnightly time scales throughout the year, tailored indicators can be developed for individual species that match key bottlenecks in their life history where recruitment is largely determined.

In this paper, we describe the 15 ecological indicators used to provide outlooks (forecasts) for salmon returns to the Columbia River. We briefly describe the role each indicator plays in the ecology of Pacific salmon and show how these same indicators may inform the recruitment variability of sablefish in the northern CC, rockfish in the central CC, and sardines in the southern CC. We also discuss emerging issues of relative importance to future climate scenarios and how we can apply existing knowledge to these (and unknown) scenarios to draw inferences on potential impacts to the ocean ecosystem.

OCEAN ECOSYSTEM INDICATORS

Our forecasting includes three basin-scale physical indicators (related to the PDO and the ENSO), five local-scale physical



FIGURE 1. Conceptual diagram showing the influence (arrows) of basin-scale PDO, NPGO, ENSO) and local-scale (upwelling, temperature, salinity) physical forces on the study region described (red circle), and resultant food chain structure. PDO = Pacific Decadal Oscillation. NPGO = North Pacific Gyre Oscillation. ENSO = El Niño–Southern Oscillation.

indicators (related to water mass properties such as temperature and salinity), and seven local-scale biological indicators (related to food chain structure and catches of juvenile salmon). These indicators have three sources: (1) various websites, (2) field collections from fortnightly oceanographic sampling along the Newport Hydrographic Line (44.7°N) since 1998, and (3) juvenile salmonid surveys conducted in June and September 1998-2013 (see http://www.nwfsc.noaa.gov/ oceanconditions for details). Indicators are compiled across different time periods that correspond to the critical life-history period of salmon or to characterize physical attributes of the system.

The Pacific Decadal Oscillation

The PDO index is defined as the leading principal component of North Pacific monthly sea surface temperature variability poleward of 20°N. Monthly values are available at http://www.jisao. washington.edu/pdo. The spatial pattern of the PDO has two phases, a warm and a cool phase, depending on the sign of sea surface temperature anomalies along the Pacific coast of North America. The oscillation between the warm and cool phases is modulated by the direction from which winds blow in the North Pacific. When the winds are primarily from the southwest, warmer conditions occur in the northern CC due to onshore transport

of subtropical waters. Conversely, when winds are primarily from the north, upwelling occurs in the open ocean (Ekman pumping), leading to cooler conditions in the northern CC. Recent work indicates that ocean conditions during both winter and summer are biologically relevant to multiple species in the CC (Black et al., 2011); therefore, we use a winter (December through March) and a summer (May through September) PDO index to characterize the basin-scale forcing and ocean conditions.

The Oceanic Niño Index

The Oceanic Niño Index (ONI) is currently used by NOAA to provide forecasts of El Niño activity and is defined as the three-month running mean of sea surface temperature anomalies in the Niño 3.4 region of the equatorial Pacific (5°N-5°S, 120°-170°W). An El Niño event is defined to occur when the ONI index exceeds 0.5°C for five consecutive months (http://www.cpc.ncep.noaa.gov/ products/analysis_monitoring/ensostuff/ ensoyears.shtml). We use the ONI values for January through June to characterize El Niño activity, as these are the months when most El Niño events are generated at the equator. We have observed that a persistent phase change in either the PDO index or the ONI index leads to rapid changes in ocean conditions (indexed by temperature and salinity properties and

zooplankton community composition) in the northern CC. Therefore, we consider both the PDO and ONI as strong drivers of ocean conditions in this region.

Temperature and Salinity

Variations in marine survival of salmon often correlate with variations in ocean conditions. For example, cold conditions are generally more productive and therefore good for Chinook (Oncorhynchus tshawytscha) and coho (O. kisutch) salmon, whereas warm conditions are not (Pearcy, 1992). We use multiple measures of ocean temperature and salinity to capture different oceanographic processes that can be favorable or unfavorable for salmon survival. Sea surface temperature (SST) data are from the National Data Buoy Center buoy 46050 (http://www. ndbc.noaa.gov/station history.php? station=46050) located 37 km offshore on the Newport Hydrographic Line. We use a composite May to September average, which characterizes surface temperatures during the main upwelling season. We augment the SST data with measurements of temperature and salinity collected from our indicator station (NH-5) located five nautical miles (9.3 km) off Newport, Oregon. Juvenile salmon inhabit the upper water column in the photic zone where productivity is highest (Pearcy, 1992; Emmett et al., 2004). The temperatures across the upper 20 m are therefore averaged to index conditions for the preferred habitat of juvenile salmon. Further, temperature and salinity from a depth of 50 m are used to characterize the types of water that upwell onto the continental shelf during the summer months. Deepwater temperature and salinity are good indices of the strength of upwelling because the sources of very cold, salty waters are usually deeper (and have higher nutrient content) than waters that are warmer and fresher.

Copepod Species

As plankton, copepods drift with the ocean currents and are therefore good indicators of the type and the sources of

water transported into the northern CC. Copepod biodiversity (or species richness) is the number of copepod species in a plankton sample. During summer, species richness is low because sub-Arctic waters dominate, and these waters naturally contain zooplankton assemblages of low diversity (Hooff and Peterson, 2006). During winter, the opposite pattern prevails-coastal waters are fed by the poleward flowing Davidson Current, which brings a highly diverse assemblage of subtropical copepods to the northern CC. Although copepod biodiversity changes greatly on a seasonal cycle, basin-wide climatological indices, such as the PDO and ENSO, can also influence diversity in coastal waters. During negative (cool) periods of the PDO, species diversity is low, and when the PDO is positive (warm) or during El Niño events, species diversity is high (Hooff and Peterson, 2006). To index the biological response to climatological indices during the summer upwelling months, we use the monthly copepod diversity anomaly (seasonal cycle removed) from May to September because this is the period of strongest upwelling in the northern CC.

These seasonal and interannual changes in copepod diversity are further illustrated by anomalies of the biomass of "northern" species (which are dominants in the coastal Gulf of Alaska and Bering Sea) and "southern" species (which are dominants in oceanic waters offshore of Oregon and in coastal waters off central and southern California) (Peterson and Miller, 1977). The presence of coastal, sub-Arctic species indicates transport of coastal, sub-Arctic waters from the north; likewise, the presence of subtropical species indicates transport of subtropical water into the northern CC from offshore of Oregon or from the south via the poleward Davidson Current (Bi et al., 2011; Keister et al., 2011). Transport also appears to be related to the PDO. When the PDO is in negative phase, waters that feed the CC and upwell onto the shelf are more sub-Arctic, leading to coldwater copepod species domination in the

zooplankton off Oregon during summer and to positive anomalies of cold-water copepods. In contrast, when the PDO is in positive phase, subtropical water dominates the coastal CC, leading to positive anomalies of warm-water copepods and negative anomalies of cold-water copepods (Hooff and Peterson, 2006; Chhak et al., 2009; Bi et al., 2011; Di Lorenzo et al., 2013). Species within these two groups are often referred to as "indicator" or "sentinel" species, because changes in their abundances typically indicate a substantial shift in ecosystem structure. Although the two groups are correlated, they capture differences in transport that can greatly alter the productivity of the food chain. The significance of alternating copepod communities is that coldwater copepod species have relatively high concentrations of lipids, whereas the warm-water species are relatively deplete of lipids (Lee et al., 2006). Thus, the base of the pelagic food chain in the coastal upwelling zone off Oregon can have very different bioenergetic and nutritional content, depending on the phase of the PDO. To index the copepod response to climatological indices during the summer upwelling months, we use anomaly values averaged over May through September because this is the period of strongest upwelling in the northern CC.

Biological Spring Transition

The biological spring transition is defined as the date each year when the copepod community has transitioned from a winter (warm water) community to a summer (cold water) community (Keister et al., 2011); it can be thought of as a measure of when the poleward Davidson Current has been replaced by equatorward-flowing shelf waters that appear after the onset of the coastal upwelling season. We suggest that the timing of the onset of the summer copepod community may be a more useful indicator of the physical transition from seasonal downwelling to seasonal upwelling because it indicates the first appearance of the kind of food chain that seems most favorable for salmon, sardines, and sablefish. This community is dominated by large, lipid–rich copepods, euphausiids, and juvenile forage fish that help fuel a lipid-rich and productive food web.

Ichthyoplankton

It is difficult and expensive to sample the juvenile fish species that young salmon feed upon during their first few months at sea. However, the abundance of the larval stages of these species during the months preceding the ocean entry of juvenile salmon is thought to be a good indicator of food availability when young salmon go to sea (Daly et al., 2013). Therefore, to index the food available to juvenile salmon, we use the abundance of latestage fish larvae (ichthyoplankton) averaged from January to March.

Juvenile Salmon Catch

The catches of yearling Chinook salmon in June and catches of juvenile coho salmon in September from pelagic trawl surveys are used to index the relative ocean abundance of these two species of juvenile salmonids.

Fish Recruitment Data

The suite of ocean indicators described above characterizes ocean conditions for salmon during their first summers at sea and are hypothesized to influence

William T. Peterson (bill.peterson@noaa.gov) is Senior Scientist and Oceanographer, National Oceanic and Atmospheric Administration (NOAA), Northwest Fisheries Science Center (NWFSC), Newport, OR, USA. Jennifer L. Fisher is Faculty Research Assistant, Jay O. Peterson is Research Associate, and Cheryl A. Morgan is Senior Faculty Research Assistant, all at the Cooperative Institute for Marine Resources Studies, Oregon State University, Newport, OR, USA. Brian J. Burke is Fisheries Biologist and Kurt L. Fresh is Fisheries Biologist, both at NOAA, NWFSC, Seattle WA, USA. survival during this critical time period. However, we have very little abundance or survival data for this time period, so we correlate ocean conditions with the abundance of adult Chinook salmon that return to the Columbia River two years later. Counts of adult salmon passing Bonneville Dam are found on the Columbia River Data Access Real Time website (http://www.cbr.washington.edu/ dart/query/adult_graph_text). Sablefish recruitment data are obtained from the Pacific Fisheries Management Council (http://www.pcouncil.org/groundfish/ stock-assessments/by-species/sablefish) and sardine data from the Pacific Fishery Management Council Stock Assessment and Fishery Evaluation Report (http:// www.pcouncil.org/coastal-pelagicspecies/stock-assessment-and-fisheryevaluation-safe-documents). The rockfish recruitment index is derived from the recruitment patterns of ten rockfish species (see Ralston et al., 2013, for details)

MATCHING OCEAN INDICATORS TO FISH RECRUITMENT Salmon

Salmon returns to the Columbia River are linked to the PDO, with higher returns of adult spring-run Chinook salmon (fish that return to spawn from mid-March to May) typically occurring when the PDO is in negative phase (before 1977 and after 1998) and lower returns occurring during positive PDO years (1978-1997) (Figure 2). Returns were so low in the mid-1990s that many Columbia River salmon stocks were listed as threatened or endangered. Fall-run Chinook salmon (fish that return to spawn from August through mid-November) exhibited a similar pattern, except that responses to both negative and positive phases of the PDO were not pronounced until after the regime shift in 1998 when returns began to increase significantly, continuing to the present, with record returns reported for fish returning in 2013 and 2014. There have been two recent pronounced "regime shifts" in the Pacific Northwest, when the PDO shifted sign in 1977 and 1998. Anomalies of salmon returns also changed sign two or three years following each regime shift. The correlations of the PDO with spring or fall Chinook salmon (not shown) are both highly significant (p < 0.01), and the variance explained is 47% and 41%, respectively.

Table 1 shows values for each of the 15 indicators, ranked and color-coded based on their impact to salmon, shown in Table 2. The color-coding illustrates the degree to which each individual



FIGURE 2. Bar chart showing the values of (A) the Pacific Decadal Oscillation integrated (PDO) from May through September annual anomalies of and the number of (B) adult spring Chinook and (C) fall Chinook salmon passing Bonneville Dam (the most downstream dam on the Columbia River). The two vertical lines mark the two recent "regime shifts" (major shifts in the sign of the PDO) in 1976 and 1998. Note that two or three years after each regime shift, the anomalies of salmon returns changed sign.

indicator suggests either "good" (green), "neutral" (yellow), or "poor" (red) conditions for salmon based on the number that returned to spawn. Patterns are readily observed with this color-coding system. For example, most of the indicators for 1998 and 2005 were red, indicating poor ocean conditions for salmon during the summers of those two years. Catches of juvenile Chinook and coho salmon during at-sea surveys in June and September, respectively, in those two years were very poor (1998: rank 15 out of 16 for Chinook and 11 out of 16 for coho salmon; 2005, rank 16 out of 16 for Chinook and rank 14 out of 16 for coho salmon, Table 2), indicating poor survival during the first few weeks (Chinook salmon) or months (coho salmon) that the juveniles were at sea. Not surprisingly, adult returns of Chinook salmon entering the ocean in 1998 and 2005 were the two lowest out of the 16 years (Figure 3). In stark contrast, ocean conditions were very good in 2008 (almost all green) and mostly good to neutral during 1999-2001 and during 2011-2012. Each of these years was characterized by negative values of the PDO and ONI, as well as cooler ocean temperature. Adult returns of Chinook salmon that entered the ocean during these years were the highest in the past 16 years (Figure 3).

Individual indicators can provide good insights into the drivers of recruitment. For example, the northern copepod biomass indexes the lipid content of the food chain and seems to be a good indicator of the source waters that feed the northern CC. However, we have found that composite indicators seem to have higher explanatory power (Burke et al., 2013). Table 1 provides example composite indices (compiled from the 15 indicators), the Principal Component (PC) scores PC1 and PC2. This procedure reduces the number of variables in the data set as much as possible, while retaining the bulk of information contained in the data (a sort of weighted averaging of the indicators). The first principal component (PC1) explains 52% of the ecosystem

variability among years, while the second principal component explains 14%. The PC1 scores compiled from the 15 ocean indicators explain 60% of the variance in adult salmon returns and account for more of the variance than did the PDO alone (Figure 3).

Sablefish, Sardine, and Rockfish

The first principal component (PC1) of the 15 indicators also explains 36% of the variability in sablefish recruitment in the northern CC and 49% of the variability in sardine recruitment in the southern CC (Figure 3). However, there was no significant relationship between PC1 and rockfish recruitment to the central CC. PC1 is a composite index of biophysical indicators tailored to the critical lifehistory period for salmon in the northern CC, which is thought to be during their first summer at sea (May through September). Similar to salmon, juvenile sablefish and sardines develop during the spring and summer (May through September). Sablefish larvae first appear in deep, offshore waters in winter and move onto the shelf as they reach the juvenile stage in spring and early summer (McFarlane and Beamish, 1992). Sardine eggs are spawned in spring and hatchlings reach juvenile stage by summer. Therefore, it is not surprising that the indicators developed for salmon hold promise for sablefish and sardine. On the contrary, the critical developmental time period for rockfish is the autumn-winterspring (October through May; Ralston et al., 2013). Rockfish spawn in autumn and winter, and larvae and pelagic juveniles are most abundant from December to June (Wyllie Echeverria, 1987; Laidig, 2010). Because many of the indicators are compiled over the summer to match the life history of salmon, it is not surprising that ocean conditions during this time period are not related to the recruitment of rockfish that develop during a different

TABLE 1. Indicators presently used to forecast salmon returns to the Columbia River and to coastal rivers of Washington and Oregon. Indicators are averaged over time periods relevant to critical life-history periods of salmon, such as the months when juvenile salmon first enter the ocean or to characterize physical attributes of the system. PDO = Pacific Decadal Oscillation. ONI = Oceanic Niño Index. SST = Sea surface temperature.

Ecosystem Indicators								Ye	ar							
	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
			r				1			1		1		1		1
PDO (°C anomaly; Dec–Mar)	5.07	-1.75	-4.17	1.86	-1.73	7.45	1.85	2.44	1.94	-0.17	-3.06	-5.41	2.17	-3.65	-5.07	-1.67
PDO (°C anomaly; May–Sep)	-0.37	-5.13	-3.58	-4.22	-0.26	3.42	2.96	3.48	0.28	0.91	-7.63	-1.11	-3.53	-6.45	-7.79	-3.47
ONI (°C anomaly; Jan–Jun)	1.08	-1.10	-1.13	-0.42	0.23	0.33	0.20	0.37	-0.38	0.02	-1.05	-0.27	0.70	-0.77	-0.42	-0.38
			1				1	1	1			1		1		1
46050 SST (°C; May–Sep)	13.66	13.00	12.54	12.56	12.30	12.92	14.59	13.56	12.77	13.87	12.39	13.02	12.92	13.06	13.26	13.37
Upper 20 m T (°C; Nov–Mar)	12.27	10.31	10.12	10.22	10.08	10.70	10.85	10.60	10.61	10.04	9.33	10.19	11.01	10.02	9.62	10.09
Upper 20 m T (°C; May–Sep)	10.38	10.13	10.19	9.77	8.98	9.62	11.39	10.73	9.97	9.99	9.30	9.90	10.14	10.05	9.95	10.63
Deep temperature (°C; May–Sep)	8.61	7.63	7.74	7.56	7.45	7.81	7.89	7.97	7.83	7.58	7.48	7.73	7.89	7.86	7.56	8.30
Deep salinity (May–Sep)	33.54	33.86	33.78	33.86	33.85	33.68	33.66	33.77	33.85	33.88	33.87	33.72	33.61	33.74	33.75	33.70
			1									- 1				
Copepod richness anomaly (no. species; May–Sep)	4.4	-2.8	-3.6	-1.3	-1.4	1.7	1.2	4.1	2.5	-0.9	-1.0	-0.9	2.9	-2.4	-1.5	-3.2
N. copepod biomass anomaly (mg m ⁻³ ; May–Sep)	-0.58	0.09	0.19	0.15	0.28	-0.08	0.05	-0.77	0.14	0.14	0.31	0.14	0.25	0.42	0.40	0.35
S. copepod biomass anomaly (mg m ⁻³ ; May–Sep)	0.62	-0.30	-0.28	-0.29	-0.30	0.09	0.22	0.55	0.10	-0.10	-0.31	-0.22	0.24	-0.15	-0.23	-0.26
Biological transition (day of year)	263	134	97	79	108	156	132	238	180	81	64	65	169	82	125	91
lchthyoplankton (mg 1,000 m ⁻³ ; Jan–Mar)	0.12	0.90	1.80	1.25	1.05	0.53	0.58	0.83	0.59	0.60	1.84	0.89	1.65	0.61	0.99	1.16
Chinook salmon juvenile catches (no. km ⁻¹ ; Jun)	0.26	1.27	1.04	0.44	0.85	0.63	0.42	0.13	0.69	0.86	2.56	0.97	0.89	0.46	1.32	1.38
Coho salmon juvenile catches (no. km ⁻¹ ; Sep)	0.11	1.12	1.27	0.47	0.98	0.29	0.07	0.03	0.16	0.15	0.27	0.01	0.03	0.30	0.13	NA
Principal Component scores (PC1)	6.58	-2.18	-2.93	-1.56	-2.07	2.19	3.11	4.28	1.00	-0.24	-4.41	-0.96	1.67	-1.40	-2.07	-1.01
Principal Component scores (PC2)	0.04	0.21	0.42	-1.04	-2.20	-1.73	2.24	-0.73	-1.18	0.15	-0.78	0.58	-0.35	1.24	0.96	2.16

time period. The cold water "northern" copepod population is known to be a good index of alongshore transport (Bi et al., 2011, Keister et al., 2011). When the northern copepod anomaly is compiled over the critical development time period for rockfish (October through May), this single indicator explains 42% of the variability in the pattern of rockfish recruitment in the central CC (not shown). These initial results with an existing suite of indicators, and a single indicator, are promising. However, to rigorously apply this approach to other species, we would want to select indicators that best represent the ocean conditions when and where those species are developing.

DISCUSSION

The strength of our combined bio/ physical indicator approach comes from the fact that biological indicators are more likely to directly influence (or correlate with conditions that influence) the success of marine fish species during the critical first year at sea compared to relying solely on a single indicator such as the PDO. Indeed, when temporal variations in the local physical and biological indicators were compared to the PDO, we gained new insights into the mechanisms that lead to success or failure of salmon runs and recruitment of other commercially important fishes. These results have led to one of our major working hypotheses: that the returns of salmon and recruitment of other fishes seems to be related to environmental variability due to interannual variations in the bioenergetic content of their food base (juvenile pelagic fish and euphausiids), which is in turn driven by variations in species composition of phytoplankton and copepods. That is, when the PDO is in a negative phase, the base of the food chain is anchored by lipid-rich cold-water copepods, and when the PDO is in positive phase, lipid-poor warm-water copepods dominate. The mechanism that links the PDO with copepods (and ultimately fish) is through the transport processes that control the source waters that feed the

TABLE 2. Indicators presently used to forecast salmon returns to the Columbia River and to coastal rivers of Washington and Oregon. The values of each indicator from Table 1 are ranked from high to low and color-coded based on their impact on salmon. Lower numbers (1–5) indicate better ocean ecosystem conditions, or "green lights" for salmon growth and survival. Higher numbers (12–16) indicate poor ("red light") conditions.

Ecosystem	Year															
Indicators	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
PDO (°C anomaly; Dec-Mar)	15	6	3	11	7	16	10	14	12	9	5	1	13	4	2	8
PDO (°C anomaly; May–Sep)	10	4	6	5	11	15	14	16	12	13	2	9	7	3	1	8
ONI (°C anomaly; Jan–Jun)	16	2	1	5	12	13	11	14	7	10	3	9	15	4	5	7
46050 SST (°C; May–Sep)	14	8	3	4	1	7	16	13	5	15	2	9	6	10	11	12
Upper 20 m T (°C; Nov–Mar)	16	10	7	9	5	13	14	11	12	4	1	8	15	3	2	6
Upper 20 m T (°C; May–Sep)	13	10	12	4	1	3	16	15	7	8	2	5	11	9	6	14
Deep temperature (°C; May–Sep)	16	6	8	4	1	9	12	14	10	5	2	7	13	11	3	15
Deep salinity (May–Sep)	16	3	7	4	5	13	14	8	6	1	2	11	15	10	9	12
Copepod richness anomaly (no. species; May–Sep)	16	3	1	7	6	12	11	15	13	10	8	9	14	4	5	2
N. copepod biomass anomaly (mg m ⁻³ ; May–Sep)	15	12	7	8	5	14	13	16	9	11	4	10	6	1	2	3
S. copepod biomass anomaly (mg m ⁻³ ; May–Sep)	16	3	5	4	2	11	13	15	12	10	1	8	14	9	7	6
Biological transition (day of year)	16	11	7	3	8	12	10	15	14	4	1	2	13	5	9	6
lchthyoplankton (mg 1,000 m ⁻³ ; Jan–Mar)	16	8	2	4	6	15	14	10	13	12	1	9	3	11	7	5
Chinook salmon juvenile catches (no. km ⁻¹ ; Jun)	15	4	5	13	9	11	14	16	10	8	1	6	7	12	3	2
Coho salmon juvenile catches (no. km ⁻¹ ; Sep)	11	2	1	4	3	6	12	14	8	9	7	15	13	5	10	NA
Mean of ranks	14.7	6.1	5.0	5.9	5.5	11.3	12.9	13.7	10.0	8.6	2.8	7.9	11.0	6.7	5.5	7.6
Rank of the mean rank	16	6	2	5	3	13	14	15	11	10	1	9	12	7	3	8

salmon-rich waters of the northern CC. Both Bi et al. (2011) and Keister et al. (2011) show that alongshore transport is linked with the PDO, such that when a greater proportion of the water entering the northern CC is from both the coastal Gulf of Alaska and from the sub-Arctic side of the North Pacific Current, lipidrich copepods dominate, whereas when the PDO is in positive phase, a greater proportion of water entering the northern CC is from the subtropical branch of the North Pacific Current. This concept is discussed in somewhat greater detail in Batchelder et al. (2013). We suggest that our correlations of ocean indicators with recruitment indicate causal relationships, because there is a mechanistic link between basin-scale physical forcing associated with the PDO, NPGO, or ENSO and the biological response of recruitment. These correlations are practical examples of "fisheries oceanography in action," that is, of how ocean ecosystem indicators (and knowledge of ocean conditions) could be used to inform management decisions for endangered salmon and for other exploited fish populations such as sablefish, sardines, and rockfish.

It might seem surprising that our suite of indicators developed for the northern CC hold promise for understanding variations in recruitment of sablefish (a fish that lives throughout the CC) and sardines (a fish that spawns in the southern CC, where recruitment is presumably set), and that a single indicator (northern copepod biomass) holds promise for rockfish recruitment to the central CC. We suggest that these relationships with ocean conditions in the northern CC and fish recruitment throughout the CC exist because transport in the CC is driven by large (basin)-scale forcing associated with the PDO, ENSO, and the NPGO. Although we have only shown biophysical data collected from the Newport Hydrographic Line at 44.7°N, we know these data are highly correlated with other long-term time series of hydrography and zooplankton off southern British Columbia at 49-50°N (Mackas et al.,

2006, 2007), Washington State at 46-48° (Lamb, 2011), and Trinidad, California, at 41°N (Bjorkstedt et al., 2012). Thus, it is logical to conclude that correlations exist between biophysical data off Newport, Oregon, and recruitment of fishes further south. Chelton and Davis (1982), Chelton et al. (1982), and McGowan et al. (1998) demonstrated clear links between transport of water to the southern CC and North Pacific climate variability as indexed by sea level along the west coast of North America, a time series that looks very much like the PDO (Mantua et al., 1997). However, the relationship between climate variability and zooplankton species composition is largely unknown in the southern CC because there are little to no data available on species composition of copepods from this region. Unfortunately, the small "southern" copepod species in this region are severely undersampled by the large mesh nets used to sample the zooplankton.

We originally hypothesized that coastal upwelling would be a leading driver of ocean productivity that would greatly influence fish recruitment. However, we do not use any of the standard indices of upwelling (e.g., total amount of upwelling in a given season, length of the upwelling season, or date of spring transition; Bograd et al., 2009) to characterize ocean conditions because these indices primarily reflect the timing and volume of water that upwells, not the quality of the water (temperature, nutrient content) nor its productivity. Standard upwelling indices also do not adequately reflect the advective loss of coastal production to offshore areas that are out of reach of coastal species such as salmon. Furthermore, there is likely an optimal combination of frequency and duration of upwelling events that leads to maximum production (e.g., Peterman and Bradford, 1987; Roy et al. 1992); however, this relationship has not been developed for coastal upwelling systems (but see the modeling of Yokomizo et al., 2010).

Stock assessments produce rigorous estimates of interannual variations of recruitment. Presently, the direct incorporation of environmental variability into formal stock assessment models remains an elusive goal for most fished species. We have illustrated some promising relationships between environmental



FIGURE 3. The relationship of (A) fall Chinook salmon returns to Bonneville Dam, (B) sablefish recruitment, (C) sardine recruitment to the southern California Current, and (D) rockfish recruitment to the central California Current versus first principal component (PC1) of 15 biophysical indicators. Outlier years (plots A, C) were determined using Cook's Distance and were excluded from the analysis (Cook, 1979).

variability and fish recruitment. As a starting point, we suggest that environmental indicators be examined alongside formal stock assessments to better understand how recruitment variability might be related to environmental variability. Historically, salmon managers used age-structured models and returns of "jack salmon" (precocious males) to rivers as an index of the number of adult salmon returning in subsequent years. Presently, some managers use our information on ocean conditions and "outlooks" for salmon returns alongside their stock estimates to better understand how ocean conditions affect salmon survival. Therefore, managers are beginning to incorporate variable ocean conditions into their age-structured models. Augmenting the stock assessment models with environmental data should lead to better forecasts of adult returns (in the case of salmon) and better understanding of recruitment variability (in the case of sablefish, sardines, and rockfish). Ultimately, physical and biological indicators produced by global climate models may be used to provide management



advice relevant to fish recruitment that should be useful for long-range planning.

Variability in productivity of the CC occurs at decadal time scales, and should be taken into account when considering recruitment variability and fish growth. It is now well established that the North Pacific Ocean exhibits dramatic shifts in climate every 10-30 years. These shifts occurred in 1926, 1947, 1977, and 1998 and were caused by eastward/westward shifts in the location of the Aleutian Low in winter, which resulted in changes in wind strength and direction over the Gulf of Alaska and the CC (Mantua et al., 1997). Changes in large-scale wind patterns led to alternating states of either a warm or a cold ocean regime, which was accompanied in turn by a dominance of warm- and cold-water copepods. Of concern for a future climate is that, since 1998, the PDO seems to have lost its decadal signature and has changed sign approximately every five years. Given the apparent strong link between the PDO, pelagic food chains anchored by copepods, and recruitment of salmon, sardines, sablefish, and rockfish, managers should be prepared for increased variability in recruitment over the coming years. This is especially true in light of the recent findings by Black et al. (in press) that variability in physical forcing and ecosystem response is increasing, suggesting that a closer watch on ocean conditions is warranted in order to be able to offer management advice in an ecosystem context.

Finally, it is noteworthy that the entire North Pacific Ocean, from the west coast of continental North America to Japan, Korea, and the east coast of Russia and into the Bering Sea, has been anomalously warm during most of 2014 (Figure 4). The present sea surface temperature patterns are not the typical patterns observed during positive PDO years when the Gulf of Alaska, the CC, and the equatorial waters are anomalously warm. We raise this issue because many of the salmon stocks around the Pacific Rim from Korea, Japan, Russia, Alaska, Canada, and the United States use the Gulf of Alaska as a feeding ground. This might be cause for concern because we have observed that anomalously warm temperatures often signal poor productivity for juvenile salmon and subsequent adult returns in the Pacific Northwest United States.

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