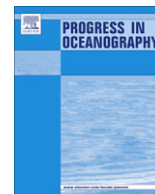




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Linking predators to seasonality of upwelling: Using food web indicators and path analysis to infer trophic connections

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ABSTRACT

Upwelling in eastern boundary current systems is a primary driver of ecosystem productivity. Typically, peak upwelling occurs during spring and summer, but winter upwelling may also be important to ecosystem functions. In this study, we investigated the hypothesis that winter and spring/summer upwelling, operating through indirect trophic interactions, are important to a suite of top predators in the California Current. To test this hypothesis, we collated information on upwelling, chlorophyll-*a* concentrations, zooplankton and forage fish, and related these to predator responses including rockfish growth, salmon abundance, seabird productivity and phenology (timing of egg-laying), and whale abundance. Seabird diets served in part as food web indicators. We modeled pathways of response using path analysis and tested for significance of the dominant paths with multiple regression. We found support for the hypothesis that relationships between upwelling and top predator variables were mediated primarily by intermediate trophic levels. Both winter and summer upwelling were important in path models, as were intermediate lower and mid trophic level functional groups represented by chlorophyll-*a*, zooplankton, and forage fish. Significant pathways of response explained from 50% to 80% of the variation of seabird (Cassin's auklet (*Ptychoramphus aleuticus*) and common murre (*Uria aalge*)), humpback whale (*Megaptera novaeangliae*) and Chinook salmon (*Oncorhynchus tshawytscha*) dependent variables, whereas splitnose rockfish (*Sebastes diploproa*) showed no significant response pathways. Upwelling and trophic responses for salmon were established for both the year of ocean entry and the year of return, with zooplankton important in the year of ocean entry and forage fish important in the year of return. This study provides one of the first comparative investigations between upwelling and predators, from fish to marine mammals and birds within a geographically restricted area, demonstrates often difficult to establish “bottom-up” trophic interactions, and establishes the importance of seasonality of upwelling to various trophic connections and predator demographic traits. Understanding change in the seasonality of upwelling is therefore required to assess dynamics of commercially and recreationally important upper trophic level species in eastern boundary current ecosystems.

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1. Introduction

Eastern boundary current ecosystems cover approximately 1% of the ocean surface yet contribute disproportionately to the world's fisheries catch (~20%) and support vast populations of marine wildlife including fish, seabirds, mammals, and turtles (Cushing, 1971; Pauly and Christensen, 1995). Productivity in these mid-latitude systems is supported by seasonal changes in sunlight and advective nutrient input from coastal and offshore upwelling (Mann and Lazier, 1996; Jahncke et al., 2004; Rykaczewski and

Checkley, 2008). At the base of the food chain, phytoplankton respond to upwelling-forced nutrient input by increasing growth and reproduction, with primary production increased when phytoplankton are retained in the photic layer (Kjørboe, 1993; Huete-Ortega et al., 2011). Primary production and fish production are tightly coupled and mediated by zooplankton (Cury et al., 2000; Ware and Thomson, 2005). Finally, it is thought that upper trophic level species are controlled by a balance of these “bottom-up” trophic effects and other biological interactions, such as predation and competition, which may exert “top-down” control on the mid-trophic levels of food webs (Cury et al., 2000; Suryan et al., 2006; Miller et al., 2010). Top-down and bottom-up processes may dominate in different ocean regions (Frank et al., 2006, 2007) or between

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years or decades within the same ecosystem (Hunt et al., 2002; Lit-zow and Ciannelli, 2007).

In the California Current, upwelling is a complex process with key centers of activity at specific locations, often near coastal headlands (Hickey, 1979; Checkley and Barth, 2009; Garcia-Reyes and Largier, 2012). Upwelling occurs with pulses of northwesterly winds that last for a few days to about 2 weeks and are interspersed with periods of calm or “relaxation” events (Largier et al., 2006). Phytoplankton responses generally lag upwelling by ~4–8 days (Dugdale and Wilkerson, 1989; Service et al., 1998; Dugdale et al., 2006), while changes in zooplankton biomass lag primary productivity by weeks to months, depending on species, water temperature and other hydrographic characteristics (Hayward and Venrick, 1998). Phytoplankton and zooplankton responses also depend on the seasonality of upwelling events. The phenology (i.e., annual timing) of upwelling depends on latitude, with earlier initiation and peaks at southerly latitudes (Bograd et al., 2009). South of ~40°N (Cape Mendocino, California), average monthly upwelling values are positive in most months, though less intense in winter than in spring and summer. For example, upwelling at 39°N starts in January/February and peaks in May/June each year. North of ~40°N, mean monthly upwelling values in winter are largely negative, i.e., reflective of southerly (poleward) winds and downwelling; in this region upwelling peaks later in the year, often in July/August.

Bottom-up processes are thought to dominate food web interactions in the California Current (Ware and Thomson, 2005). While a considerable body of literature exists on the effects of upwelling on upper trophic level predators, rarely has the seasonality of upwelling been coupled with varying pathways of response and examined in a systematic fashion for multiple top predators. One key reason for this is that difficulties arise in measuring upwelling, phytoplankton concentrations, zooplankton, forage fish and upper trophic level predator responses on appropriate temporal and spatial scales (Croll et al., 1998, 2005). For example, previously in the California Current, relationships have been established between upwelling and the diet composition and reproductive success of seabirds (e.g., Miller and Sydeman, 2004; Schroeder et al., 2009), but these studies have lacked a clear understanding of intermediate trophic steps. Another difficulty is study length; Jahncke et al. (2008) summarized upwelling, chlorophyll-a, zooplankton prey (krill), and responses of seabird predators, but this study was limited to 2 years which provided only a limited snapshot of upwelling and trophic interaction variability. Lastly, despite the fact that pulses of upwelling often begin in January or February each year (Bograd et al., 2009; Garcia-Reyes and Largier, 2012) and a series of recent investigations have shown the importance of early season upwelling (Logerwell et al., 2003; Abraham and Sydeman, 2004, 2006; Bograd et al., 2009; Schroeder et al., 2009; Black et al., 2010, 2011), winter upwelling is often neglected. Mechanistically, winter winds may result in effective upwelling if the ocean is less stratified during that time of year resulting in isopycnal shoaling even if winds are weaker (Schroeder et al., 2009). There also is growing evidence suggesting that winter and spring/summer upwelling influence species differently; some species responses relate to winter upwelling while others relate mostly to the summer mode (Black et al., 2011).

Some of the earliest, strongest and most variable winds and upwelling in California are found between 36°N (Monterey Bay) and 39°N (Point Arena), which we refer to as the Gulf of the Farallones (GoF) region. We focus on the GoF for this study as it is well known for high ecosystem productivity and supports substantial fisheries and wildlife populations. Our overarching hypothesis is that predator productivity and population variation in the GoF is affected by seasonal variation in upwelling indirectly through intermediate trophic levels represented by chlorophyll-a, zoo-

plankton, and forage fish biomass. To address this hypothesis we analyzed seasonal variation in upwelling and direct and indirect pathways of response for a suite of predators including fish, seabirds, and marine mammals. Based on the study by Black et al. (2011), we predicted that pathways of response from seasonal upwelling to predators would vary, with some species responding more to winter upwelling and others to summer upwelling. Likewise, we expected some would respond more strongly to variability in zooplankton biomass, and others to forage fish. Additionally, we investigated whether seabirds responded similarly to the seasonality of upwelling by examining different response variables (i.e., timing of reproduction and reproductive success). To test our hypothesis and predictions, we first developed conceptual models from upwelling through lower and mid trophic levels to the growth of rockfish, abundance of whales and salmon, and phenology and reproductive success of seabirds. This study is important as climate change is predicted to affect the amplitude (intensity) and phasing (timing) of upwelling (Bakun, 1990; Snyder et al., 2003; Bakun et al., 2010). Observations have already linked climate change to proxies of upwelling intensification in the GoF region including increasing wind stress and decreasing ocean temperatures (Garcia-Reyes and Largier, 2010). Upwelling timing has also become more variable (Schwing et al., 2006), with substantial ecosystem consequences (Brodeur et al., 2006; Sydeman et al., 2006). Some climatic changes and environmental response variables such as temperature may directly affect species at all trophic levels while others generally influence only higher trophic levels and mostly indirectly (Moloney et al., 2011), but these impacts are not well known. Therefore, it is both critical and timely to investigate the seasonality of upwelling, trophic connections, and predator responses in a comprehensive manner, as we present in this study.

2. Methods

We integrated and modeled data available from a variety of sources. The data sets (Table 1) include estimates of (1) winter and spring/summer upwelling (based on Black et al. (2011), see below for details), (2) chlorophyll-a concentrations, (3) mesozooplankton (copepod and krill) abundance and community structure, (4) forage fish (juvenile rockfish *Sebastes* spp.) abundance, (5) splitnose rockfish (*Sebastes diploproa*) otolith growth, (6) seabird (Cassin's auklet, *Ptychoramphus aleuticus*; common murre, *Uria aalge*) timing of breeding and reproductive success, (7) Chinook salmon (*Oncorhynchus tshawytscha*) abundance, and (8) humpback whale (*Megaptera novaeangliae*) abundance. We selected these species and variables as they characterize vital parts of the epipelagic food web in the region, encompassing species responsible for key trophic interactions and representing a diverse suite of top predators for the outer continental shelf ecosystem of the north-central California Current. Due to challenging data requirements for this investigation, including monthly-resolved upwelling data and annualized data on chlorophyll-a, zooplankton, forage fish, and predators, our study was limited to 10 years, 1997 through 2006.

2.1. Predictor variables

2.1.1. Upwelling

The Bakun upwelling index ($\text{m}^3/\text{s}/100 \text{ m coastline}$) is calculated by NOAA's Pacific Fisheries Environmental Laboratory. Data were downloaded from <ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon>. Monthly values for upwelling at 36°N, 122°W and 39°N, 125°W were used in this study. Data treatment is described below.

Table 1

Data sets used in the path analyses. Upwelling was the independent variable, and seasonal modes were produced using Empirical Orthogonal Function (EOF) analysis for two sites. Chlorophyll-a concentrations for two sites were combined using EOF analysis for the lowest intermediate trophic level, as were copepods and euphausiids for a zooplankton trophic level. The third intermediate level included in path models for piscivore predator species was forage fish, represented by juvenile rockfish abundance. Predator response variables included rockfish growth, humpback whale abundance, reproductive success and phenology for two seabird species (Cassin's auklet and common murre), and Chinook salmon abundance in the year of ocean entry and year of return for two populations.

Variable/species	Location	Parameters	Sampling/summary time scales
Upwelling	36°N and 39°N	Bakun Upwelling Index $\text{m}^3/\text{s}/100 \text{ m}$ coastline	Hourly/Monthly
Chlorophyll	Bodega Bay	SeaWiFS Chl-a ($9 \times 9 \text{ km}$) mg/m^3	Daily/Monthly
	Farallon Islands		Daily/Monthly
Copepods	Central Oregon	Copepod Biomass $\text{mg C}/\text{m}^3$	Bi-weekly/Annual
		Northern Copepod Index	Bi-weekly/Annual
Euphausiids <i>Thysanoessa spinifera</i>	Gulf of Farallones	Abundance % wet mass (g)	Weekly/Annual
Rockfish <i>Sebastes</i> spp.	Central California	Growth of Splitnose Rockfish <i>S. diploproa</i>	Annual
		Juvenile Rockfish Abundance	Daily/Annual
Humpback whale <i>Megaptera novaeangliae</i>	California	Abundance	Annual
Cassin's auklet <i>Ptychoramphus aleuticus</i>	Gulf of Farallones	Reproductive Success Mean chicks/pair	Annual
		Phenology Mean egg laying date	Weekly/Annual
Common murre <i>Uria aalge</i>	Gulf of Farallones	Reproductive Success Mean chicks/pair	Annual
		Phenology Mean egg laying date	Daily/Annual
Chinook salmon <i>Oncorhynchus tshawytscha</i>	Sacramento River	Abundance	Annual
	Russian River		

2.1.2. Chlorophyll

Satellite remotely-sensed chlorophyll-a concentrations (mg/m^3) were obtained from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS; <http://oceancolor.gsfc.nasa.gov/SeaWiFS/>). Monthly level-3 mapped 9-km resolution data were obtained. We assessed changes in chlorophyll-a concentrations for two sites in the region, around the Farallon Islands (37.708°N, 123.125°W) and the Bodega Bay NOAA buoy (Station 46013, 38.208°N, 123.375°W). For each location, we averaged the values for four adjacent 9-km \times 9-km cells (pixels), thereby providing chlorophyll-a concentrations for 324 km^2 of ocean habitat at each site. The four cells were one with coordinates closest to the location and the adjacent cells directly to the east, southeast, and south of the first. Chlorophyll-a concentrations from both sites were averaged together and temporally to produce a single annual estimate for inclusion in the path analyses.

2.1.3. Zooplankton

Data for copepods included two measures of biomass ($\text{mg C}/\text{m}^3$): total copepod biomass and the “Northern Copepod Index” (NCI). Data were obtained from field surveys off central Oregon (Newport Hydrographic Line, 44.65°N, Hoeff and Peterson, 2006). Copepods were collected using a 0.5-m, 0.202-mm plankton net and were sampled bi-weekly during the months of May–September; the bi-weekly data were averaged to produce monthly values. The biomass anomalies of three species from neritic sub-arctic waters, *Pseudocalanus minus*, *Acartia longiremis*, and *Calanus marshallae*, were averaged to produce the NCI. This data set represents the longest-running and most comprehensive copepod sampling program for the central-northern California Current, and though it is located ~800 km to the north of our general study area, numerous relationships have established these copepod indices as important for GoF predators (Sydeman and Thompson, 2010; Sydeman et al., 2011; Sydeman, Peterson and Black, unpublished data).

We estimated krill (*Thysanoessa spinifera*) availability based on the diet composition of Cassin's auklet food samples (average of daily samples, percent wet mass (g) comprised of adult and juvenile *T. spinifera* relative to other prey species). Field and laboratory methods for auklet diet sampling are described by Abraham and Sydeman (2006). Briefly, provisioning adult auklets capture prey at sea and bring undigested food to chicks at the colony once per day. Provisioning adults were caught at the Southeast Farallon Island colony (37°42'N, 123°00'W) and the contents of the pouch were gently massaged into glass vials or plastic whirlpak bags. Prey

items were identified, enumerated and weighed by M. Galbraith at the Institute of Ocean Sciences (Sidney, British Columbia). Over the years 2002–2006, *T. spinifera* in the auklet diet was positively related to *T. spinifera* measured in the Gulf of the Farallones (Spearman rank correlation: $\rho = 0.975$, $p = 0.0048$). We used the seabird diet as a proxy for *T. spinifera* availability as this time series was longer than other available measurements.

2.1.4. Forage fish

The availability of juvenile rockfish (*Sebastes* spp.) was similarly indexed by the diet of a seabird, the common murre. Field methods for murre diet sampling are described by Mills et al. (2007). Juvenile rockfish abundance is expressed as the average proportion of identified prey species captured by murre and delivered to offspring at nest sites on Southeast Farallon Island (proportion = juvenile rockfish/total number of forage fish identified). Mills et al. (2007) and Sydeman et al. (2009) show that the proportion of juvenile rockfish in the murre chick diet indicates relative abundance of juvenile rockfish in the environment as measured by mid-water trawls ($r^2 = 0.81$). We use seabird diet as a proxy for juvenile rockfish availability as this approach (i.e., using seabird diet) matches the approach used to index the euphausiid *T. spinifera*.

2.2. Response variables

2.2.1. Splitnose rockfish growth

Methods for generating splitnose rockfish growth chronology are detailed by Black et al., (2008). Briefly, rockfish were obtained by research and commercial fishing vessels between 35 and 39°N. Otoliths were extracted from the fish, embedded in resin, thin-sectioned along a dorsal–ventral axis perpendicular to the sulcus, mounted on a glass slide, and polished. The dendrochronology technique of crossdating was applied to ensure that all growth increments had been correctly identified and assigned the correct calendar year of formation. Next, otolith increment widths were measured from the margin to the focus, though the first few (3–5) years of growth were excluded given that young fish may have different habitat and food requirements than adults. Measurement time series were detrended with negative exponential functions to remove age-related growth declines then averaged with respect to the calendar year to produce the growth-increment chronology. Splitnose rockfish are predators of a wide variety of prey including euphausiids, copepods and other crustaceans (Brodeur and Pearcy, 1984).

2.2.2. Cassin's auklet and common murre reproductive success and timing of breeding

Reproductive success and phenology data for seabirds were collected at Southeast Farallon Island by PRBO Conservation Science under contract with the U.S. Fish and Wildlife Service/Farallon National Wildlife Refuge. Methods to determine reproductive success and timing of breeding (mean egg laying date) are provided by Ainley et al. (1995) and Sydeman et al. (2001, 2009). In short, a sample of focal breeding pairs was monitored throughout each nesting season. Individual nest sites were studied at 1–7 day intervals. Cassin's auklets are planktivorous and prey include euphausiids (Manuwal, 1974), mysids and copepods (Sydeman et al., 2001), though Abraham and Sydeman (2004) report that two species of euphausiid (*Euphausia pacifica* and *T. spinifera*) comprise about 80% of auklets' diets. Murres are piscivorous and their diets largely contain juvenile rockfish, anchovies, squid and smelt (Baltz and Morejohn, 1977; Croll, 1990; Scott, 1990; Roth et al., 2008).

2.2.3. Chinook salmon abundance

The 'Sacramento Index' for Chinook salmon, calculated by the Pacific Fisheries Management Council, is the sum of ocean harvest south of Cape Falcon, Oregon, recreational harvest in the Sacramento River, and adult spawner escapement to the Sacramento River (O'Farrell et al., 2009). Chinook returns to the Russian River were monitored by the Sonoma County Water Agency. Adult Chinook were observed and counted by videotape as they returned upstream and passed over fish ladders (fish/year). We analyzed the Sacramento Index and the Russian River returned adult abundances, and lagged abundance data 2 years to test for the effect of ocean conditions on these populations during their year of ocean entry. Chinook have a varied diet and major prey groups include euphausiids, anchovy, herring and rockfish (Brodeur and Pearcy, 1992).

2.2.4. Humpback whale abundance

We used estimates of humpback whale abundance (individuals/year) from mark-recapture analysis of individually known whales off California and Oregon. Whales were identified using photographic surveys (Calambokidis, 2009). Estimates of abundance were based on the two-sample Petersen capture-recapture method. As for other baleen whales, krill are a primary prey (Croll et al., 2005), but humpback whales also consume forage fish (Witteveen et al., 2011), including juvenile rockfish (Kieckhefer, 1992).

2.3. Data treatment

We calculated anomaly statistics for all variables except humpback whale abundance. Anomalies were calculated by subtracting long-term monthly or annual mean values from monthly or annual values. All data sets fit the assumption of normal distribution of residuals with the exception of humpback whale abundance. To meet this requirement, estimates of humpback whale abundance were de-trended to remove the strong trend of increasing abundance, and we used the residuals for our analyses. Based in part on the analysis described by Black et al. (2011; though our study addressed only two upwelling locations compared to their five), we used Empirical Orthogonal Function (EOF) analysis to describe the dominant modes of seasonality in upwelling. From monthly upwelling anomalies we found two interpretable EOFs that proxy winter (EOF2_{upwelling}) and summer (EOF1_{upwelling}) upwelling (Fig. 1, details of results are explained below). We also conducted an EOF analysis for the period 1997–2006 on the three zooplankton variables NCI, anomalies of overall copepod biomass and *T. spinifera* abundance. An average for May–September was calculated for both copepod data sets prior to the EOF analysis. The resulting first EOF (EOF1_{zooplankton}) was used in the path analysis. All vari-

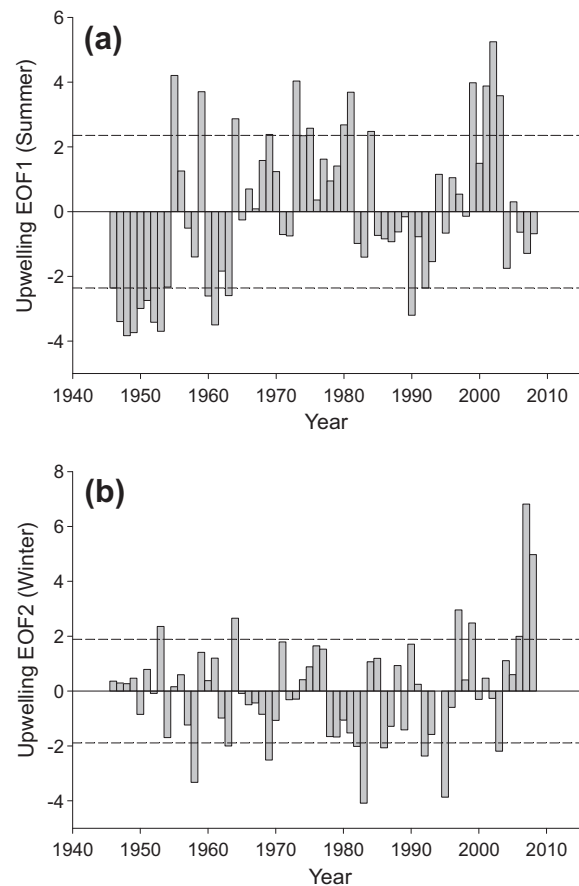


Fig. 1. (a) EOF (spring/summer) and (b) EOF (winter) of upwelling index at 36°N, 122°W and 39°N, 125°W. Dashed lines indicate 1 standard deviation. See Appendix A1 for month-latitude loadings.

ables were represented with annual data values for the path analysis, with the driver variable being either winter (EOF2_{upwelling}) or summer (EOF1_{upwelling}) upwelling.

2.4. Pathways of response

Structured models with multiple intermediate trophic levels (phytoplankton, zooplankton and forage fish) to test effects of a driver variable (seasonal upwelling) on a predator's response are suitably quantified with path analysis because of its capacity to analyze systems with multiple causality (Petraitis et al., 1996). Like Wells et al. (2008), we tested conceptual models of pathways of response by path analysis and multiple regression. Path models were determined *a priori*, but unlike Wells et al. (2008), who tested the effect of eight environmental variables, our analyses were conducted with upwelling as the sole exogenous variable in all models. In our models, multiple causality is the possible paths of the effect of upwelling on predator response. Models for planktivore response variables (rockfish growth and auklet phenology and reproductive success) included chlorophyll-*a* concentration and zooplankton as intermediate variables. Models for piscivore response variables (whale abundance, salmon abundance and murre phenology and reproductive success) included chlorophyll-*a* concentration, zooplankton and juvenile rockfish abundance as intermediate variables.

Using EOF1_{upwelling} and EOF2_{upwelling}, path analyses were run separately for spring/summer and winter upwelling, respectively. Path analyses were run using the program *Stata* (v.8) and the command *pathreg*. With this command, multiple conceptual

models can be run simultaneously. Each model tests the correlations of all variables in a given path. On constructed path diagrams, each segment of the path was labeled with its corresponding “beta” (standardized regression) coefficient. Once diagrams were complete, direct and indirect effects were calculated. The direct effect is the beta coefficient between upwelling and the response variable. Indirect effects were calculated as the product of all beta coefficients in a given path; the total indirect effect for each model is then the sum of all indirect effects (Mitchell, 2001). We determined the dominant path by

comparing the total indirect effect to the direct effect; the larger value indicated the dominant path. If the dominant pathway of response was indirect, then the indirect path was specified as the one with the highest effect value.

To determine statistical significance, path analysis was coupled with regression analyses (Petraitis et al., 1996). We conducted multiple regression analyses on variables in the identified dominant paths in the path analysis. Owing to the relatively small sample size, models were considered significant at $p < 0.1$ (for a justification of this approach see Grosbois et al., 2008).

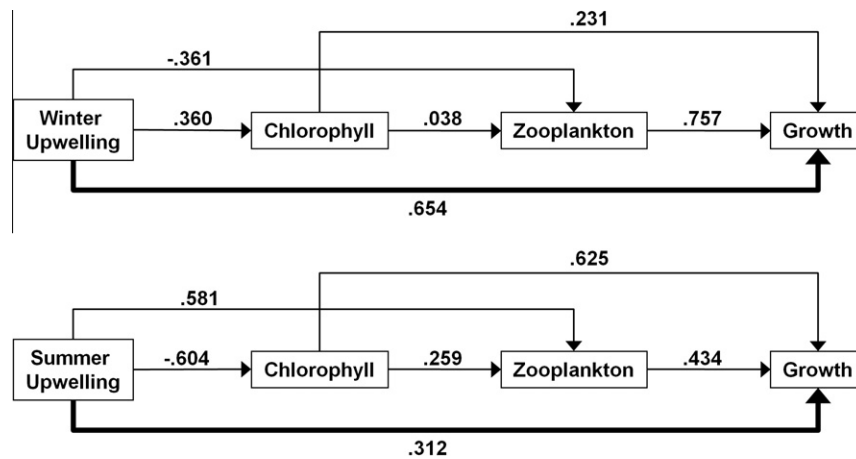


Fig. 2. Path diagrams for seasonal upwelling and splitnose rockfish growth. For all path Figs. 2–7, beta coefficients are shown along their respective path segments and the dominant path is shown in bold.

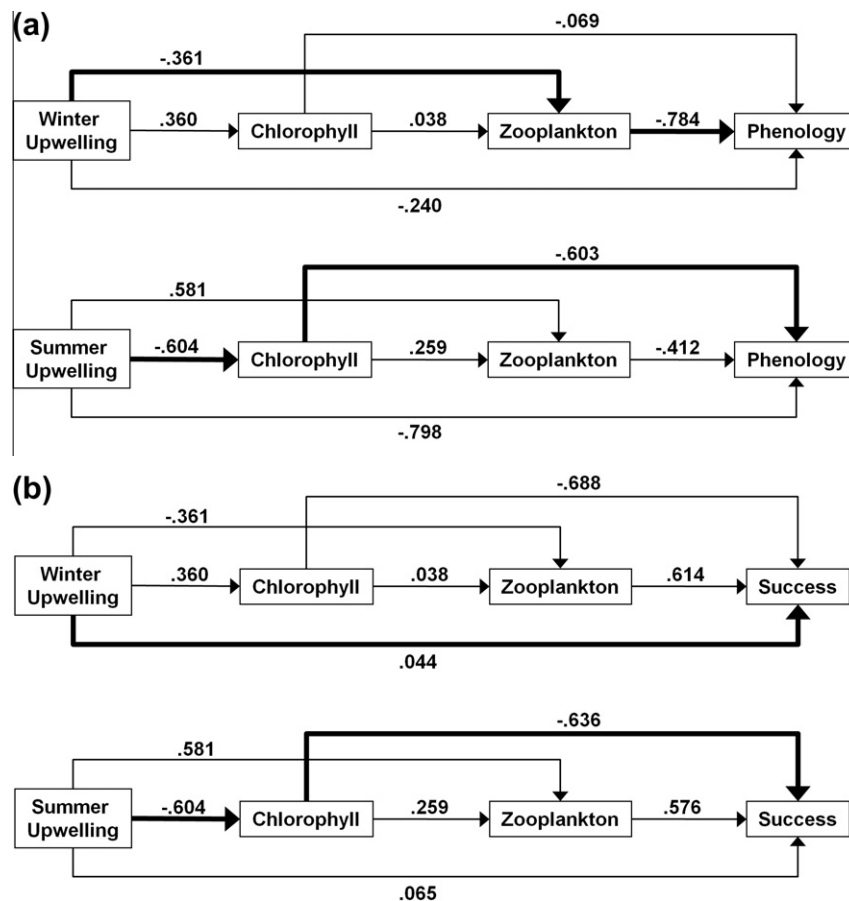


Fig. 3. Path diagrams for seasonal upwelling and Cassin's Auklet (a) phenology and (b) reproductive success.

3. Results

3.1. Seasonal modes of upwelling and lower trophic level response

The first EOF of upwelling explained 23.2% of the variance and loaded heavily on the months of April–August for both 36°N and 39°N (Fig. 1, Appendix A1). The second EOF of upwelling explained ~15% of the variance and loaded heavily on December–March for both locations. Over the study period, EOF1 (hereafter interpreted as “summer upwelling”) was well above one standard deviation of the mean in 1999 and again from 2001 to 2003, whereas weaker spring/summer upwelling was found from 2004 to 2008 and in 1997–1998. EOF2 (hereafter “winter upwelling”) was anomalously high in 2007–2008. For zooplankton, the first EOF explained 64.1%

of the variation, and loaded approximately twice as heavily on each of the copepod measurements than krill abundance (Appendix A2).

3.2. Pathways of response for top predators

Path analysis diagrams are shown in Figs. 2–7, with the calculated dominant pathways of response shown in bold; the effect value for each direct and total indirect path is given in Table 2. Growth of splitnose rockfish was directly affected by winter and summer upwelling, with winter dominant (larger beta coefficient, Fig. 2). Cassin's auklet phenology (timing of egg-laying) was indirectly affected by winter upwelling via zooplankton, and indirectly affected by summer upwelling through chlorophyll-a (Fig. 3a). Cassin's auklet reproductive success was directly affected by

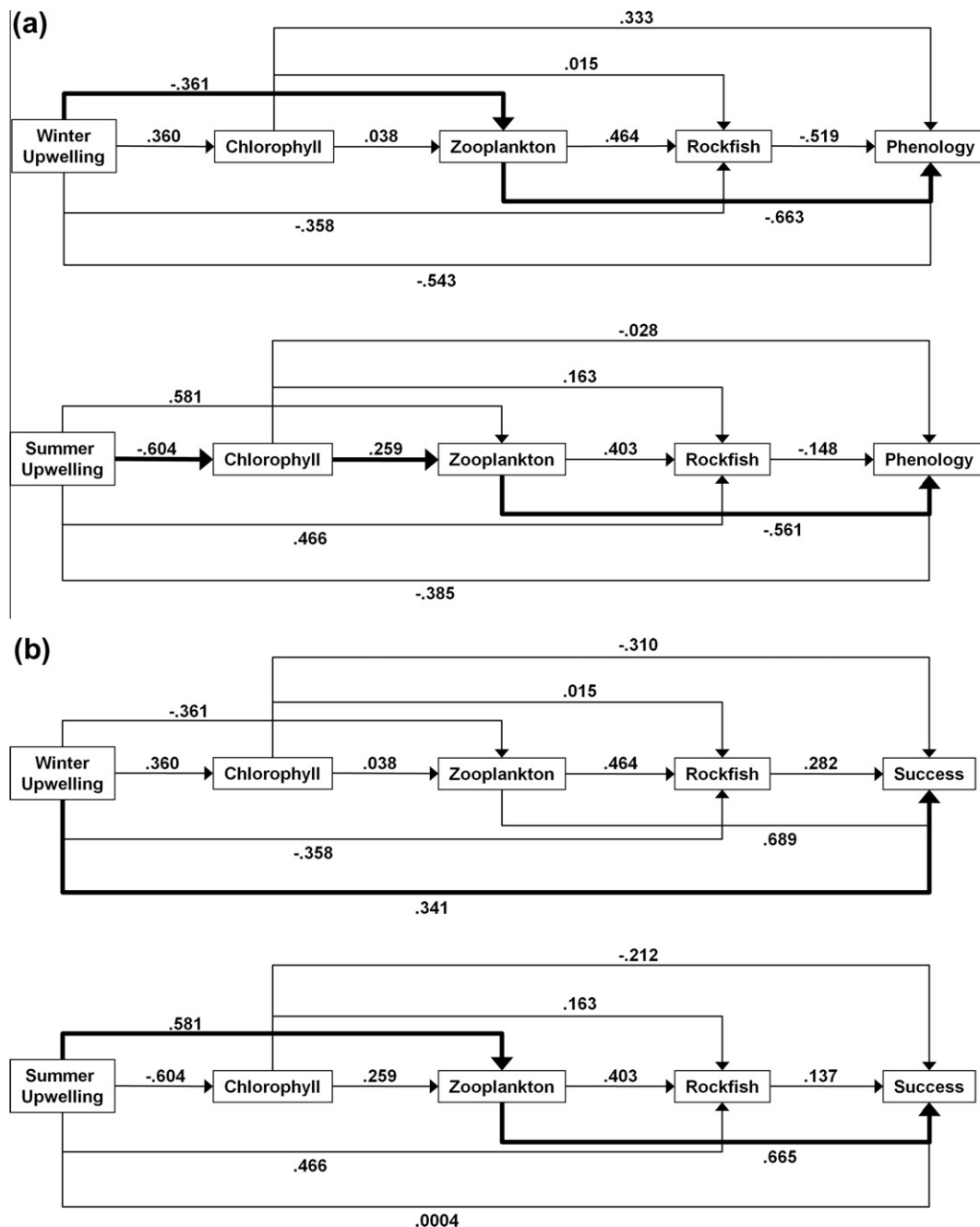


Fig. 4. Path diagrams for seasonal upwelling and common murre (a) phenology and (b) reproductive success.

winter upwelling, whereas there was an indirect effect of summer upwelling through chlorophyll-a (Fig. 3b). As was seen for the auklet, common murre phenology was indirectly affected by winter upwelling through zooplankton. The path from summer upwelling was indirect through chlorophyll-a and zooplankton (Fig. 4a). Murre reproductive success was directly affected by winter upwelling, while the path from summer upwelling worked through zooplankton (Fig. 4b). Humpback whale abundance was indirectly affected by summer upwelling with the intermediate step of forage fish (juvenile rockfish) and directly affected by winter upwelling (Fig. 5).

For salmon, we modeled abundance against upwelling and intermediate trophic levels by investigating conditions during both the year of [ocean] entry (YoE) and the year of return (YoR). For the Sacramento River Chinook, we found dominant direct paths from winter upwelling in both YoE and YoR, and indirect paths via chlorophyll-a and forage fish for summer upwelling in YoE and YoR, respectively (Fig. 6a and b). For the Russian River Chinook in the YoE, there was an indirect path of effect of summer upwelling through zooplankton and a dominant path of effect of winter upwelling (Fig. 7a). For Russian River Chinook in the YoR, indirect paths for both winter and summer upwelling were found; the path from winter upwelling operated through chlorophyll-a whereas the path from summer upwelling was through rockfish (Fig. 7b). In summary, we found eight direct paths of response, seven for winter and one for summer, and 12 indirect paths, three for winter and nine for summer. The 12 indirect pathways of response included five models with chlorophyll-a as an intermediate step, five models with zooplankton, and three models with forage fish.

Results of the regression analyses are shown in Table 3. Split-nose rockfish growth did not relate significantly to either winter or summer upwelling or any intermediate trophic levels. Humpback whale abundance showed a significant indirect relationship with summer upwelling through rockfish. For both seabirds, timing of breeding showed significant indirect inverse relationships with winter upwelling through zooplankton (Fig. 8a and b), indicating earlier egg-laying dates with more winter upwelling and zooplankton. The Cassin's auklet phenology model for summer included chlorophyll-a as well as upwelling as significant components, and these relationships were negative (Fig. 8c). The model for common

murre phenology and summer upwelling was also negative (Fig. 8d). Notably, this is the only model that included more than one intermediate variable (chlorophyll-a and zooplankton), but our results showed that zooplankton was significant whereas chlorophyll-a was not. Reproductive success of Cassin's auklet had a significant relationship with summer upwelling through chlorophyll-a, but unexpectedly chlorophyll-a itself was not related to auklet breeding success. Last, reproductive success of common murre showed no significance with winter upwelling, but demonstrated a significant indirect positive relationship with zooplankton and summer upwelling (Fig. 8e).

Sacramento River Chinook were not significantly related to winter upwelling in either YoE or YoR, but demonstrated significant indirect relationships with summer upwelling through rockfish (YoR) and chlorophyll-a (YoE). Notably, the relationship with summer upwelling and rockfish was positive (Fig. 9a), while the relationship with chlorophyll-a was negative (similar to that of auklet reproductive success). Russian River Chinook were unrelated to winter upwelling in both YoE and YoR, but had a significant indirect positive relationship with summer upwelling through zooplankton in the YoE (Fig. 9b). Although rockfish and chlorophyll-a were indirect components in the YoR models (summer and winter, respectively), they were not significant.

4. Discussion

To address our primary hypothesis of indirect effects from upwelling to predators, we examined a variety of response variables (growth, timing, productivity and abundance) across a diverse selection of taxa, including fish (rockfish and salmon), seabirds (auklets and murre), and mammals (humpback whales). The variety of predators and response variables examined makes this study unique with respect to physical–biological coupling and predator–prey interactions in the California Current, and upwelling ecosystems more generally (Cury and Shannon, 2004; Jahncke et al., 2004; Chavez and Messie, 2009). By decomposing the variance of the upwelling index using EOF analysis, we identified distinct upwelling modes attributable to seasons (see also Black et al., 2011). Subsequently, to infer and compare trophic relationships, we used path analysis and multiple regression to link winter and

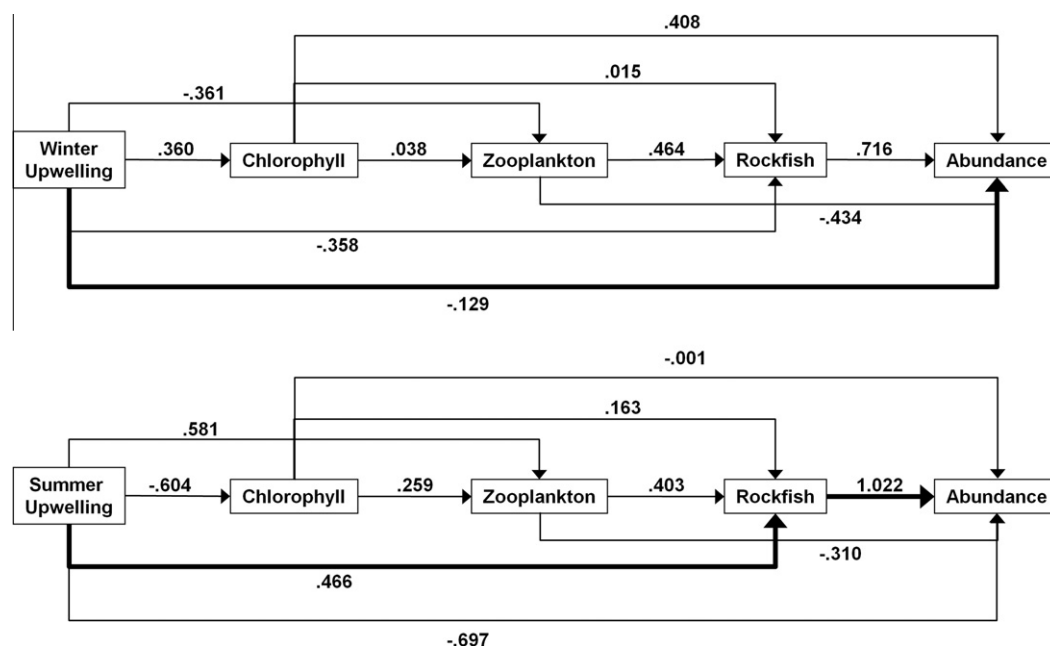


Fig. 5. Path diagrams for seasonal upwelling and humpback whale abundance.

summer modes of upwelling with predator responses. While the literature provides numerous examples of bottom-up forcing in predator species (see Ware and Thomson (2005) and references therein), here we provide a novel perspective for a predator community within the Gulf of the Farallones (GoF). To our knowledge, this is the first empirical study to investigate and compare bottom-up interactions for fish, birds, and mammals in a unified manner, facilitating generalizations about the relationships between upwelling and consumers in eastern boundary current systems. Moreover, by creating and analyzing seasonal modes of upwelling, we expanded upon the work of Wells et al. (2008) who focused on three species of seabirds and spring and summer upwelling periods, and Black et al., (2011) who linked seasonal variation in upwelling to a suite of predator responses, but without the intermediate trophic steps that provide mechanistic understanding.

4.1. Seabird-based food web indicators

The intermediate trophic levels examined in this study provide a simplified yet appropriate representation of the epipelagic food web in the GoF. The use of SeaWiFS ocean color data as a proxy for phytoplankton concentration has become standard in marine ecology (Chavez et al., 2011). The idea to use seabird diets to proxy the availability of zooplankton and forage fish is not new (Cairns, 1987; Piatt et al., 2007; Mills et al., 2008), but the application of these data to provide insight into the productivity or abundance of other species of seabirds, let alone marine mammals or fish, is different. While some proxies of prey abundance based on seabirds have previously been defined, we also support the cautious approach advocated by Durant et al. (2009) in using “reverse inference” to infer prey availability in the environment based on

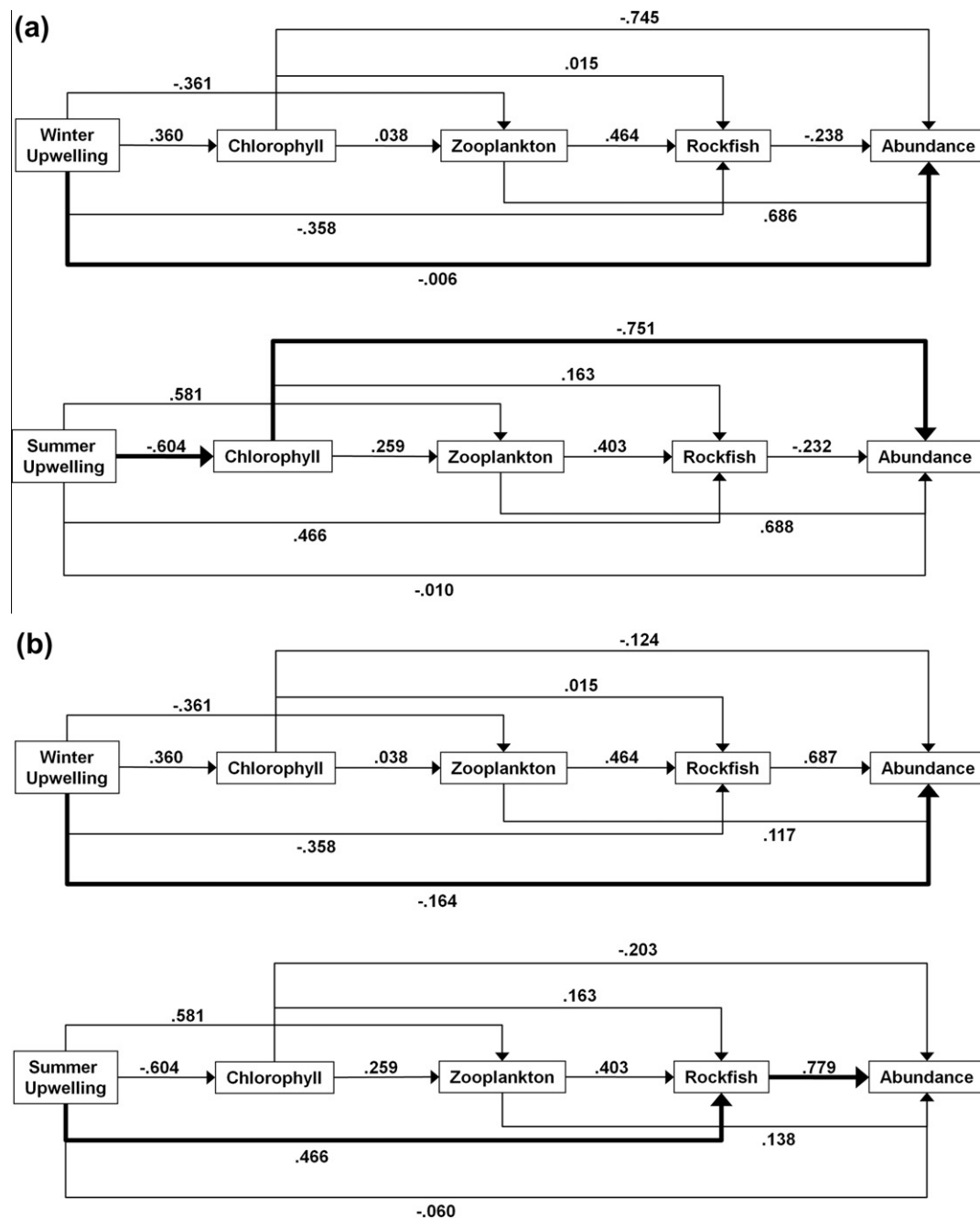


Fig. 6. Path diagrams for seasonal upwelling and Chinook salmon abundance, Sacramento River, for year of (a) ocean entry and (b) adult return.

seabird data. Using seabirds, or any variable as a proxy for another variable not measured directly, requires calibration. Optimally, to provide an accurate estimate of the response in question the proxy will demonstrate a tight linear relationship with the response variable, but rarely is this well known. Fortunately, in this case, we previously examined the relationship between juvenile *Sebastes* spp. in common murre diet and abundance in the environment (Mills et al., 2007). The fit between the proxy and response variable is linear, with the proxy explaining ~80% ($r^2 = 0.81$) of the variation in the response variable. Calibration for the use of auklet diet composition as a proxy for the abundance of the euphausiid *T. spinifera* in the environment has not been previously published, but we provide initial details for this relationship in the Methods. In both cases, our calibration (linear fit, high explanatory power) justifies reverse inference and the use of the seabird diet as a proxy for prey

availability in the environment. Based on the foraging ambits of these species (90 km for murre and 60 km for auklets), the proxies certainly represent prey abundance in the greater Gulf of the Farallones region.

We also simplified the modeled food web by conducting EOF analyses on net-sampled zooplankton (from central Oregon) combined with the seabird proxy for *T. spinifera*. These variables loaded more strongly on the zooplankton net samples from Oregon but all loadings were positive. Presumably due to the strong southern flow of the California Current, the lipid-rich cold-water copepod species are a robust component in food webs for northern California species and have previously been shown to positively correlate with predator responses considered here, such as Cassin's auklet reproductive success (Sydemann and Thompson, 2010). With the combination of both zooplankton information collected from

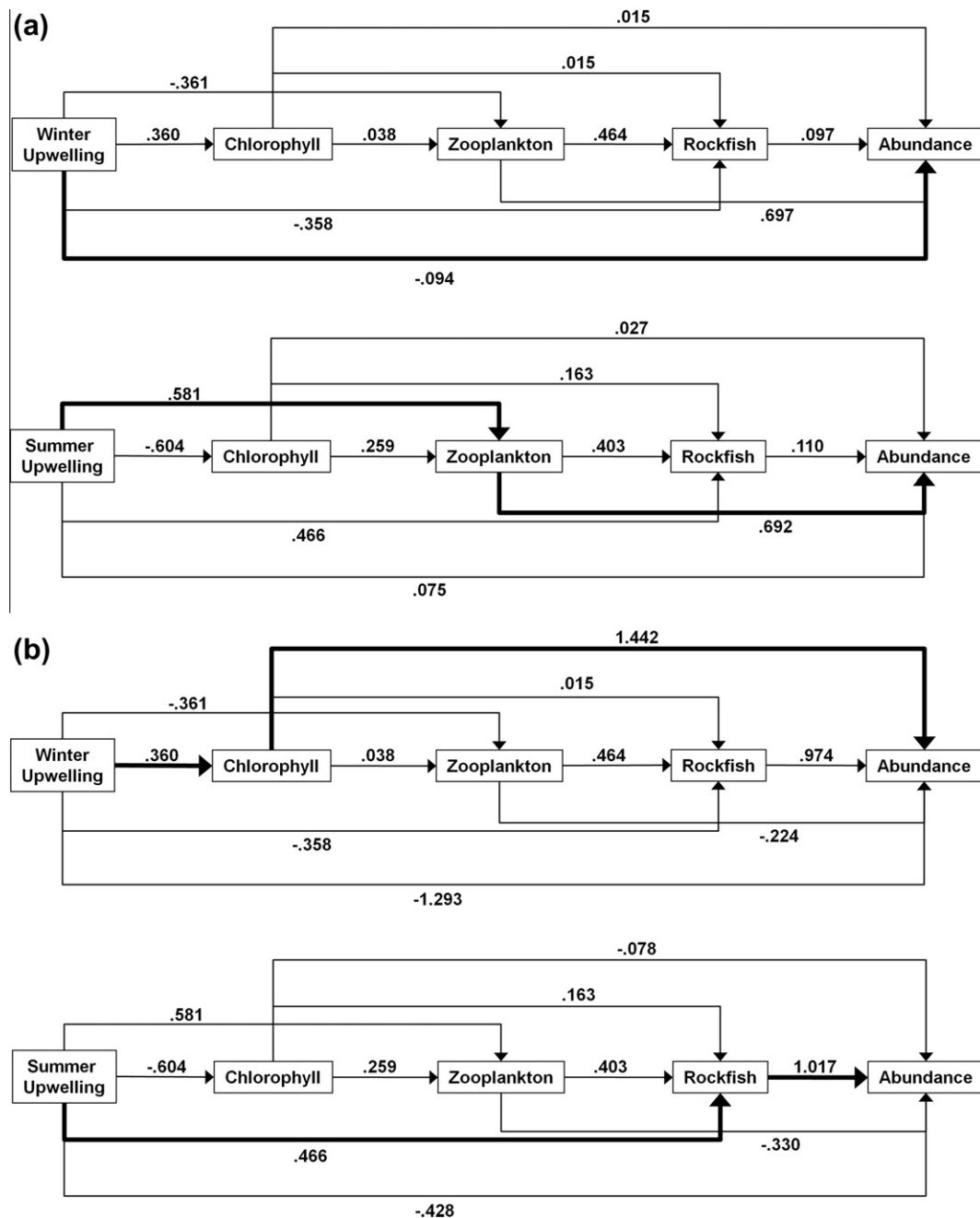


Fig. 7. Path diagrams for seasonal upwelling and Chinook salmon abundance, Russian River, year of (a) ocean entry and (b) adult return.

Table 2

Direct and indirect effects of pathways of responses relative to seasonal upwelling. Shading indicates the dominant path. See Methods for details of assessment.

Species/response	Upwelling season	Direct effect	Indirect effect
Splitnose Rockfish Growth	Winter	0.654	−0.180
	Summer	0.312	−0.193
Cassin's Auklet Phenology	Winter	−0.240	0.247*
	Summer	−0.798	0.189*
Cassin's Auklet Reproductive Success	Winter	0.044	−0.461
	Summer	0.065	0.629*
Common Murre Phenology	Winter	−0.543	0.617*
	Summer	−0.385	−0.301*
Common Murre Reproductive Success	Winter	0.341	−0.496
	Summer	0.0004	0.484*
Humpback Whale Abundance	Winter	−0.129	−0.199
	Summer	−0.310	0.109*
Chinook Abundance, Sacramento River (Year of Ocean Entry)	Winter	−0.006	−0.384
	Summer	−0.010	0.621*
Chinook Abundance, Sacramento River (Year of Return)	Winter	−0.164	−0.438
	Summer	−0.060	0.601*
Chinook Abundance, Russian River (Year of Ocean Entry)	Winter	−1.293	0.096
	Summer	−0.428	0.455*
Chinook Abundance, Russian River (Year of Return)	Winter	−0.094	−0.286
	Summer	0.075	0.337

* Denotes significance (see Table 3).

Table 3Results for multiple regression. The dominant path for effect of upwelling on the response is noted as direct or indirect by listing the intermediate variable or variables of that dominant indirect path. An exception is Cassin's auklet phenology and summer upwelling: upwelling is also listed because of the resulting significant individual effect in the model. Owing to the relatively small sample size, significance was considered when $p < 0.1$ (for a justification of this approach see Grosbois et al., 2008); NS: not significant.

Response	Dominant path	N	Multiple regression			
			Model results		Significant factor results	
			R ²	p-value	t	p > t
<i>Splitnose rockfish growth</i>						
Winter upwelling	Direct	10	0.20	0.191		
Summer upwelling	Direct	10	0.01	0.782		
<i>Cassin's auklet phenology</i>						
Winter upwelling	Zooplankton	10	0.52	0.074	−2.77	0.028
Summer upwelling	Chlorophyll	9	0.69	0.030	−2.49	0.047
	Upwelling				−3.63	0.011
<i>Cassin's auklet breeding success</i>						
Winter upwelling	Direct	10	0.17	0.236		
Summer upwelling	Chlorophyll	9	0.63	0.050		NS
<i>Common murre phenology</i>						
Winter upwelling	Zooplankton	10	0.61	0.038	−4.19	0.009
Summer upwelling	Chlorophyll	9	0.80	0.034		NS
	Zooplankton				−2.74	0.041
<i>Common murre breeding success</i>						
Winter upwelling	Direct	10	0.004	0.860		
Summer upwelling	Zooplankton	10	0.50	0.088	2.04	0.081
<i>Humpback abundance</i>						
Winter upwelling	Direct	10	0.01	0.753		
Summer upwelling	Rockfish	10	0.60	0.041	3.00	0.020
<i>Chinook abundance, Sacramento River (Year of Ocean Entry)</i>						
Winter upwelling	Direct	10	0.12	0.334		
Summer upwelling	Chlorophyll	10	0.63	0.051	−2.04	0.088
<i>Chinook abundance, Sacramento River (Year of Return)</i>						
Winter upwelling	Direct	10	0.15	0.262		
Summer upwelling	Rockfish	10	0.64	0.028	2.79	0.027
<i>Chinook abundance, Russian River (Year of Ocean Entry)</i>						
Winter upwelling	Direct	9	0.15	0.311		
Summer upwelling	Zooplankton	9	0.62	0.053	2.70	0.036
<i>Chinook abundance, Russian River (Year of Return)</i>						
Winter upwelling	Chlorophyll	7	0.28	0.512		NS
Summer upwelling	Rockfish	7	0.50	0.254		NS

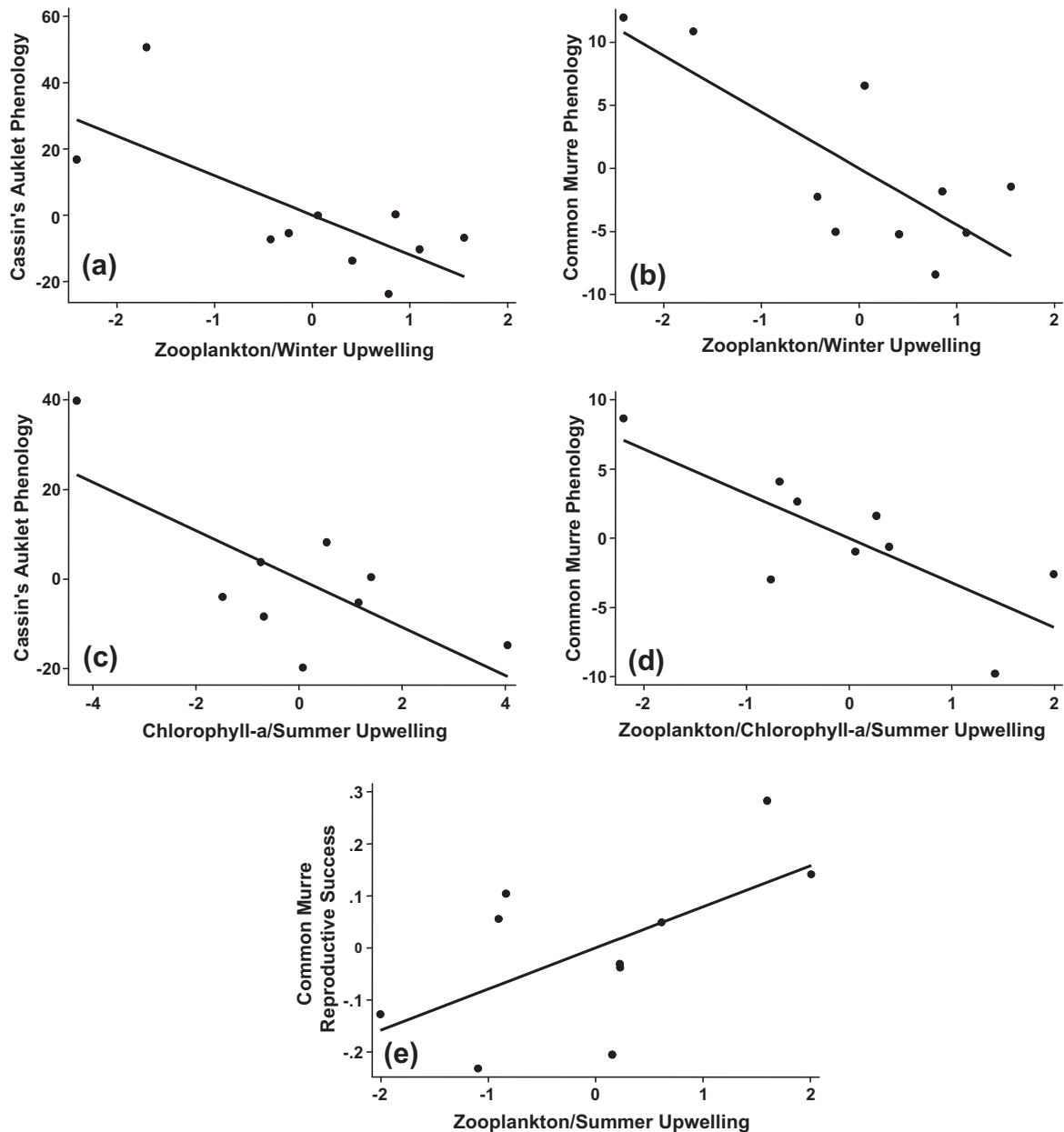


Fig. 8. Added variable plots for seabirds: (a) Cassin's auklet phenology predicted by zooplankton adjusted by winter upwelling, (b) common murre phenology predicted by zooplankton adjusted by winter upwelling, (c) Cassin's auklet phenology predicted by chlorophyll-a adjusted by summer upwelling, (d) common murre phenology predicted by zooplankton adjusted by chlorophyll-a and summer upwelling and (e) common murre reproductive success predicted by zooplankton adjusted by summer upwelling.

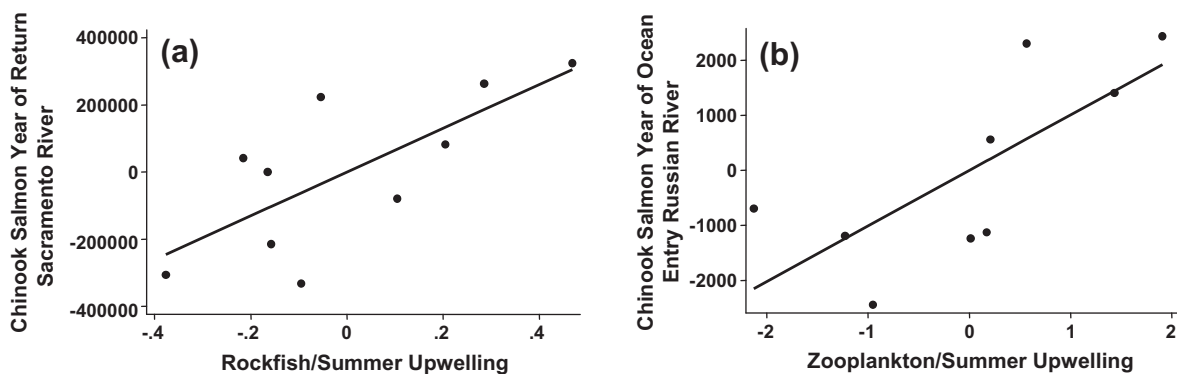


Fig. 9. Added variable plots for Chinook salmon: (a) adult return abundance in the Sacramento River predicted by rockfish adjusted by summer upwelling and (b) ocean entry abundance in the Russian River predicted by zooplankton adjusted by summer upwelling.

seabird diet studies as well as field-sampled zooplankton, we consider EOF1_{zooplankton} to be a representation of relative zooplankton biomass.

4.2. Direct or indirect effects?

Path analysis showed that dominant modes of response from upwelling to predators were indirect (12 of 20 models). None of the selected direct paths were significant (defined as $p < 0.1$, given our relatively small sample size), while 83% of the indirect paths were significant (Table 3), thereby supporting our primary hypothesis. Probably, the inclusion of additional or different prey data would have produced even more significant indirect models. Furthermore, our findings follow a lack of evidence for direct correlations between upwelling and predator response (Black et al., 2011), which provides confirmation of the indirect relationship.

While our primary hypothesis was supported, the lack of direct effects, or indirect effects operating through habitat variability, cannot be dismissed. For example, when upwelling is strong, there is considerable cross-shelf transport in water masses and planktonic materials (Peterson et al., 1979). Therefore, with stronger upwelling the volume of coastal cold-water habitat enlarges, and it is well-known that California Current predators often respond to changes in hydrographic habitat characteristics (Hyrenbach and Veit, 2003; Barlow et al., 2008). To demonstrate these kinds of relationships, however, we would have needed to investigate changes in range or distribution for the predators under consideration. We also did not assess any physiological or metabolic response variables. Therefore, we note that our general conclusion of indirect effects applies only to the type of responses evaluated in this study which include demographic (breeding success, abundance) and life history (phenology).

The one species that showed only direct effects of upwelling, splitnose rockfish, is ectothermic. For this rockfish, the relationships with upwelling were positive, indicating greater growth in years of more upwelling. While insignificant in this study, Black et al. (2011) found significance of this relationship, but they used a much longer time series (60 years). Generally speaking, growth of ectothermic fish is positively related to water temperature (Brander, 2005), but upwelling and surface temperature in the California Current are inversely related (Checkley and Barth, 2009). As cooler temperatures are associated with upwelling, we expected a decrease, not an increase in rockfish growth with increasing upwelling. For this species, it is also possible that we did not include the correct food web prey indicator in the path models to secure indirect relationships. Splitnose rockfish are known to primarily consume euphausiids (Love et al., 2002). Our zooplankton functional group included information on copepods and euphausiids (relative abundance of *T. spinifera*), yet the deeper-water habitats of splitnose rockfish are known to support a different species of euphausiid, *E. pacifica*. Therefore, it seems reasonable to suggest that the unexpected relationship between splitnose rockfish growth and upwelling may be related to a prey species that was not well-represented by our zooplankton functional group. It is also possible that upwelling does have a direct effect on rockfish metabolism and growth, but the mechanism for this relationship is presently unknown.

4.3. Indirect effects and trophic connections

Of the 10 models showing significant indirect pathways of response (Table 3), all but one showed only one intermediate trophic step. The one model showing two steps was the timing of breeding of common murre related to summer upwelling, which included chlorophyll-a and zooplankton in the dominant path (Fig. 4a). However, chlorophyll-a was not significant when zooplankton

was in the model, indicating that zooplankton was the driving factor. Indeed, seabird phenology was the only response that had indirect paths for both winter and summer upwelling. For murre timing, the seasonal path models were consistent in showing negative (i.e., earlier) timing with increasing zooplankton biomass, with winter effects slightly stronger than summer effects (winter upwelling, zooplankton → phenology $\beta = -0.663$ vs. summer upwelling, zooplankton → phenology $\beta = -0.561$). Murres are known to consume euphausiids during the pre-egg-laying period (Sydeman et al., 1997) and generally initiate nesting in late April each year (Reed et al., 2009; Schroeder et al., 2009), so it is reasonable that winter upwelling operating through zooplankton is the primary determinant of murre phenology. Similarly, auklets showed an indirect model from winter upwelling to phenology acting through zooplankton, with stronger winter effects (winter upwelling, zooplankton → phenology $\beta = -0.784$ vs. summer upwelling, chlorophyll-a → phenology $\beta = -0.603$; Fig. 3a). The summer upwelling – timing relationship for auklets is a bit surprising as this species initiates nesting in March or April each year (Schroeder et al., 2009). As seabird laying dates were the only phenological responses investigated we conclude that winter upwelling operating via zooplankton biomass primarily determines timing variation for seabirds in this system. While this result has been previously suggested (Abraham and Sydeman, 2004; Schroeder et al., 2009), this is the first study to link upwelling, zooplankton and seabird laying dates using path analysis. Moreover, since we investigated two biological characteristics (phenology and breeding success) for each of two species of seabirds, we were able to examine the effects of seasonal upwelling in the context of similarities or differences within and between species. Path analysis indicated similarities across both species for both phenology and breeding success, but differences across responses for each species.

Of the remaining indirect models, all involved summer upwelling and two included chlorophyll-a (auklet breeding success, Sacramento YoE salmon), two included juvenile rockfish (humpback abundance, Sacramento YoR salmon), and two included zooplankton (murre breeding success and Russian YoE salmon). Salmon and humpback whales are known to consume juvenile *Sebastes* spp. as prey (Kieckhefer, 1992; Mills et al., 2007), so based on food habits for these species these models appear to be reasonable. Our finding of a significant indirect pathway of response for humpback whale abundance, however, was unexpected as abundance of this long-lived, slowly reproducing species would probably not respond on the interannual time scale, but rather over many years or decades. A reproductive variable similar to what we have used for seabirds or some measure of body condition might have been better for this analysis, but these data are not available. Mortality (Ford et al., 2009) and calving rates (Perryman et al., 2002) of other whale species has been linked to environmental conditions, but these variables would alter abundances in a detectable way only over multiple years. Nonetheless, we found that interannual deviations (residuals) from the humpback whale population trend were related to summer upwelling and juvenile rockfish abundance. We interpret this relationship as reflective of a change in distribution of whales, or some behavioral attribute that affected whale distribution or behavior and thereby altered or biased the abundance estimates, rather than demonstrating actual changes in whale abundance. Murres are also known to consume large quantities of juvenile rockfish (Roth et al., 2008), and their breeding success has been previously related to juvenile rockfish abundance (Ainley et al., 1995; Field et al., 2010), yet in this study murre breeding success was related to zooplankton. Based on net samples taken throughout the GoF over 25 years, juvenile rockfish were generally low in abundance during the 10 years of this study (Field et al., 2010), so it may be that another prey species, possibly northern anchovy (*Engraulis mordax*) which was not sampled, related more clo-

sely to murre breeding success during this decade. For Cassin's auklet breeding success the summer upwelling model included chlorophyll-*a* as a component, but this factor was not significant, indicating that upwelling was probably the key factor. Despite the fact that juvenile rockfish abundance has been related to murre productivity in previous studies (Wells et al., 2008; Field et al., 2010), in this study, zooplankton was a better predictor of predator growth, timing, reproductive success, and abundance. This may be related to the fact that the trophic chain to rockfish also includes the zooplankton functional group.

4.4. Salmon year of ocean entry or year of return

A unique aspect of this study is that we examined the relationships between Chinook salmon returns (abundance) against upwelling and intermediate trophic levels in the year of return (YoR) as well as lagged 2 years to the year of ocean entry (YoE). We found a consistent result for the year of return, where summer upwelling was indirectly related to abundance through juvenile rockfish. For the Russian River, however, the model was not statistically significant undoubtedly due to the small sample size (Table 3). In the year of ocean entry, models of summer upwelling through chlorophyll-*a* (Sacramento) and zooplankton (Russian) were significant. Thus, the pathway of response for the effect of summer upwelling on juvenile salmon (year of ocean entry) has significant intermediate steps at lower trophic levels (chlorophyll-*a* and zooplankton), whereas the pathway of response for adult salmon (year of return) has an intermediate step at mid trophic levels (juvenile rockfish). It has been previously shown that adult Chinook salmon prey upon juvenile rockfish (Merkel, 1957; Hunt et al., 1999; Mills et al., 2007) and other fish species (Peterson et al., 1982; Brodeur, 1990), while zooplankton can be prevalent in the diets of juveniles (Baldwin et al., 2008). Our results corroborate these findings and show that the ontogenic changes in the prey use may be reflective of oceanographic-food web interactions that affect survival and returns at appropriate time lags.

5. Conclusions

In summary and conclusion, seabird phenology was related to both winter and summer upwelling through zooplankton and seabird breeding success was related to summer upwelling through zooplankton. Humpback whale abundance was related to summer upwelling through juvenile rockfish, and salmon abundance was significantly related to summer upwelling through juvenile rockfish in the year of return and through zooplankton in the year of ocean entry. Thus, winter upwelling is important to timing variables, summer upwelling is important to demographic variables, and both zooplankton and forage fish are important intermediate trophic connections. We demonstrate bottom-up trophic control and conclude, as hypothesized, that most predator responses are indirect and varied in accordance with known predator food habits. Knowledge of food habits is therefore critical to predicting predator response to changes in the seasonality of upwelling in eastern boundary current ecosystems in the future. Upwelling is predicted to both intensify and change in seasonality as a result of global warming (Bakun, 1990; Snyder et al., 2003). The path analysis and modeling framework developed and tested here reflect hypotheses that can be modified to examine, in more detail, predictions of predator responses to future climate variability and upwelling change. Depending on how climate change influences the seasonality of upwelling, different species and responses may be impacted. The evidence-based pathways of response demonstrated in this study should have great relevance to understanding upwelling and ecosystem dynamics in the decades to come.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.poccean.2012.02.001](https://doi.org/10.1016/j.poccean.2012.02.001).

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