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## Upwelling and the condition and diet of juvenile rockfish: A study using $^{14}\text{C}$ , $^{13}\text{C}$ , and $^{15}\text{N}$ natural abundances

**Abstract**—Juvenile *Sebastes jordani* individuals sampled in late spring 1995, 1996, and 1997 near Monterey Bay, California, were analyzed for  $\Delta^{14}\text{C}$ ,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ . As anticipated, a strong negative correlation was found between mean annual juvenile rockfish  $\Delta^{14}\text{C}$  and the preceding 3-month average Bakun upwelling index for this region. The sensitivity of this isotopic response by juvenile rockfish to upwelling variations was similar to that previously observed in surface-water inorganic carbon in nearby Half Moon Bay (Robinson 1981). This indicates that the  $\Delta^{14}\text{C}$  of surface-dwelling marine fish can be used as a measure of fish feeding in freshly upwelled  $^{14}\text{C}$ -depleted water. However, we found no correlation between this parameter and fish somatic condition as measured by deviations in the regressions of individual fish (1) weight on length, (2) otolith size on fish length, or (3) total lipid content on dry weight. This questions the role upwelling plays in affecting juvenile rockfish condition. Also unrelated to fish condition were fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , implying that the condition of juvenile *S. jordani* is unaffected by variation in the consumption of specific, isotopically discernible food resources.

The advection of nutrients critical to plant life is facilitated by the upwelling of subsurface water and has long been recognized as an important process for both neritic and open ocean ecosystems (Smith 1968; Cushing 1975; Hermann et al. 1989). The transport of micro- and macronutrient-rich deep water to the photic zone via winds, internal waves, and ocean currents can significantly stimulate primary, and subsequently secondary, production when those nutrients are otherwise limiting to plant and microbial growth. These processes are thought to play a pivotal role in determining the spatial, temporal, and taxonomic patterns of life in the ocean. Although nutrient supply and overall ecosystem productivity are necessarily intimately linked, it has proven more difficult to directly demonstrate by field measurement that a relationship exists between upwelling (nutrient supply) and the health and abundance of the more diffuse and mobile higher consumers.

The rockfishes (*Sebastes*) are one such example. This genus forms one of the most important segments of the U.S.

West Coast groundfish fishery. Management of these stocks is based almost exclusively on age-structured models that estimate an allowable biological catch (ABC) using the  $F_{50}$  criterion (Ralston 1998). Because of extreme interannual variability in rockfish reproductive success (Leaman and Beamish 1984), experience has shown that rockfish ABCs depend primarily on the recent history of recruitments to the fishery. Consequently, management of the resource stands to significantly benefit from improvements in forecasting rockfish year-class strength.

Rockfish year-class strength is largely established during the larval period (i.e., 0–60 d in age; Ralston and Howard 1995), and variability in the coastal upwelling regime is thought to be particularly important in controlling the physical environment of young-of-the-year (Larson et al. 1994). Larval survival is hypothesized to be adversely affected by reduced upwelling because of inadequate inputs of inorganic nutrients to the photic zone and consequent reduced organic production of larval prey (Cury and Roy 1989). Conversely, elevated upwelling may affect larval survival negatively, presumably because of increased turbulence in the water column (Lasker 1978). Optimum conditions for larval survival are thus predicted to occur at times and places of intermediate levels of upwelling. Empirical evidence in support of this hypothesis is provided by Ainley et al. (1993), who reported a dome-shaped relationship between upwelling in January–February and juvenile rockfish abundance later in the year. Their study was based on data collected off central California over an 18-yr period. However, such observations must be tempered by the fact that conventional field sampling and measurement techniques (e.g., midwater trawling) have demonstrated significant seasonal, interannual, and spatial variability in young-of-the-year rockfish densities (Larson et al. 1994). Thus, the statistical problems associated with such sampling and observational studies are significant.

We therefore proposed that measurement of  $^{14}\text{C}$  abundance in individual juvenile *Sebastes* could be useful in studying the relation between upwelling and fish health and survival because relative  $^{14}\text{C}$  depletion in surface water dissolved inorganic carbon (DIC) has been found to be a highly conservative marker or tracer of upwelling in this region. Robinson (1981) found a very large seasonal cycle in surface-water  $\Delta^{14}\text{C}$  (see *Methods* for definition) in Half Moon Bay, California. The magnitude of this signal is partly due to the natural difference in  $\Delta^{14}\text{C}$  between surface water in equilibrium with the atmosphere and subsurface water that has “aged” (lost  $^{14}\text{C}$  by radioactive decay) since its last contact with the atmosphere (e.g., Southon et al. 1990; Stuiver and Braziunas 1993). However, this natural dichotomy between equilibrated surface water and deep water was exacerbated by the large addition of  $^{14}\text{C}$  to the atmosphere (and subsequently the surface ocean) during atomic weapons testing in 1950–1960. This resulted in a massive increase in atmospheric  $\Delta^{14}\text{C}$  and subsequent elevations in ocean surface water  $\Delta^{14}\text{C}$ , contributing greatly to the  $\Delta^{14}\text{C}$  difference between surface and recently advected deep water. For example, seasonal  $\Delta^{14}\text{C}$  variations along the central California coast in 1978–1979 were in excess of 100‰ (Robinson 1981). In addition, interannual  $\Delta^{14}\text{C}$  variations in the Gulf of California in the decades following nuclear testing were found to

be in excess of 30‰, again strongly influenced by variations in upwelling linked to El Niño–Southern Oscillation (ENSO) events (Frantz et al. 2000). With the decline in atmospheric  $\Delta^{14}\text{C}$  following the cessation of aboveground nuclear testing, surface water  $\Delta^{14}\text{C}$  has begun to level off or decline as the bomb  $^{14}\text{C}$  is diluted by the large oceanic carbon reservoir (e.g., Peng et al. 1998; Frantz et al. 2000). Conversely,  $\Delta^{14}\text{C}$  in subsurface ocean layers have increased somewhat as bomb  $^{14}\text{C}$  is mixed downward (e.g., Peng et al. 1998).

Because the  $\Delta^{14}\text{C}$  in surface water DIC determines the  $\Delta^{14}\text{C}$  of the marine consumer food base produced in surface waters via photosynthesis, we believed that the  $\Delta^{14}\text{C}$  in marine animal consumers such as juvenile rockfish could provide at least a qualitative measure of their feeding in and exposure to recently upwelled versus nonupwelled water. If this is the case, then hypotheses relating upwelling to fish condition, survival, and abundance can be tested by looking for consistent relationships between these measures and  $\Delta^{14}\text{C}$  in individual fish.

Necessary for the determination of  $\Delta^{14}\text{C}$  is the measurement of stable carbon isotope abundances ( $\delta^{13}\text{C}$ —see *Methods*). This measurement allows carbon isotope fractionation by biological processes to be factored out of the radiocarbon measurement.  $\delta^{13}\text{C}$  variation in animal consumers is also a useful measure of diet variability because diet  $\delta^{13}\text{C}$  largely determines consumer  $\delta^{13}\text{C}$ . The same is also true of stable nitrogen isotope abundances ( $\delta^{15}\text{N}$ —see *Methods*), which can be determined readily in parallel with  $\delta^{13}\text{C}$ . The ranges of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in a juvenile *Sebastes* population can then be used as a qualitative measure of diet variability within that population. We sought to establish what these ranges were in samples of Monterey Bay *Sebastes* juveniles and to see if diet variations among individuals as measured by these parameters were related to fish condition.

*Methods*—Pelagic juvenile *S. jordani* were collected using a midwater trawl in the Monterey Bay area during the annual rockfish recruitment cruise conducted by the National Marine Fisheries Service (NMFS) Tiburon Laboratory, which was conducted in three legs or sweeps during May–June 1995–1997. This study focused on this species because of previous knowledge of its ecology and because of its relative abundance and ecological importance in central California (Lenarz 1980; Ainley et al. 1993). The midwater trawl sampled a cross-sectional area of 100 m<sup>2</sup> and was fitted with a 9.5-mm codend liner. For each year sampled, the distribution and abundance of 15 species of *Sebastes* was assessed, and an annual index of year-class strength was estimated. The index of year-class strength was corrected for differences in age structure by adjusting all trawl catches of young-of-the-year rockfish to a common age of 100 d by (1) measuring the standard length of all specimens, (2) ageing a subsample for each year of the survey, (3) estimating the age of each specimen from year-specific regressions of age on length, and (4) adjusting the relative weight of each fish by application of an exponential mortality model that assumed a constant natural mortality rate of 0.04 d<sup>-1</sup> (see Ralston and Howard [1995] for details). Final calculation of the index was computed as the log-transformed mean relative abundance over seven spatial strata. All trawls were at a standard

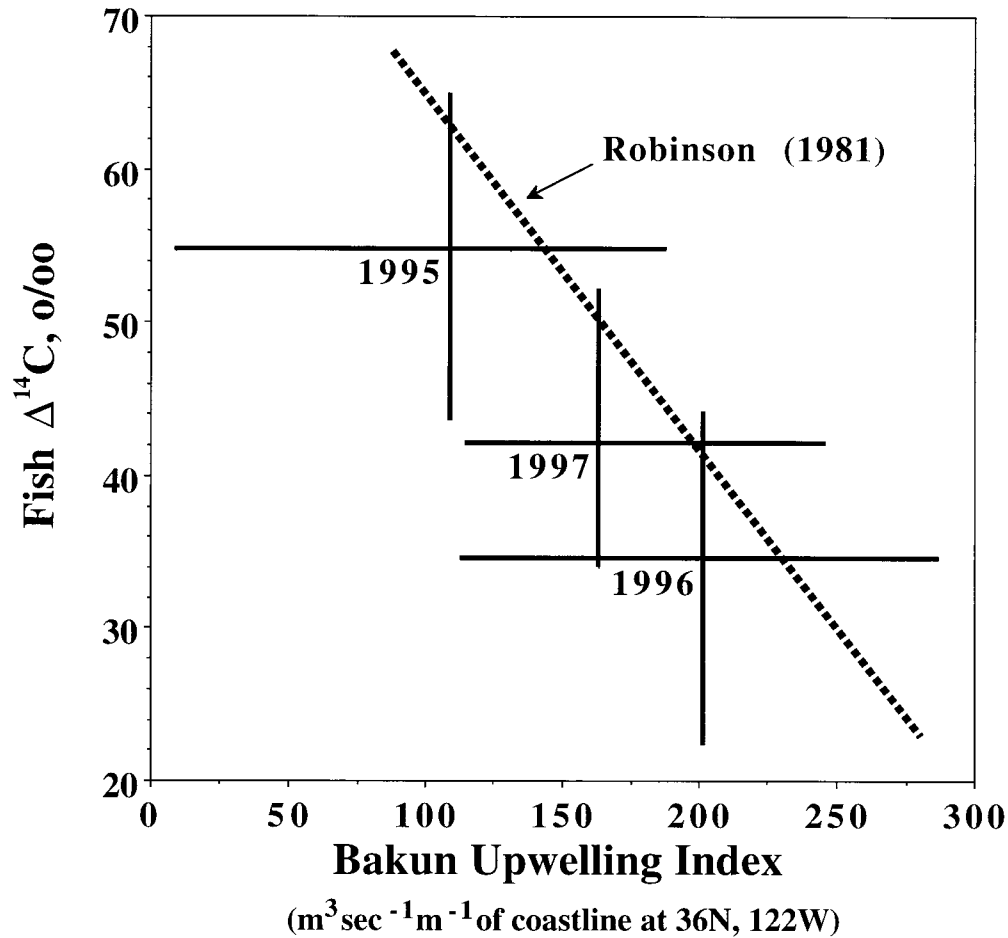


Fig. 1. Upwelling versus radiocarbon abundance in *Sebastes jordani* juveniles in or near Monterey Bay, California, in late spring 1995–1997. Vertical lines denote range of values encountered in each year. Horizontal lines denote range of monthly mean upwelling values reported for the 3 months prior to each yearly fish sampling (<ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon>). Diagonal dashed line indicates mean trend between upwelling and surface-water–dissolved inorganic radiocarbon in Half Moon Bay, California, in 1978–1979 as reported by Robinson (1981).

depth of 35 m, were of 15 min duration, and were conducted at a series of fixed stations in and near Monterey Bay.

Somatic condition measures of the young-of-the-year rockfish sampled above included otolith anomaly, wet weight anomaly, and total lipid anomaly. At sea, specimens of *S. jordani* were placed in whirl-packs and frozen at  $-80^{\circ}\text{C}$ . In the laboratory fish samples were defrosted, length and wet weight were measured, and the sagittal otoliths were removed. The logarithm of wet weight was regressed on the logarithm of standard length, and the residual was used as an index of somatic condition (= weight anomaly). Otolith size was determined using the results of a principal component analysis that combined three separate otolith length measurements (i.e., length, height, and perimeter) into one. Composite otolith size was then regressed on standard length, and the residual (with sign changed) was used as another index of condition over the life span of the fish (Suthers et al. 1992). Total lipid was extracted from selected fish using methods outlined in Norton et al. (2001). Speci-

men total lipid content was also regressed on standard length, and the residual deviation from the mean trend (= lipid anomaly) was determined. In theory, these three somatic condition measures should be positively correlated with one another, with positive anomalies representing specimens in good condition. Of the remaining fish not consumed by lipid analysis, muscle was excised from individual fish covering a range of fish sizes and prepared for isotope analyses by first submerging samples in a dilute HCl solution to remove inorganic carbon that could potentially include  $^{14}\text{C}$  contamination. All muscle excision and subsequent handling of the fish was done with uncontaminated surfaces (clean gloves, acid-rinsed tweezers and sample containers, and so on).

To determine stable isotope abundances, tissue carbon and nitrogen were converted to  $\text{CO}_2$  and  $\text{N}_2$  and analyzed on a Nuclide 6-60 isotope ratio mass spectrometer to determine  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively (e.g., Rau et al. 1990, 1992). A split ( $\sim 20$ – $50 \mu\text{mol}$ ) of the  $\text{CO}_2$  gas of each sample was

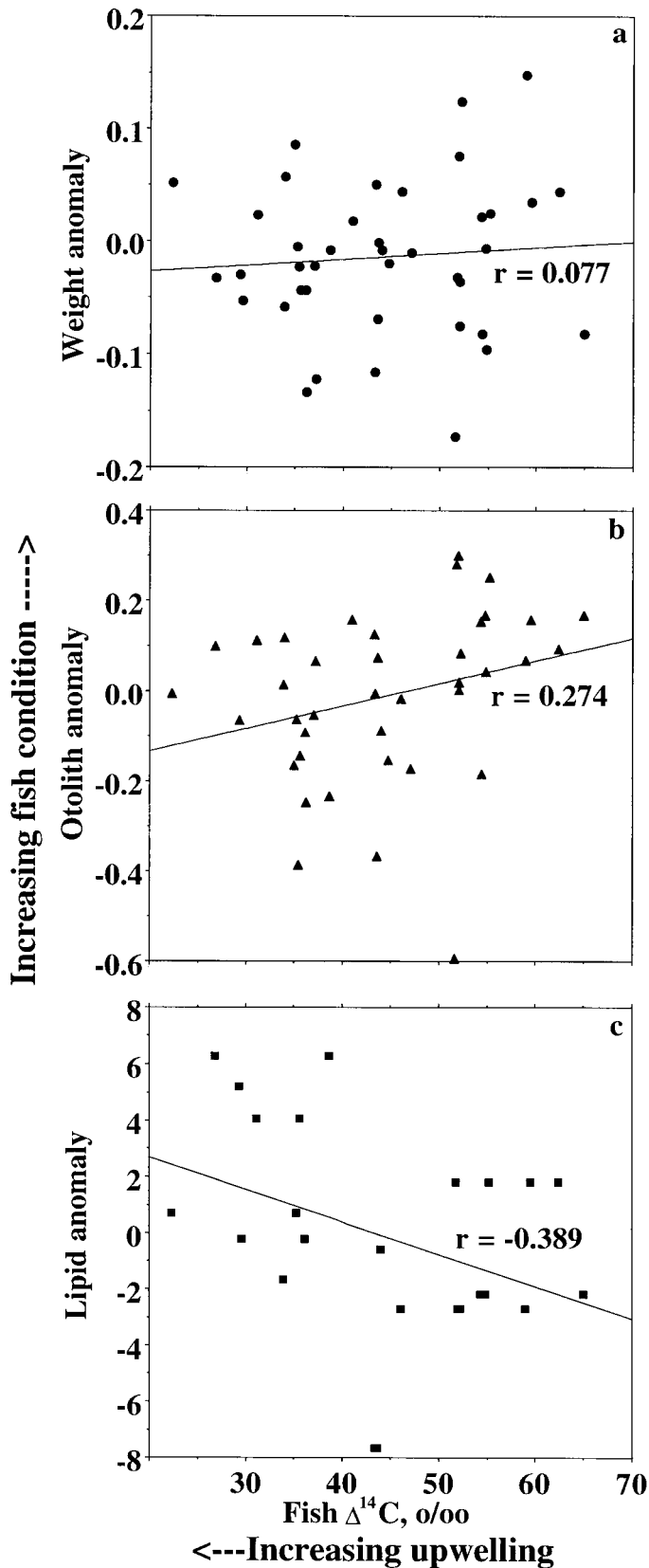


Fig. 2. Radiocarbon abundance versus (a) weight, (b) otolith, and (c) lipid anomalies in juvenile *Sebastes jordani* collected in or near Monterey Bay, California, in late spring 1995, 1996, and 1997. Lipid anomalies are station means for 1995 and 1996 only. Increas-

ing anomaly values imply better fish health and condition. Lines denote linear regression of data. The correlation coefficient,  $r$ , in each figure is not significantly different from 0 at the 95% confidence level.

$$\Delta^{14}\text{C} = \delta^{14}\text{C} - 2(\delta^{13}\text{C} + 25)(1 + \delta^{14}\text{C}/1,000),$$

where

$$\delta^{14}\text{C} = 1,000(^{14}\text{C}/^{12}\text{C}_{\text{sample}} - ^{14}\text{C}/^{12}\text{C}_{\text{standard}})/^{14}\text{C}/^{12}\text{C}_{\text{standard}},$$

$$\delta^{13}\text{C} = 1,000(^{13}\text{C}/^{12}\text{C}_{\text{sample}} - ^{13}\text{C}/^{12}\text{C}_{\text{PDB standard}})$$

$$\div ^{13}\text{C}/^{12}\text{C}_{\text{PDB standard}}, \quad \text{and}$$

$$\delta^{15}\text{N} = 1,000(^{15}\text{N}/^{14}\text{N}_{\text{sample}} - ^{15}\text{N}/^{14}\text{N}_{\text{air standard}})$$

$$\div ^{15}\text{N}/^{14}\text{N}_{\text{air standard}}.$$

That is, these values increase (decrease) as the heavier isotope increases (decreases) relative to the lighter isotope of either C or N as denoted above. Units are in parts per thousand (per mil, ‰) with a typical analytical precision of  $\pm 5\text{‰}$ ,  $0.2\text{‰}$ , and  $0.3\text{‰}$  for  $\Delta^{14}\text{C}$ ,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ , respectively.

*Fish  $\Delta^{14}\text{C}$* —Initial fish  $\Delta^{14}\text{C}$  ranged 22.3–84.1‰ (see Web Appendix 1: [http://www.aslo.org/lo/toc/vol\\_46/issue\\_6/1565a1.pdf](http://www.aslo.org/lo/toc/vol_46/issue_6/1565a1.pdf)). However, there was reason to suspect that the two highest values in the 1995 collection resulted from  $^{14}\text{C}$  contamination, and these values were removed from consideration in the following interpretation. The revised  $\Delta^{14}\text{C}$  range is similar to, to somewhat lower than, the few data available for other eastern Pacific Ocean near-surface-dwelling fishes (Percy and Stuiver 1983; Williams et al. 1987; Druffell and Williams 1991). Consistent with the observation that surface water DIC  $\Delta^{14}\text{C}$  in this region is inversely correlated with upwelling (Robinson 1981), we found that mean annual fish  $\Delta^{14}\text{C}$  was negatively correlated with the mean Bakun upwelling index for the 3 months preceding fish collection (Fig. 1). To our knowledge, this is the first evidence that fish  $\Delta^{14}\text{C}$  is sensitive to upwelling and that variations in this parameter can be used as a qualitative, if not quantitative, measure of fish exposure to and feeding in freshly upwelled water.

Assuming then that  $\Delta^{14}\text{C}$  variation among individual fish sampled from a common area provides a measure of variation in upwelling exposure experienced by these fish: Is there a relationship between upwelling and fish condition as hypothesized? As Fig. 2a–c demonstrates, no statistically significant relationship is evident between fish  $\Delta^{14}\text{C}$  and fish condition measures represented by interannual weight, otolith, or lipid anomalies. A similar lack of correlation was evident when intra-annual condition anomalies were com-

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pared to fish  $\Delta^{14}\text{C}$ . We therefore conclude that upwelling effects on fish condition are not evident in these data, questioning what, if any, role upwelling played in affecting rockfish health and condition in the region and time period studied.

If, as expected, fish condition correlates positively with survival (*see, e.g.,* Ferron and Leggett 1994), one might further infer from our data that young-of-the-year survival is also unrelated to upwelling. However in this region, *S. jordani* pelagic juveniles were most abundant in 1996, when upwelling was greatest, whereas fish were least abundant in 1995, when upwelling was lowest (S. Ralston, W. H. Lenarz, and D. P. Woodbury in prep.). Thus, during the 1995–1997 period, there is a suggestion that upwelling has a beneficial influence on fish survival. In contrast, Ralston (1995) showed that during 1985–1989, upwelling during the winter spawning season (January–March) was negatively correlated with the growth of larval *S. jordani*, and that growth was uncorrelated with survival. More recent information indicates that the statistical power of the latter comparison was low and that a positive relationship between *S. jordani* growth and survival does exist, albeit weak (S. Ralston, W. H. Lenarz, and D. P. Woodbury in prep.).

These apparently incongruous findings could be due to a relatively broad dome-shaped response of growth and survival to upwelling conditions (i.e., growth and survival may gradually decline on either side of an “optimum upwelling window”; Cury and Roy 1989; Ainley et al. 1993; Ralston 1995). However, such dome-shaped relationships are not evident in our comparisons of upwelling to fish condition (Fig. 2) or to survival (above) in 1995–1997. To more fully test such a model, measurements over a broader range of environmental conditions than afforded by this study are required.

*Fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$* —Fish  $\delta^{13}\text{C}$  (–22.8 to –17.9‰, Web Appendix 1) fell within the range observed in plankton in Monterey Bay (Rau et al. 2001), consistent with previous observations that animal  $\delta^{13}\text{C}$  largely reflects that of the available food base (e.g., Rau et al. 1992). Fish  $\delta^{15}\text{N}$  (6.7–9.8‰) averaged several per mil higher than plankton  $\delta^{15}\text{N}$  (Rau et al. 1998), in keeping with  $^{15}\text{N}$  enrichment seen in higher elements of the marine consumer food web (e.g., Rau et al. 1992). Because animal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  variations are largely controlled by the stable isotope abundance variations in their food (Gearing 1991), a correlation between these measures and fish condition would imply that the latter parameter is affected by differences in diet among individuals. That is, do fish that are in better condition consume food sources that are isotopically distinct from fish in poorer condition? In this study, the answer is no: We found no significant trend (not shown) in isotope abundance in relation to any of the three fish condition measures conducted. However, this study cannot address the possibility that dietary components did change across the range in fish condition encountered but that these dietary components were isotopically indistinguishable, resulting in no significant change in fish  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  with fish condition.

*Conclusions*—Mean annual fish  $\Delta^{14}\text{C}$  in this study displayed a significant negative correlation with regional upwelling in the months that preceded fish collection, consistent with fish  $\Delta^{14}\text{C}$  being a recorder of the exposure of each fish to recently upwelled  $^{14}\text{C}$ -depleted water. Contrary to expectations, no significant relationship between fish  $\Delta^{14}\text{C}$  (upwelling) and three separate measures of fish condition were found. As well, we found no relationship between stable carbon and nitrogen isotope abundances and fish condition. These observations, therefore, provide no evidence that variations in upwelling and diet affect juvenile rockfish condition, at least within the time span and location of the study. The relationships between upwelling and juvenile rockfish growth and survival also appear to be weak. To test the veracity of these conclusions, it would be of interest to apply our approach across a larger geographic and temporal range and to other fish species. Such research could advance our understanding of the relation between physical ocean processes, such as upwelling and fish ecology.

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## Occurrence and ecological implications of pyrophosphate in estuaries

**Abstract**—Loading of bioavailable phosphorus, traditionally measured as soluble reactive phosphorus (SRP), contributes to the eutrophication of aquatic ecosystems. However, polyphosphates are also bioavailable but escape detection by the standard method used for measuring SRP.  $^{31}\text{P}$  nuclear magnetic resonance spectrometric analysis of sediment extracts and enzymatic assay of surface waters reveal heretofore unreported presence of pyrophosphate (Ppi) in coastal wetlands. We show that the accumulation of Ppi (the smallest chemical form of polyphosphate) in coastal wetlands is related to human impact and can occur in quantities that exceed that of SRP. We further

demonstrate that Ppi is readily utilized by microbes in coastal wetland sediments in the presence of nitrogen and carbon and can serve as a reservoir of orthophosphate. Thus, Ppi accumulation in estuaries will subsidize the in situ biogeochemical phosphorus cycle. This has important ecological implications for trophic responses and estuarine productivity.

Phosphorus (P) plays a vital role in controlling biotic production in a wide range of ecosystems, ranging from freshwater lakes (Hecky and Kilham 1988) to open oceans (Clark