Spatial patterns of recruitment in a demersal fish as revealed by seabird diet

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ABSTRACT: Understanding recruitment in demersal fish requires determination of larval survival and delivery to appropriate settling habitats. Sanddabs *Citharichthys* sp. are an abundant neritic fish of Central California, an area of persistent upwelling. 'Upwelling shadows' develop in the lee of coastal promontories, retain surface waters, and may promote spatial variation in fish settlement. To test this hypothesis, we studied the diet and foraging dimensions of a seabird (*Cepphus columba*) specializing in sanddab consumption at windward and leeward sites over a 6 yr period. We integrated the bird's take of sanddab with information on upwelling intensity and variability and sanddab larval abundance based on net sampling. Seabird diet at both sub-colonies was variable, but dominated by Age 1 sanddabs. Sanddabs were more prevalent in the diet of guillemots at the leeward site, and diet was more variable at the windward site. Persistent upwelling led to regional increases in sanddab larval abundance which, in turn, resulted in enhanced recruitment to leeward waters, as reflected in seabird diet. Pulsed upwelling was related to apparent increased recruitment in windward waters. This study is one of the first to suggest that seabird diet can be used as an indicator of spatial variability in recruitment and settlement of demersal forage fish.

KEY WORDS: Pigeon guillemot · Sanddab · Diet · Larval abundance · Coastal promontory · Upwelling shadow · Relaxation · Demersal fish settlement

INTRODUCTION

Recruitment in open marine fish populations is dependent on larval survival and settlement (Caley et al. 1996, Levin 1996). For neritic species, settlement may be affected by spatial variability in oceanographic processes that affect the distribution of larvae as they reach settlement age (Jenkins & Black 1994, Wing et al. 1998). In eastern boundary current systems, upwelling promotes ocean productivity, but strong, persistent upwelling may advect icthyplankton away from suitable coastal habitats (Cury & Roy 1989). Recent research has shown that the effect of upwelling on advective processes depends, in part, on coastal topography; in particular, 'upwelling shadows' on the leeward sides of coastal promontories can act as retention areas even when upwelling is strong and persistent (Wing et al. 1995, 1998). Moreover, nutrients entrained within upwelling shadows facilitate primary and sec-

ondary productivity for weeks longer than in areas outside shadows (Graham & Largier 1997).

We tested the hypothesis that recruitment of a demersal fish in an upwelling system varies spatially, with recruitment greater in either windward or leeward habitats depending on the interplay of upwelling effects and coastal topography. While increased upwelling (i.e. more intense and/or more persistent) should increase regional productivity and hence survival of larvae in general, Ekman transport of these larvae could differ on the 2 sides of a coastal promontory (Fig. 1). In windward habitats, increased upwelling may lead to increased offshore advection, reduced recruitment and a reduced Age 1 population the following year. In leeward habitats, increased upwelling may result in an upwelling shadow that will retain larvae and their food. This, in turn, may lead to increased larval recruitment and an increased Age 1 population. Conversely, the Age 1 population should
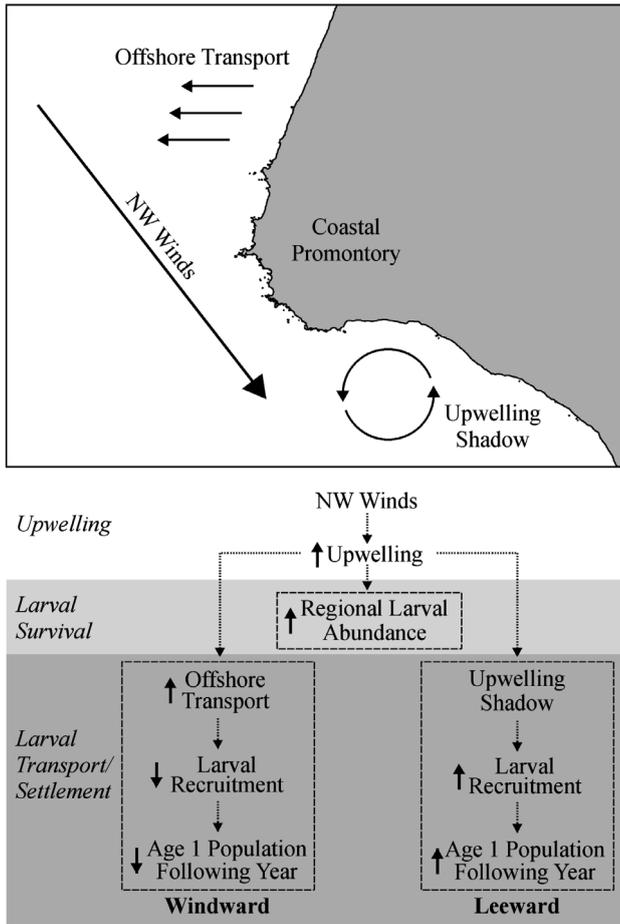
Fig. 1. Theoretical diagram showing the cascading effects of upwelling winds on demersal fish recruitment to windward and leeward habitats around a coastal promontory in Central California

be increased at windward sites and reduced at leeward sites when prior-year upwelling is weak and/or variable. Variable upwelling should result in more relaxation events, and thus, a reduction in net offshore transport at windward sites.

We tested this hypothesis by integrating regional upwelling indices with net samples of sanddab *Citharichthys* sp. larval abundance and diet of a nearshore seabird, the pigeon guillemot *Cepphus columba*, collected upstream and downstream from a coastal promontory. Traditional methods for estimating demersal fish recruitment involve trawl samples to estimate age-specific abundance (Caley et al. 1996). We used a similar approach, but substituted trawl samples with seabird diet, which provides a proxy to abundance of Age 1 individuals. This approach is based on research showing that seabirds can be used as reliable indicators of change in prey populations (Sunada et al. 1981, Cairns 1992, Hatch & Sanger 1992, Montevecchi & Myers 1995, 1996, Miller & Sydeman 2004, Abraham &

Sydeman 2006). However, our approach is novel because we integrate the seabird data with net samples and use seabird diet to test hypotheses of fish settlement to local neritic habitats, a new application.

MATERIALS AND METHODS

Study area, diet and foraging observations. We studied sanddabs *Citharichthys* sp., birds *Cepphus columba* and upwelling at the Point Arguello Promontory, north of Point Conception, Central California (Fig. 2). We defined the promontory as extending from Point Michelle in the north to Sudden Ranch in the south. The coastal habitat here supports ~500 pairs of breeding pigeon guillemots (D. P. Robinette unpubl. data), with the birds nesting in rock crevices. Though guillemots typically take a diverse array of prey (Follett & Ainley 1976, Ewins 1993, Litzow et al. 2000), prey specialization has been observed at both the individual and colony level (Golet et al. 2000, Litzow et al. 2000). Specialization is an ideal trait for an indicator species if the predator does not switch to a single alternate prey in the absence of the dominant prey (Anderson & Gress 1984, Monaghan 1996). This is the case for guillemots at Point Arguello.

We obtained information on diet composition and foraging dimensions of guillemots at 2 sub-colonies,
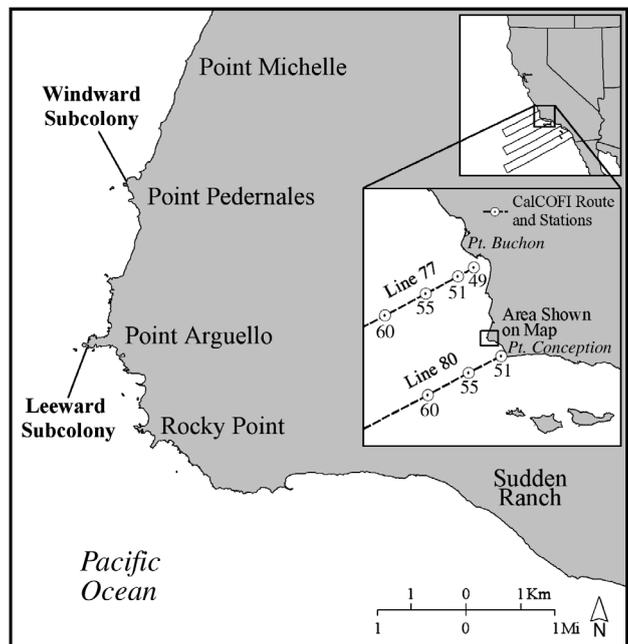

Fig. 2. Map of the Point Arguello Promontory showing the Point Pedernales (windward) and Point Arguello (leeward) sub-colonies. The larger inset map shows nearshore sampling stations along California Cooperative Oceanic Fisheries Investigations (CalCOFI) Lines 77 and 80. The entire CalCOFI survey route is shown in the smaller inset map

1 windward and 1 leeward of the Point Arguello Promontory. Point Pedernales, our windward site, is located approximately 3 km northeast of Point Arguello (Fig. 2). Our leeward site was on the south side of Point Arguello. We made observations during the chick-rearing seasons at Point Pedernales from 2000 to 2002 and again from 2004 to 2005 (n = 132 h total) and at Point Arguello from 2001 to 2005 (n = 206 h total). During chick-rearing, adults return to breeding crevices with whole prey items in their bills. Adults typically land on the rocks outside crevices, allowing identification of prey type. We located 18 crevices at Point Pedernales and 34 at Point Arguello. Because not all crevices are active during a given year, the annual number of crevices used in our analyses ranged from 7 to 9 at Point Pedernales and from 10 to 25 at Point Arguello. We made observations with binoculars and a spotting scope from approximately 30 m. We identified prey to the lowest taxonomic level possible (usually family) and estimated prey size as a multiple of guillemot bill length. Over all years, we identified a total of 684 prey items at Point Pedernales (windward) and 1201 at Point Arguello (leeward). We used percent sanddab as our basic index of sanddab take by the birds. We calculated percent sanddab as the percent of total identified prey items that were sanddabs. To examine if guillemots take an alternate dominant prey in some years, we also calculated diet diversity using the Shannon-Wiener diversity index given in Brower et al. (1998):

$$H' = -\Sigma p_i \log_{10} p_i$$

where p_i is the proportion of total identified prey items from prey group i. This index has a range of values from zero to $\log(S)$, where S is the total number of species in the sample.

Pigeon guillemot foraging directions. Beginning in 2004, we recorded the directions foraging guillemots were leaving in and returning to Point Arguello; in 2005, we extended this effort to Point Pedernales. We made flight observations concurrently with diet observations. At each point, we divided our field of view into north, northwest, west, southwest and south. When birds left the colony, we recorded the direction the bird was last observed flying. For returning birds, we recorded the direction from which they came into view. We recorded a total of 149 departing and 183 returning flights in 2004 and 175 departing and 201 returning flights in 2005 at Point Arguello. We recorded a total of 378 departing and 229 returning flights at Point Pedernales in 2005.

Sanddab larval abundance. We estimated regional sanddab larval abundance using data from the California Cooperative Oceanic Fisheries Investigations (Cal-COFI). CalCOFI surveys are conducted on a quarterly

basis (winter, spring, summer and fall). We used data from bongo tows conducted at nearshore stations along CalCOFI Lines 77 and 80 (Fig. 2). Ohman & Smith (1995) have described the methods. Data were standardized by soaking time and provided as number of larvae m^{-2}. Occasionally, 1 or 2 stations were missed during a particular quarterly survey. Additionally, differences among stations can differ by orders of magnitude. We therefore calculated the geometric mean of larval abundance across stations. We calculated geometric means by transect in order to control for transect effects during statistical analyses. Additionally, because sanddab spawning is triggered by temperature changes associated with upwelling and can continue past the upwelling season (Rackowski & Pikitch 1989), we calculated geometric means of larval abundance for 3 time periods based on CalCOFI surveys: (1) spring and summer, (2) fall and (3) spring, summer and fall.

Upwelling indices. The peak upwelling season along the Central California coast occurs from April through August (Hickey 1979). We estimated the intensity and variability of upwelling using monthly upwelling indices calculated for 36° N, 122° W by the Pacific Fisheries Environmental Laboratory (www.pfeg. noaa.gov). We calculated indices using the same time periods used for larval abundance. We used data from April through August for spring to summer larval abundance, September through November for fall, and April through November for spring, summer and fall. We estimated annual upwelling *intensity* by summing monthly values to create cumulative upwelling indices (CUI) for each time period. We also calculated period-specific estimates of upwelling *variability* by calculating the standard deviations of upwelling within a period.

Statistical analyses. We used tests of homogeneity based on the Pearson goodness-of-fit chi-squared statistic to determine if foraging directions varied by sub-colony and year. We compared 2004 and 2005 at Point Arguello, as well as Point Arguello and Point Pedernales in 2005. To determine which upwelling variables influenced regional larval abundance and at which temporal scales these processes were working, we created predictive linear models with larval abundance measured at the 3 time periods as dependent variables and upwelling intensity and variability at the 3 time periods as independent variables. We used Mallows' C_p criterion to determine the best model for each dependent variable (Mallow 1973). We put 2 limitations on model selection. First, the maximum number of independent variables used was 3 — the CalCOFI transect plus 2 upwelling variables. Second, we did not use upwelling variables containing fall values to predict the previous spring to summer larval abundance. The dependent variable (larval abundance for the respec-

tive time period) was log transformed in these analyses to meet assumptions of linear models (Nur et al. 1999). We present standardized regression coefficients (Kutner et al. 2005) to compare among models. Finally, we used the upwelling and larval abundance variables with the strongest association (as indicated by the standardized regression coefficient) in linear models relating these variables to proportion of sanddab in guillemot diet. Based on the mean guillemot bill length reported by Ewins (1993) and the age-class lengths of sanddabs reported by Rackowski & Pikitch (1989), we determined that guillemots in our study were taking Age 1 sanddabs. We therefore used a lagged approach in our models, relating upwelling and larval abundance in yr^x to diet in yr^{x+1}. When modeling the effects of upwelling on guillemot diet, we controlled for larval abundance; when modeling the effects of larval abundance, we controlled for upwelling. Both models used logit-transformed percent sanddab and controlled for Cal-COFI transect impacts. We estimated separate slopes for windward and leeward sites for the respective variable of interest (larval abundance or upwelling)

Table 1. *Cepphus columba.* Diet composition (% total observations yr^{-1}) and diet diversity (*H'*, Shannon-Wiener index) of pigeon guillemots breeding at the Point Pedernales (windward) sub-colony in 2000 to 2002 and 2004 to 2005

Prey taxon	2000	2001	2002	2004	2005
Sanddab (*Citharichthys* sp.)	23.73	57.50	29.11	60.42	43.95
Anchovy (*Engraulis mordax*)	0.00	1.25	0.00	2.08	3.24
Smelt (Family Osmeridae)	0.00	0.00	6.33	0.00	0.00
Squid (*Loligo* sp.)	0.00	1.25	0.00	0.00	0.00
Rockfish (*Sebastes* sp.)	1.69	0.00	5.70	0.00	4.42
Saury (*Cololabis saira*)	0.00	0.00	0.00	0.00	1.18
Octopus (*Octopus* sp.)	6.78	5.00	9.49	0.00	1.18
Sculpin (Family Cottidae)	15.25	7.50	17.09	14.58	2.95
Cuskeel (Family Ophidiidae)	0.00	1.25	0.00	2.08	1.47
Kelpfish (Family Clinidae)	1.69	0.00	0.00	2.08	2.95
Greenling (*Hexagrammos* sp.)	0.00	1.25	1.27	0.00	3.24
Shrimp (*Crangon* sp.)	0.00	0.00	3.16	6.25	12.68
Blenny (*Hypsoblennius* sp.)	0.00	0.00	0.63	2.08	1.18
Lingcod (*Ophiodon elongatus*)	1.69	2.50	6.33	0.00	0.29
Sardine (*Sardinops sagax*)	0.00	0.00	0.00	2.08	0.00
Midshipman (*Porichthys* sp.)	20.34	18.75	11.39	4.17	10.62
Surfperch (Family Embiotocidae)	0.00	0.00	1.27	0.00	0.00
Gunnel (Family Pholididae)	3.39	1.25	1.27	4.17	2.65
Prickleback (Family Stichaeidae)	15.25	0.00	6.96	0.00	4.13
Sandcrab (*Blepharipoda occidentalis*)	5.08	1.25	0.00	0.00	2.06
Poacher (Family Agonidae)	1.69	1.25	0.00	0.00	0.00
Combfish (*Zaniolepis* sp.)	3.39	0.00	0.00	0.00	1.47
n	59	80	158	48	338
Diversity (*H'*)	0.90	0.63	0.93	0.62	0.89

in a single model when a statistically significant difference between the slopes was detected. We used STATA 8.2 statistical software (STATA 2005) for all statistical analyses except for tests of homo-geneity, which were done by hand.

RESULTS

Sanddab consumption by guillemots

A total of 23 prey species and groups were taken (Tables 1 & 2). Sanddabs were the dominant prey at both sites in all years. Percent sanddab *Citharichthys* sp. was strongly negatively correlated with diet diversity at both sites, indicating guillemots *Cepphus columba* did not switch to a single alternate prey species in years when sanddabs were less available (windward: r = −0.900, p = 0.019; leeward: r = −0.900, p = 0.019). Sanddab consumption at the leeward site was more consistent than at the windward site. Annual percent sanddab ranged from ~41 to 64% of the diet at the leeward site (Table 2) and from ~24 to 60% of the diet at the windward site (Table 1). The coefficient of variation (CV) for the windward site (38.24) was more than

twice that of the leeward site (17.36). Overall, mean (±SE) annual percent sanddab was greater at the leeward site (50.28 ± 3.90, n = 5) than at the windward site (42.94 ± 7.34); the take of sanddab between the sites among years was not significantly correlated (r = −0.400, p = 0.300).

Foraging directions

There were among-year differences in the directions guillemots left and returned to Point Arguello (leaving: χ^2 = 26.93, df = 4, p < 0.005; returning: χ^2 = 26.07, df = 4, p < 0.005). However, the majority of guillemots left and returned from the south and southwest in both years (Fig. 3). The most pronounced differences were that guillemots foraged more to the south in 2004 and more to the southwest in 2005. Guillemots from Point Pedernales mainly foraged to the north and northwest (Fig. 4). There were differences in foraging directions between Point Pedernales and Point Arguello (leaving: χ^2 = 221.46, df = 4, p < 0.005; returning: χ^2 = 246.40, df = 4, p < 0.005). Together, these data suggest that guillemots from Arguello forage leeward, while guillemots from Pederanles forage windward of the promontory.

Table 2. *Cepphus columba.* Diet composition (% total observations yr^{-1}) and diet diversity (H', Shannon-Wiener index) of pigeon guillemots breeding at the Point Arguello (leeward) sub-colony in 2001 to 2005

Prey taxon	2001	2002	2003	2004	2005
Sanddab (*Citharichthys* sp.)	64.04	53.06	46.75	41.45	46.13
Anchovy (*Engraulis mordax*)	0.44	0.00	0.41	15.65	5.99
Smelt (Family Osmeridae)	0.00	9.18	0.00	7.83	0.00
Squid (*Loligo* sp.)	0.44	1.02	0.00	2.61	0.70
Rockfish (*Sebastes* sp.)	1.32	1.02	7.32	3.77	3.17
Saury (*Cololabis saira*)	0.00	0.00	0.00	0.29	0.35
Sablefish (*Anoplopoma fimbria*)	0.44	0.00	0.00	0.00	0.00
Octopus (*Octopus* sp.)	8.77	15.31	16.67	0.00	0.70
Sculpin (Family Cottidae)	1.32	0.00	10.57	2.03	0.00
Cuskeel (Family Ophidiidae)	0.00	1.02	0.00	2.61	1.41
Kelpfish (Family Clinidae)	0.00	0.00	0.41	3.19	0.70
Greenling (*Hexagrammos* sp.)	0.00	0.00	0.41	0.29	0.70
Shrimp (*Crangon* sp.)	1.75	1.02	0.81	6.09	27.82
Blenny (*Hypsoblennius* sp.)	0.44	0.00	0.00	0.29	1.06
Lingcod (*Ophiodon elongatus*)	0.00	0.00	0.41	0.00	2.46
Sardine (*Sardinops sagax*)	0.44	0.00	0.00	0.87	0.35
Midshipman (*Porichthys* sp.)	11.40	8.16	10.16	4.06	4.93
Surfperch (Family Embiotocidae)	0.44	0.00	0.81	3.19	0.00
Gunnel (Family Pholididae)	1.75	1.02	1.63	1.45	0.00
Prickleback (Family Stichaeidae)	4.82	9.18	0.81	0.29	1.76
Sandcrab (*Blepharipoda occidentalis*)	0.00	0.00	0.00	0.00	0.70
Poacher (Family Agonidae)	1.32	0.00	2.44	2.32	0.00
Combfish (*Zaniolepis* sp.)	0.88	0.00	0.41	1.74	1.06
n	228	98	246	345	284
Diversity (H')	0.60	0.65	0.74	0.91	0.73

Upwelling, regional larval abundance and guillemot diet

Spring to summer upwelling variability was the best predictor of regional larval abundance for all 3 time periods (Table 3). Fall upwelling variability was also a good predictor of fall larval abundance, and fall upwelling intensity predicted spring to fall larval abundance. Overall, the strongest relationship was between spring to summer upwelling variability and spring to fall larval abundance. Thus, upwelling variability during the spring to summer period appears to be driving regional larval abundance, and the effects of this variability last through fall. The relationship is negative, illustrating that fewer larvae are present when upwelling variability is greatest (Fig. 5).

There was a strong, significant relationship between the proportion of sanddab in the guillemot diet and the spring to summer upwelling variability when controlling for location and larval abundance (Table 4). Furthermore, the effects of upwelling differed between windward and leeward sites, with the tightest relationship and steepest slope occurring with windward diet (Fig. 6).
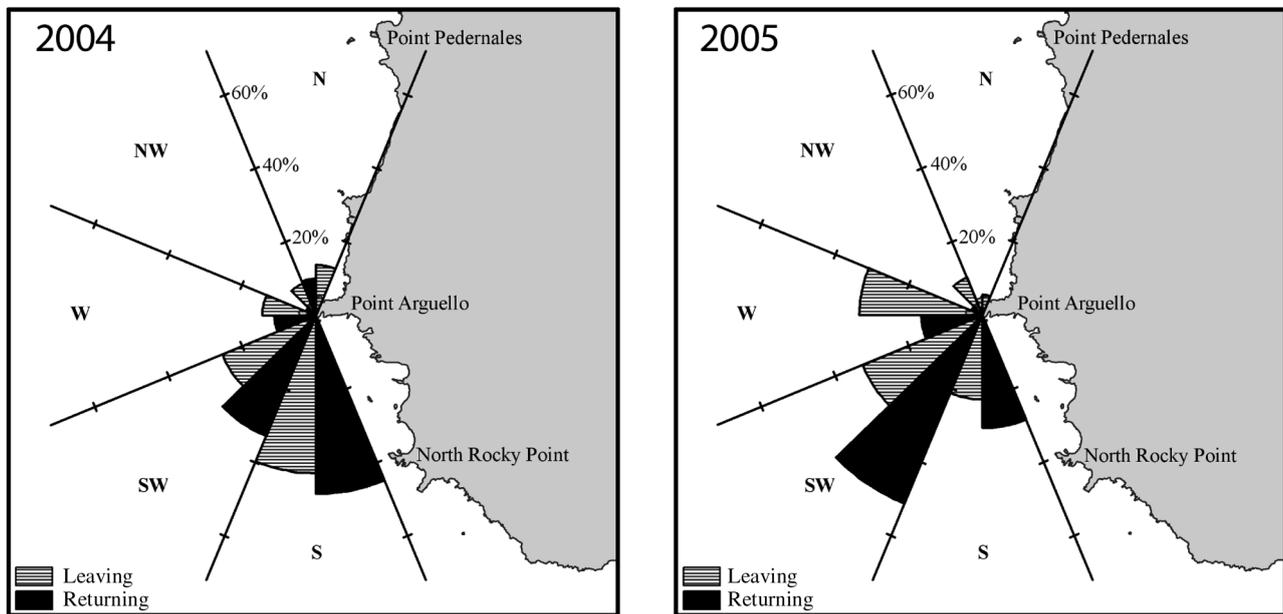

Fig. 3. *Cepphus columba.* Percent of total guillemots observed leaving and returning in each direction during foraging bouts from Point Arguello (leeward) in 2004 and 2005
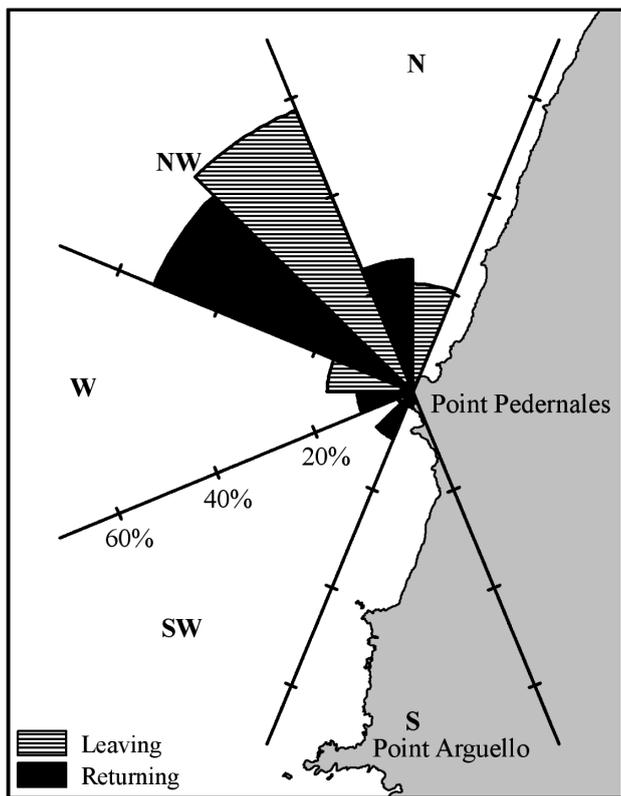
Fig. 4. *Cepphus columba*. Percent of total guillemots observed leaving and returning in each direction during foraging bouts from Point Pedernales (windward) in 2005

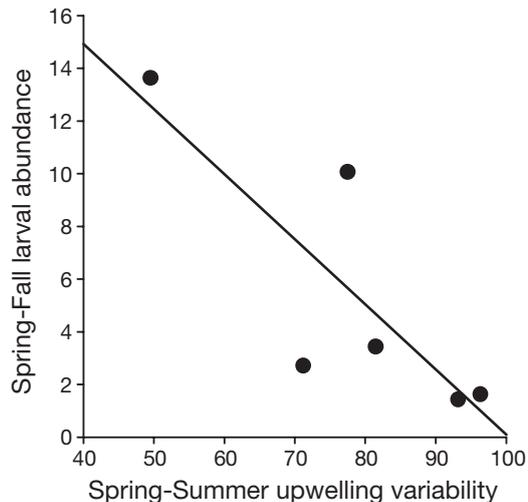Fig. 5. *Citharichthys* sp. Scatter plot and regression line of spring to fall larval sanddab abundance versus spring to fall upwelling variability

There was also a strong, significant relationship between guillemot diet and spring to fall larval abundance when controlling for location and upwelling variability (Table 5). The effects of larval abundance also differed between sites. Though the slopes for windward and leeward sites were similar, the strongest relationship by far was with leeward diet (Fig. 7). Thus, it appears that windward diet is most affected by variability in Ekman transport during the spring to summer of the previous year, while leeward diet is most affected by larval abundance in the spring to fall of the previous year.

DISCUSSION

Our results suggest that persistent upwelling is more important than upwelling intensity in determining regional sanddab *Citharichthys* sp. larval abundance. If upwelling, regardless of intensity, is short-lived, regional nutrient and phytoplankton concentrations will diminish quickly. Persistent upwelling, however, will have a prolonged impact on regional productivity and thus increase larval survival. Our results support this hypothesis in that more persistent (i.e. less variable) upwelling in our study led to increased regional larval abundance.

The benefits of an upwelling shadow are similar to those of persistent upwelling in that nutrient enrichment and primary productivity are prolonged. In essence, an upwelling shadow is a circulating body of water driven by upwelling-favorable winds (Graham & Largier 1997). The nutrients retained in this circulation provide for prolonged algal blooms, and thus, prolonged food availability for zooplankton. Though we

Table 3. *Citharichthys* sp. Optimal predictive models of sanddab larval abundance versus upwelling intensity and variability using Mallows' C_p criterion for each of 3 time periods (spring to summer, fall, and spring to fall). Each model used 0, 1, or 2 upwelling variables and included California Cooperative Oceanic Fisheries Investigations (CalCOFI) transect effects; k: total number of parameters in the model, includes 1 for transect effect. Standardized regression coefficients (beta) are shown. **Bold:** model with the overall best fit

Optimal predictive model	Independent variable	Beta	p
Spring–Summer, $k = 2$, $R^2 = 0.347$	Spring–Summer upwelling variability	−0.588	0.057
Fall, $k = 3$, $R^2 = 0.798$	Spring–Summer upwelling variability	0.800	0.001
	Fall upwelling variability	−0.328	0.073
Spring–Fall, $k = 3$, $R^2 = 0.845$	**Spring–Summer upwelling variability**	**−0.940**	**<0.001**
	Fall upwelling intensity	**0.441**	**0.017**

Table 4. *Citharichthys* sp. Effects of spring to summer upwelling variability on logit-transformed percent sanddab controlling for spring to fall larval abundance. Site-specific effects (differing between windward and leeward sites) are included. Note slopes for upwelling variability differ significantly between sites ($F_{1,5}$ = 48.67, p <0.001). Linear model: $F_{4,5}$ = 36.83, p <0.001, R^2 = 0.967

Factor	Coefficient	SE	t	p
Location	−3.072	0.434	−7.08	0.001
Larval abundance	0.144	0.017	8.28	<0.001
Upwelling variability				
Windward site	0.069	0.006	11.27	<0.001
Leeward site	0.031	0.006	5.13	0.004

Table 5. *Citharichthys* sp. Effects of spring to fall larval abundance on logit-transformed percent sanddab controlling for spring to summer upwelling variability. Site-specific effects (differing between windward and leeward sites) are included. Note slopes for larval abundance differ significantly between sites ($F_{1,5}$ = 12.22, p = 0.017). Linear model: $F_{4,5}$ = 10.97, p = 0.011, R^2 = 0.898

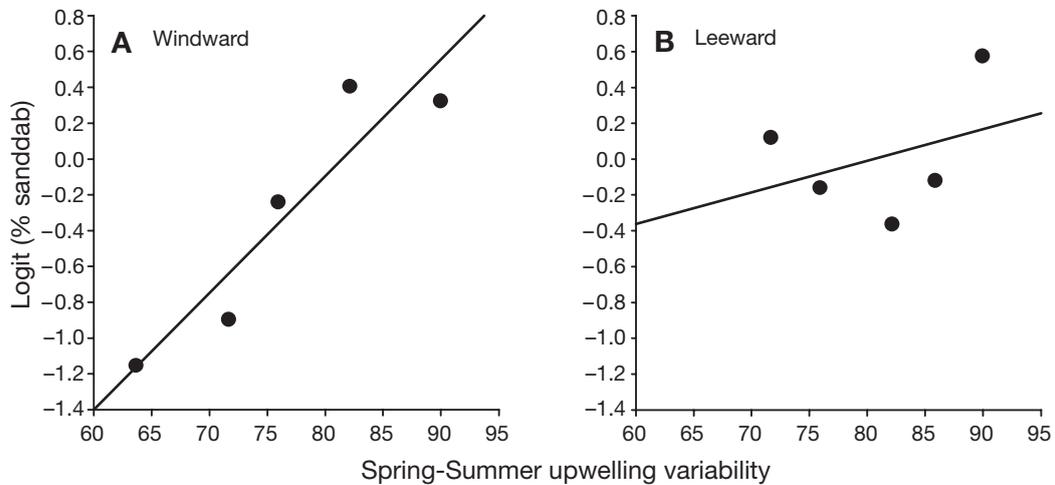| Factor	Coefficient	SE	t	p
Location	0.496	0.233	2.13	0.087
Upwelling variability	0.066	0.010	5.76	0.002
Larval abundance				
Windward site	0.112	0.032	3.47	0.018
Leeward site	0.224	0.037	6.00	0.002

Fig. 6. *Citharichthys* sp. Scatter plots of logit-transformed percent sanddab in the guillemot *Cepphus columba* diet versus spring to summer upwelling at the: (A) windward and (B) leeward sub-colonies. Values plotted are residuals from the linear model presented in Table 4
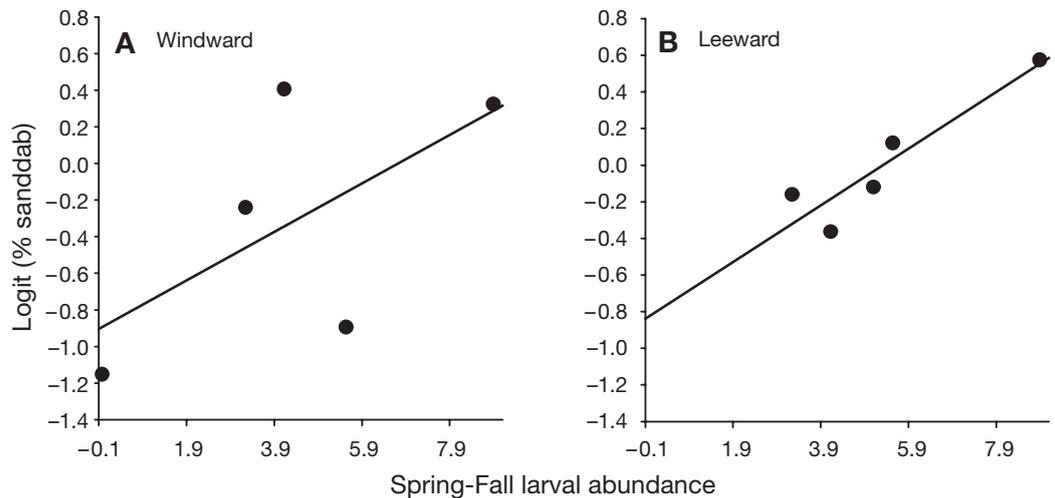

Fig. 7. *Citharichthys* sp. Scatter plots of logit-transformed percent sanddab in the guillemot *Cepphus columba* diet versus spring to fall larval abundance at the: (A) windward and (B) leeward sub-colonies. Values plotted are residuals from the linear model presented in Table 5

expect an upwelling shadow in the lee of Point Arguello, to our knowledge one has never been documented. Trainer et al. (2000) observed a diatom bloom in the lee of Point Arguello that lasted for over 3 wk, suggesting the presence of a small, nearshore shadow.

Our results further support the idea of an upwelling shadow in the lee of Point Arguello. Leeward diet had the strongest relationship with prior-year larval abundance, suggesting larvae are not being transported offshore from leeward habitats. Though the relationship between leeward diet and prior-year upwelling variability was significant, it was weak. Thus, variable upwelling may contribute to increased sanddab in the leeward diet during the following year. We expected this relationship to be opposite, since upwelling shadows should be prolonged and more effective during persistent upwelling. However, our results suggest that the upwelling shadow is simply acting as a buffer, minimizing the direct effects of upwelling by maintaining nutrient levels (and thus larval survival) in the leeward area during periods of high variability. This would explain the lower variability in diet at the leeward site. Overall, it appears that the number of larvae fed into the shadow is more important in determining leeward sanddab recruitment than the upwelling event that created the shadow.

Conversely, upwelling variability was very important in determining windward diet, with increased upwelling variability leading to increased sanddab in the windward diet. When upwelling is variable, there are more relaxation events. Relaxation decreases the net offshore transport of larvae by allowing displaced larvae to drift back to nearshore habitats. This has been documented for larvae of other marine species (see Graham & Largier 1997).

Sanddabs have a long (approximately 270 to 320 d) 5-stage larval cycle, with the earliest stages acting as passive drifters and the later stages capable of remaining nearshore (Sakuma & Larson 1995). Thus, hydrodynamics during the early larval stages are important in determining the alongshore distribution of settlement-age sanddabs. This is likely why spring to summer upwelling variability had the most impact on windward diet the following year. Sakuma & Larson (1995) and Sakuma & Ralston (1995) suggest that early-stage sanddab larvae reside on the offshore side of upwelling fronts. During upwelling events, the larval pool is pushed offshore over the mid-shelf region, where they are subject to further displacement—mid-shelf transport during the upwelling season is offshore and equatorward (Dever 2004, Ohashi & Wang 2004, Dong & Oey 2005).

Conversely, inner shelf transport appears to be very different from mid-shelf transport (Cudaback et al. 2005). In the absence of upwelling-favorable winds,

transport over the inner shelf has an onshore tendency. Additionally, the inner shelf experiences much more poleward transport during relaxation than the mid-shelf, and transport is often poleward, even during upwelling. Thus, larvae that were displaced offshore and equatorward during upwelling can potentially be replaced through poleward transport during periods of relaxation. Cudaback et al. (2005) also noted that transport over the inner shelf responds much more consistently to relaxation than upwelling. We therefore suggest that pulses of relaxation (i.e. variable upwelling) are likely important for recruitment to windward areas and perhaps non-shadow areas in general.

Future research should verify the existence of an upwelling shadow in the lee of the Point Arguello Promontory through the use of advanced very high resolution radiometer (AVHRR) satellite imagery and the fine-scale mapping of surface currents. Additionally, more guillemot *Cepphus columba* sub-colonies should be studied in order to (1) create replicates of leeward and windward sites and (2) investigate how proximity to the apex of the promontory (i.e. Point Arguello) affects the relationships between sub-colony diet composition and larval abundance and upwelling dynamics. While guillemots at the Point Pedernales sub-colony had a strong tendency toward windward foraging, with very few trips in the leeward direction, foraging directions at the south Point Arguello sub-colony were more variable. Though the majority of the trips were in the leeward direction, there was a moderate number toward the west in 2005. Birds departing to the west can potentially forage on either side of the promontory. It is therefore possible that diet at Point Arguello is weakly influenced by windward recruitment. This may have distorted the potential correlation between diet at Arguello and upwelling variability. Preliminary data from a sub-colony on the immediate north side of Point Arguello also showed variable foraging directions, but with a tendency toward windward foraging. We propose adding this sub-colony as our windward replicate, in addition to a sub-colony located at Rocky Point (Fig. 2) as our leeward replicate. This will allow us to investigate whether sub-colonies further away from the apex show stronger correlations in support of our hypotheses. If a given sub-colony is highly dependent on a particular foraging habitat (e.g. windward versus leeward), it will be a better indicator of recruitment to that habitat than if it were influenced by recruitment patterns in both habitats.

In conclusion, this is one of the first studies to use seabird diet as a proxy for recruitment in a demersal fish. We were successful in relating some aspects of diet to the oceanographic factors that likely have a mechanistic influence on sanddab populations on leeward and windward sides of coastal promontories in

this upwelling system. While our basic premise and methodology (using seabird diet to assess demersal fish availability) is not novel (Mills et al. 2007), relating diet composition to habitat associations and potential mechanistic determinants of recruitment is new. We suggest that the concept of seabirds as indicators of forage fish can be expanded to include spatial as well as temporal components.

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