The Spatial Association of Predators and Prey at Frontal Features in the Northern California Current: Competition, Predation, or Co-occurrence?

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SUMMARY We investigated variation in the small- to meso-scale abundance and distribution of top predators in the northern California Current System (CCS) during the upwelling season of 2000 and 2002. Included were adult salmon Onchorhynchus spp., the two most abundant seabird species (83.7% of seabird biomass) --- sooty shearwater Puffinus griseus and common murre Uria aalge --- and humpback whales Megaptera novaeangliae. Emphasis was on seabirds.

We first explored variation in seabird density. Covariates, with importance assessed using general linear and information theoretic modeling, included physical features, such as sea-surface temperature, dynamic height and pyncnocline depth; biological factors, such as chlorophyll maximum; and food web factors, such as the density of three size classes of zooplankton, the density of potential piscine predators, such as adult salmon, and abundance of fish prey, such as anchovies Engraulis mordax. Flux-adjusted seabird density was estimated using continuously collected data; covariates were estimated using towed Seasoar and four-channel hydroacoustics arrays, as well as trawls for fish.

The most important factors explaining seabird occurrence were proximity to the alongshore upwelling front, the abundance of prey-sized fish, year-season, and association with certain inshore vs offshore 'biomes'. Overlap in occurrence of murres and shearwaters with adult salmon was interpreted as co-occurrence and, perhaps, competition for prey species; a negative relationship between shearwaters and abundance of forage fish was interpreted as evidence for prey depletion by co-occurring predators. Humpback whales co-occurred with the birds and salmon as well.

These predators occurred at the edges of some forage fish 'hotspots' but not others, and overlapped the areas of fish concentration mainly in the frontal region. Such a pattern has implications for modeling food web structure and trophic transfer, where data are assigned by cells of arbitrary size. Results indicate that better resolution of spatially explicit data on predator and prey species would likely improve validity of food web modeling.

FIGURE 1. The NEP GLOBEC study area in the northern CCS off Oregon, including the continental shelf and slope. Shown are SeaSoar and HTI tracks (green lines), seabird survey segments (gold diamonds), and trawl stations (red boxes). Shelf break shown in blue. Cruises during the early (June) and mature (August) phases of the upwelling period were conducted in two years, 2000 and 2002.

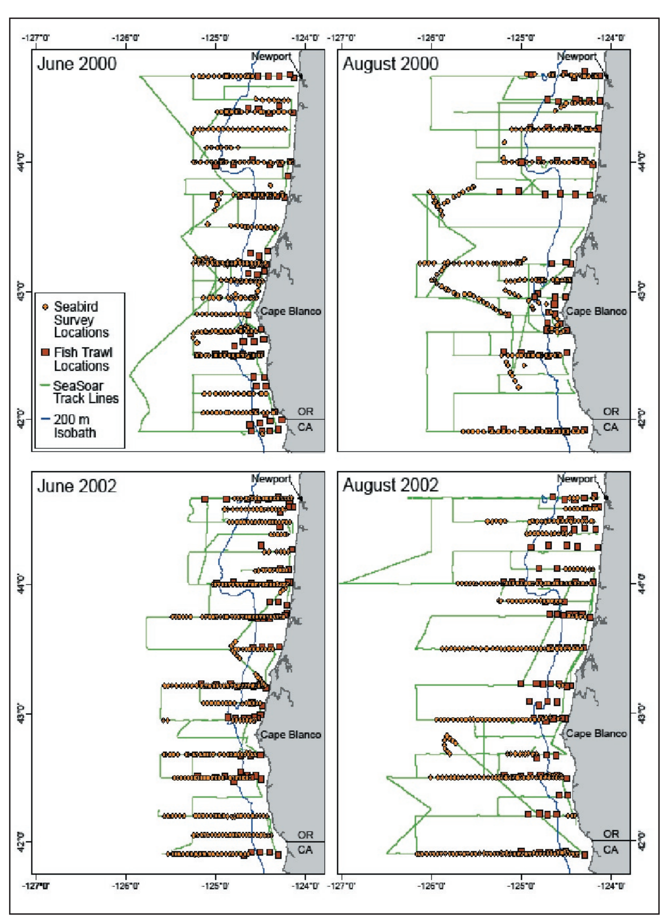

TABLE 1. ACRONYMS FOR COVARIATES USED TO MODEL BIRD DENSITY. Data derived from SeaSoar and HTI surveys, as well as fish trawls (see Fig 1).

Bird density	Flux corrected counts of individuals km^{-2}
Cruise	June vs August
DPTH	Ocean depth, m
SST	Sea surface Temp, °C
SSS	Sea surface salinity, ppt
ColDist	Sum (Colony Size*Dist^2) for all colonies; murres only
CHLMX	Chlorophyll maximum, volts
MAXDp	Depth of chlorophyll maximum, dbars
MLD	Thermal mixed-layer depth, dbars
ThSlp	Thermocline slope (Δ °C in first 20 m)
PycDp	Pycnocline depth, dbars
ZDsm	Density (ind m^{-3}) of small zooplankton, 3-4 mm
ZDmed	Density (ind m^{-3}) of medium zooplankton, 5-10 mm
ZDlg	Density (ind m^{-3}) of large zooplankton, 11-24 mm
Fish	Density (ind m^{-3}) of small fish >24 mm
DistB	Distance to feature B, at 2.0 m^2 s^2, boundary where cross-shelf gradients in dynamic height relaxed (markedly less steep), reaching the 'plateau' of the alongshore upwelling jet
DistB2	Absolute value of distance to feature B
GroupA	Individuals km^{-3} of adult salmon
GroupB	Individuals km^{-3} of clupeid fish, juvenile salmon
GroupC	Individuals km^{-3} of market squid
GroupD	Individuals km^{-3} of juvenile demersal fish
GroupE	Individuals km^{-3} of adult sardines, saury

TABLE 2. SUMMARY STATISTICS FOR ALL HABITAT FEATURES AND PREY ABUNDANCE COVARIATES USED IN THE MODELING. The two years differed markedly in productivity, with far denser concentrations of zooplankton (ZD) and forage fish in 2002.

	2000		n = 519	2002		n = 790
Covariate	Mean	SE	95% CI	Mean	SE	95% CI
Dpth	902.72	45.97	812 - 993	999.21	39.99	920 - 1077
ColDist	113.08	20.87	72.08 - 154.09	62.42	4.05	54.48 – 70.36
SeaSoar	Data					
SST	13.24	0.08	13.10 - 13.38	11.99	0.06	11.87 – 12.12
SSS	32.15	0.03	32.09 - 32.21	31.82	0.06	31.69 – 31.95
Chlmx	3.52	0.18	3.17 - 3.88	0.72	0.02	0.69 – 0.75
Max_dp (Chl)	18.71	0.61	17.51 - 19.91	18.16	0.54	17.12 – 19.21
MLD	7.02	0.22	6.60 - 7.45	6.40	0.20	6.01 – 6.78
Th_slp	2.98	0.06	2.87 - 3.09	2.60	0.05	2.50 – 2.70
Pyc_dpt	10.41	0.43	9.56 - 11.26	59.05	1.08	56.92 – 61.17
DistB	9.75	1.06	7.67 - 11.83	2.56	0.82	0.95 – 4.17
Acoustic	Data					
ZDsmall	34.70	2.63	29.54 - 39.86	120.30	16.18	88.55 – 152.05
ZDmed	7.90	0.51	6.89 - 8.91	45.12	6.75	31.86 – 58.38
ZDlarge	3.70	0.20	3.30 - 4.10	6.97	0.40	6.17 – 7.76
Fish	0.001	0.0001	0.001 - 0.002	0.003	0.003	0.003 – 0.004
Trawl	Data					
GroupA	0.42	0.05	0.32 - 0.52	0.61	0.04	0.53 – 0.70
GroupB	25.70	2.23	21.31 - 30.08	50.33	2.67	45.10 – 55.57
GroupC	0.31	0.03	0.25 - 0.38	17.00	1.34	14.37 – 19.62
GroupD	24.37	2.32	19.82 - 28.93	6.36	0.28	5.81 – 6.92
GroupE	1.17	0.16	0.86 - 1.48	11.59	0.70	10.23 – 12.96

Italics represent covariates whose 95% CIs do not overlap between years.

CONCLUSIONS

- >Top predators --- salmon, birds and whales --- occurred closely in space and time.
- >Association of avian predators with potential forage fish was strong only in the year of reduced zooplankton and forage fish abundance (2000).
- >Predator abundance, especially of seabirds and especially 2002 (prey abundant), associated mainly with the intense physical gradients (upwelling front) that marked the edge of fish 'hot spots'. Food web models rarely are sensitive enough to address the offset (edge effect) of prey with predator abundance, and therefore trophic interaction, evident in this study (e.g. Trites et al. 1999. Fisheries Centre Res Rep 7:1-106; Field et al. 2006. Progr Oceanogr 68:238-270; Ruzicka et al. 2007. Calif Coop Ocean Fish Invest Rep 48:106-128). Quantifying these spatially explicit relationships should increase sensitivity of foodweb models to climate-related alterations of marine communities, especially if fronts move or change intensity

TABLE 3. THE TOP 10 MODELS RELATING ENVIRONMENTAL AND COVARIATES TO COMMON MURRE DENSITY. Models ranked by AIC adjusted for small sample size (AIC_c); model deviance (DEV), number of parameters (k), ΔAIC_c, and AIC_c weights also given, along with sign of the slope coefficients (β) [positive (+) and negative (-) denote coefficients with 95% CI's that do not include zero, otherwise, sign denoted as zero]. Intercept-only model included for comparison.

Model	DEV	k	Δ AIC_c[1]	AIC_c Wt	β
2000					
GroupA, DistB	1258.0	5	0.00	1.00	+, -
GroupA	1280.4	4	20.36	0.00	+
DistB	1287.0	4	27.70	0.00	-
SSS	1294.4	4	34.34	0.00	+
SST	1296.7	4	36.63	0.00	+
Th_Slp	1308.6	4	48.49	0.00	-
Chlmx	1314.9	4	54.82	0.00	+
Pyc_dpt	1315.1	4	55.06	0.00	-
ColDist	1316.1	4	56.05	0.00	+
MLD	1316.8	4	56.71	0.00	-
Intercept Only	1322.2	3	60.10	0.00	
2002					
GroupE, DistB	1595.5	5	0.00	1.00	-,-
DistB	1625.5	4	28.00	0.00	-
GroupE, SST	1670.4	4	74.92	0.00	-,-
SST	1700.2	4	102.69	0.00	-
GroupE	1708.1	4	110.62	0.00	-
Th_SLP	1747.2	4	149.69	0.00	-
GroupD	1748.3	4	150.78	0.00	-
GroupC	1752.3	4	154.82	0.00	+
ColDist	1753.5	4	155.94	0.00	+
GroupA	1755.2	4	157.69	0.00	+
Intercept-only	1777.5	3	177.95	0.00	

[1] Lowest AICc in 2000 was 1268.16; lowest AICc in 2002 was 1605.57.

TABLE 4: THE TOP 10 MODELS RELATING ENVIRONMENTAL AND COVARIATES TO SOOTY SHEARWATER DENSITY. Models ranked by AIC adjusted for small sample size (AIC_c). See Tables 1 & 3 for definition of terms. Asterisks denote interactions.

Model	DEV	k	Δ AIC_c[1]	AIC_c Wt	β
2000					
Cruise, Fish, Cruise*fish	1684.4	6	0.00	0.97	-, -, -[2]
Cruise, Fish	1694.3	5	7.89	0.02	-,-
Fish	1698.8	4	10.30	0.01	-
Cruise	1705.8	4	17.33	0.00	-
ZDlg	1711.6	4	23.07	0.00	-
DistB2	1711.9	4	23.39	0.00	-
DistB	1712.1	4	23.59	0.00	-
ZDmed	1712.3	4	23.84	0.00	-
SST	1712.7	4	24.17	0.00	-
GroupA	1713.0	4	24.57	0.00	+
Intercept-only	1718.6	3	28.08	0.00	
2002					
Cruise, SST	2209.3	5	0.00	0.48	-, -
Cruise, DistB	2209.9	5	0.67	0.34	-, -
Cruise, SST, Cruise*SST	2209.2	6	1.98	0.18	-, 0, 0
Cruise, DistB, Cruise*DistB	2209.9	6	2.58	0.13	-, -, 0
SST, GroupE	2220.9	5	11.69	0.00	-, -
Crusie, GroupE, Cruise*GroupE	2222.8	6	15.61	0.00	-, -, 0
Cruise, GroupE	2226.9	5	17.63	0.00	-, -
SST	2229.5	4	18.19	0.00	-
Cruise	2232.9	4	21.62	0.00	-
GroupE	2233.4	4	22.14	0.00	-
Intercept-only	2251.9	3	28.62	0.00	

[1] Lowest AICc in 2000 was 1696.56; lowest AICc in 2002 was 2219.33.
[2] Bird density decreases more in conjunction with increased fish density on 1st cruise compared to 2nd.

FIGURE 2. Common murre density in relation to the main factors affecting occurrence: top panels, in 2000 abundance of adult salmon (competitor) and, bottom panels, in 2002 sardine/saury (potential prey). In fact, the murres and the sardines/saury overlap little, being of different 'biomes' (negative relationship). Solid line indicates Feature B, with cross hatching indicating zone of intense gradients in various biophysical features (as well as dynamic height).

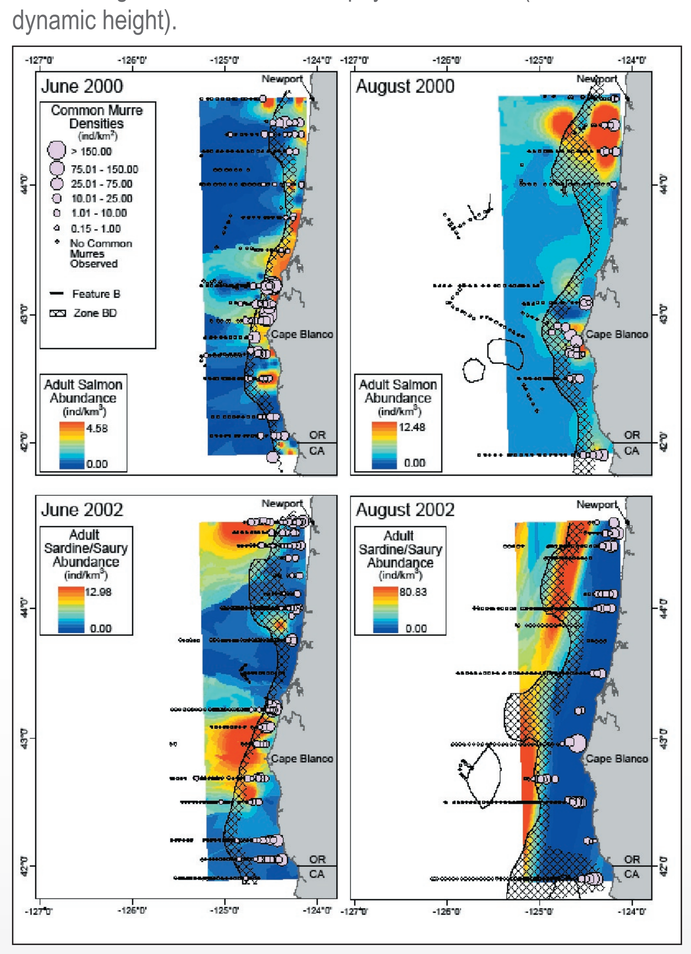

FIGURE 3. Sooty Shearwater density in relation to the abundance of forage fish. In fact, the shearwaters occurred mainly along the edge of the fish 'hot spots'. Solid line indicates Feature B, with cross hatching indicating zone of intense gradients in various biophysical features (as well as dynamic height).

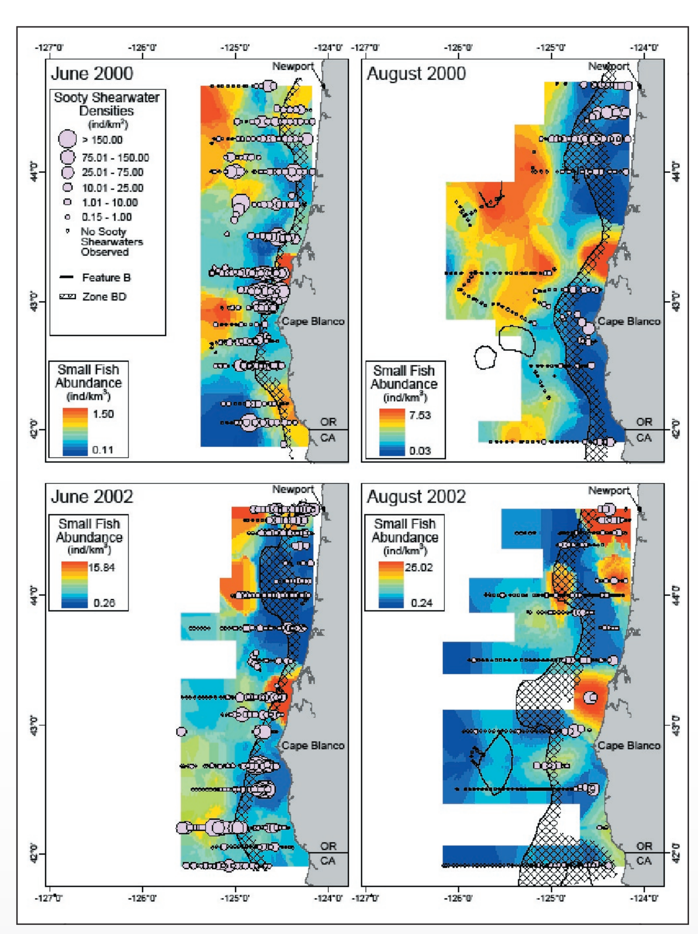

FIGURE 4. Density of humpback whales in relation to the abundance of forage fish during 2000. Whales were most concentrated in areas where other predators were abundant as well, birds and adult salmon (see Figures 2 & 3).