Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature

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Abstract: We tested the hypothesis of synchronous interannual changes in forage fish dynamics around the North Pacific Rim. To do this, we sampled forage fish communities using a seabird predator, the rhinoceros auklet (*Cerorhinca monocerata*), at six coastal study sites from Japan to California. We investigated whether take of forage fishes was related to local marine conditions as indexed by sea surface temperature (SST). SST was concordant across sites in the eastern Pacific, but inversely correlated between east and west. Forage fish communities consisted of anchovy (*Engraulis* spp.), sandlance (*Ammodytes* spp.), capelin (*Mallotus* spp.), and juvenile rockfish (*Sebastes* spp.), among others, and take of forage fish varied in response to interannual and possibly lower-frequency oceanographic variability. Take of primary forage species were significantly related to changes in SST only at the eastern sites. We found synchrony in interannual variation of primary forage fishes across several regions in the eastern Pacific, but no significant east–west correlations. Specifically in the Japan Sea, factors other than local SST or interannual variability may more strongly influence forage fishes. Predator diet sampling offers a fishery-independent, large-scale perspective on forage fish dynamics that may be difficult to obtain using conventional means of study.

Résumé : Nous testons l'hypothèse qui veut qu'il y ait des changements interannuels synchrones dans les dynamiques des poissons fourrage autour de la bordure du Pacifique Nord. C'est pourquoi nous avons échantillonné les peuplements de poissons fourrage à l'aide d'un oiseau marin prédateur, le macareux rhinocéros (*Cerorhinca monocerata*), à six sites d'étude côtiers du Japon à la Californie. Nous avons vérifié si les captures de poissons fourrage sont reliées aux conditions marines locales, telles que représentées par la température de surface de la mer (SST). Les SST s'accordent d'un site à l'autre dans l'est du Pacifique, mais il y a une corrélation inverse entre l'est et l'ouest. Les peuplements de poissons fourrage consistent, entre autres, d'anchois (*Engraulis* spp.), de lançons (*Ammodytes* spp.), de capelans (*Mallotus* spp.) et de jeunes sébastes (*Sebastes* spp.) et la capture de poissons fourrage varie en réaction à la variabilité océanographique interannuelle ou aussi peut-être de fréquence moins élevée. La capture de poissons fourrage principaux est en corrélation significative avec SST seulement dans les sites de l'est. Nous observons un synchronisme dans la variation interannuelle des poissons fourrage principaux entre plusieurs régions de l'est du Pacifique, mais aucune corrélation significative entre l'est et l'ouest. Tout particulièrement dans la mer du Japon, des facteurs autres que la SST locale et la variabilité interannuelle peuvent influencer plus fortement les poissons fourrage. L'échantillonnage du régime alimentaire des prédateurs permet d'obtenir, indépendamment de la pêche commerciale, une perspective à grande échelle de la dynamique des poissons fourrage qu'il serait peut-être difficile d'acquérir par les méthodes d'étude conventionnelles.

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Introduction

An extensive body of literature compares population dynamics of marine organisms at various trophic levels with temporal and spatial environmental variation. In the northeastern Pacific, opposing trends in the abundance of zooplankton (Brodeur et al. 1996), salmon (Hare et al. 1999), and some flatfish stocks (Hollowed et al. 2001) have been hypothesized between the Alaska Current and California Current ecosystems. These trends have been linked to the Pacific Decadal Oscillation (PDO) and other large-scale environmental forcing such as the El Niño Southern Oscillation (ENSO; Hare et al. 1999; Hollowed et al. 2001). On an even greater scale, global synchronies (or "out-of-phase" fluctuations) have been identified for various commercial species of anchovy (*Engraulis* spp.), sardine, herring, Pacific salmon (*Oncorhynchus* spp.), cod, pollock, and mackerel (Klyashtorin 1998; Beamish et al. 1999; Schwartzlose et al. 1999). Some of these quasi-global-scale observations relate to climate indices such as the Atmospheric Circulation Index, but are poorly correlated with interannual climate indices (e.g., Aleutian Low Pressure Index; Klyashtorin 1998). Freon et al. (2003) found little quantitative evidence for global synchronies of commercial coastal pelagic species worldwide and suggested that regional synchronies forced by climatic changes at the basin scale may be easier to demonstrate and understand.

Time series from fisheries landings are typically based on harvest of a single age class (adults) and may be fraught with socio-economic biases (Bakun and Broad 2003; Freon et al. 2003). Net surveys may also have some limitations in that standardized station sampling may miss patchily distributed species (Larson et al. 1994). Instead, sampling by upper trophic level predators offers an alternative tool for studying forage species (Reid et al. 1996; Mills et al. 2007). Because predators target patchy prey resources, may target juvenile age classes, and can be sampled at low cost compared with traditional net surveys, this technique is garnering substantial attention (Boyd et al. 2006). In this paper, we characterized changes in forage fish communities from the late 1970s to the early 2000s, as sampled by a piscivorous seabird, rhinoceros auklet (*Cerorhinca monocerata*), in six continental shelf regions representing at least three large marine ecosystems in the North Pacific (Fig. 1). The associated forage fish communities included small coastal pelagic species as well as juvenile, large predatory fish. We quantified change in primary forage fishes over a 10-year period (1994–2003). We tested the hypothesis that changes in primary forage species abundance in the auklet diet covaried among regions and were related to synchronous changes in local marine conditions. Fish populations in the different systems may be driven by regional processes, so we used sea surface temperature (SST) as an index of local ocean conditions. Specifically, our objectives were to (*i*) determine rhinoceros auklet diet composition from different shelf systems around the Pacific Rim, (*ii*) examine how diet composition varied spatially and temporally, and (*iii*) describe variation in relation to marine climate on local to basin scales.

Materials and methods

Ocean ecosystems

We conducted studies in three coastal ocean current sys-

tems and one transition zone. These contained six study sites: one in the western Pacific and five in the eastern Pacific.

The Tsushima Current branches off from the warm Kuroshio Current into the Sea of Japan and dominates surface flows northeastward along the western margin of the Japanese Archipelago (Park et al. 2004). Other major physical transport mechanisms in this system include mixing at the northern polar front and winter storms (Chiba and Saino 2002). The study site of Teuri Island (TEI; 44°25′N, 141°19′E) is located ∼30 km off the coast of northwestern Hokkaido.

The Subarctic Current pushes water eastward across the North Pacific, bifurcating off the coast of British Columbia. To the north in the Gulf of Alaska, persistent coastal downwelling leads to nutrient depletion in the euphotic zone and low productivity following the initial spring bloom (Coyle and Pinchuk 2003). However, other influences contribute to nutrient supply in surface waters, such as freshwater runoff, coastal and bottom topography and strong tides that generate numerous eddies and meanders, frequent storms, surface Ekman flux, and episodic upwelling (Okkonen et al. 2001; Stabeno et al. 2004). St. Lazaria Island (SLI; 56°59′N, 135°42′W) lies in the southeastern Gulf of Alaska, 8 km west of Sitka Sound. Middleton Island (MI; 59°15′N, 146°15′W) is located in the northern Gulf of Alaska, ∼80 km south of Prince William Sound and 15 km north of the shelf break.

In the California Current eastern boundary system, northwest winds cause coastal upwelling, particularly near capes and headlands (Chavez et al. 2002). Upwelling is strongest during the spring and summer and leads to nutrient enrichment and cool SST, but mixed-layer depth modifies this relationship (Chavez et al. 2002). Southeast Farallon Island (SFI; 37°42′N, 123°00′W) is situated 29 km south of Pt. Reyes, California, and 8 km east of the shelf break. Año Nuevo Island (ANI; 37°06′N, 122°20′W) lies 1 km off Pt. Año Nuevo, California, and 11 km northeast of submarine canyons extending in from the shelf break.

The Eastern Coastal Transition Zone off British Columbia shares physical characteristics with both the Gulf of Alaska and California Current. Interannually, the position and intensity of the Aleutian Low and North Pacific High atmospheric pressure centers may affect strength of horizontal transport to the north versus south (McGowan et al. 1998). Seasonally, the winter Aleutian Low drives prevailing southerly coastal winds that promote downwelling, but northward movement of the North Pacific High in summer triggers upwelling-favorable northerly winds and equatorward surface currents along the shelf break (Mackas et al. 2001). Triangle Island (TRI; 50°52′N, 129°05′W) lies in the Eastern Coastal Transition Zone ∼45 km northwest of Vancouver Island, British Columbia, and 40 km from the shelf break.

Environmental indices

Given the many different atmospheric and oceanographic processes that influence productivity in the study systems, we chose SST as an index that represented the outcome of myriad bottom-up processes in each of the various systems that could be used for comparison. Local SST measurements were not available at all sites or in all years during our

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Fig. 1. Map of North Pacific Ocean with study sites and simplified current flows (arrows). MI, Middleton Island; SLI, St. Lazaria Island; TRI, Triangle Island; SFI, Southeast Farallon Island; ANI, Año Nuevo Island; TEI, Teuri Island.
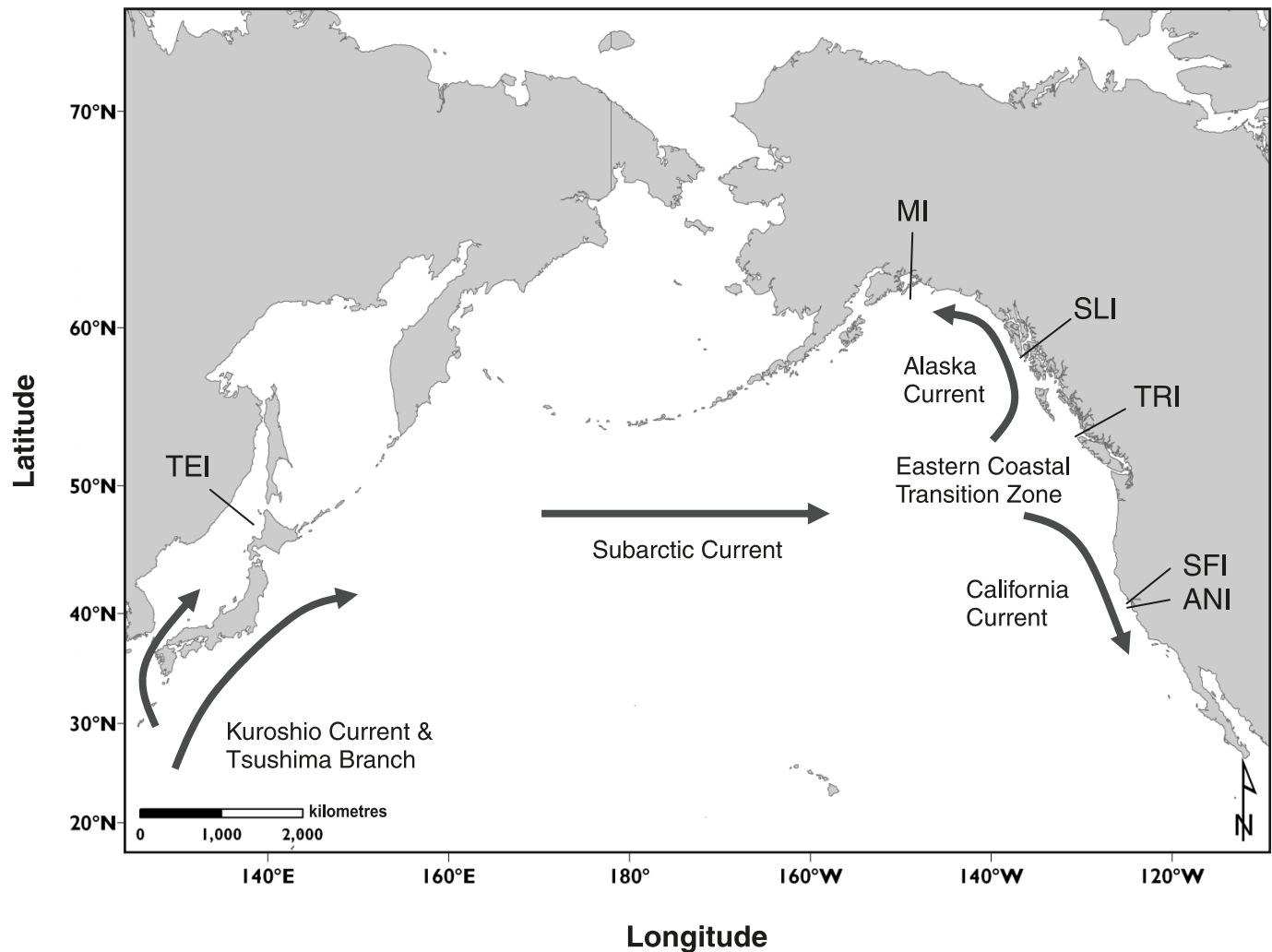
study. Therefore, we derived SST indices from the Advanced Very High Resolution Radiometer (AVHRR) satellite remote sensing system (9 km × 9 km cells; poet.jpl. nasa.gov/), available since 1985. We computed 3-month seasonal indices for a 50 km radius around each site (excluding land), comparable with auklet foraging ranges around the colonies (Kato et al. 2003; McFarlane-Tranquilla et al. 2005). AVHRR data were fairly complete within the 50 km radius around most sites in most months (see Appendix A). We compared satellite-derived SST with in situ measurements where possible (Appendix A). All correlations were highly significant, though less so as the year progressed, which we interpreted as reflecting the effects of insolation.

Forage fishes

Fishes were sampled by a piscivorous, diving marine bird (rhinoceros auklet), which is closely related to puffins and ranges throughout the North Pacific Rim. This seabird can forage to depths of 60 m, but has mean dive depths of 10–30 m (Burger et al. 1993; Kuroki et al. 2003). Fishes were collected from auklets provisioning offspring in summer (June–August), either by netting or hand-capturing the adults as they returned to the colony. Fishes were measured, weighed, and identified to species. Rhinoceros auklets are "multiple prey loaders", which typically bring 1–10 prey back to the colony in their bill following a foraging bout.

We used percent number of prey species, since we were interested in community composition. As multiple prey from one bill load are not statistically independent, individual prey items were summarized in terms of a bill-load sampling unit (Appendix B, Table B1). We calculated the proportion diet composition by number for each bill load averaged over each year as an index of prey harvest (or take). Forage communities were described using the entire time series available at each site, in some cases dating back to 1976.

Statistical analysis

Since fish data were expressed as proportions, we used a logit-transformation ($\ln[p/(1 - p)]$) prior to analysis, where p was the proportion. All analyses were performed using STATA statistical software (v.8.0, 2003; StataCorp LP, College Station, Texas). Statistical comparisons were done only

Fig. 2. Seasonal anomalies of sea surface temperature (SST, °C) during December–February (stippled bars), March–May (black bars), and June–August (gray bars) from 1985 to 2003 within 50 km around (*a*) Middleton Island (MI, 59°N), (*b*) St. Lazaria Island (SLI, 56°N), (*c*) Triangle Island (TRI, 50°N), (*d*) Southeast Farallon Island (SFI, 37°N), and (*e*) Año Nuevo Island (ANI, 37°N) in the eastern Pacific and (*f*) Teuri Island (TEI, 44°N) in the western Pacific. Note different scales of various panels.
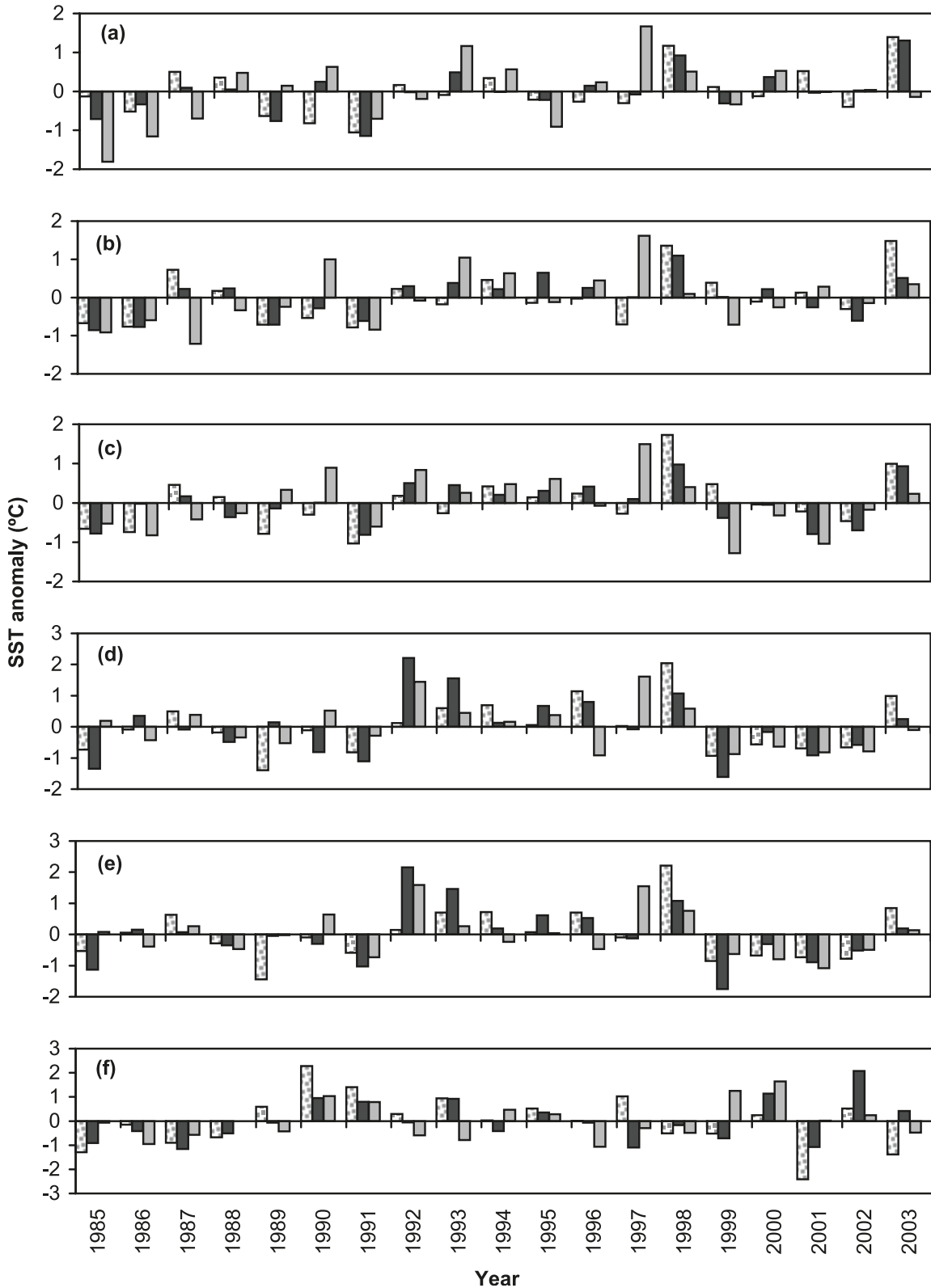
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Table 1. Spearman rank correlations of sea surface temperature (SST) between sites in (*i*) December–February, (*ii*) March–May, and (*iii*) June–August 1985–2003.

Latitude (°N)	Site	Western Pacific (TEI)	Eastern Pacific			
			MI	SLI	TRI	SFI
December–February						
59	MI	–0.79**				
56	SLI	–0.60**	0.90**			
50	TRI	–0.51**	0.82**	0.96**		
37	SFI	–0.21	0.47**	0.56**	0.63**	
37	ANI	–0.25	0.46**	0.51**	0.57**	0.96**
March–May						
59	MI	0.33				
56	SLI	0.12	0.67**			
50	TRI	0.14	0.63**	0.80**		
37	SFI	0.20	0.39*	0.64**	0.86**	
37	ANI	0.19	0.45**	0.70**	0.92**	0.97**
June–August						
59	MI	0.07				
56	SLI	–0.15	0.75**			
50	TRI	–0.11	0.56**	0.70**		
37	SFI	–0.21	0.23	0.32	0.68**	
37	ANI	–0.45**	0.23	0.39*	0.73**	0.90**

Note: TEI, Teuri Island; MI, Middleton Island; SLI, St. Lazaria Island; TRI, Triangle Island; SFI, Southeast Farallon Island; *, $p \leq 0.10$; **, $p \leq 0.05$.

for years in which sampling took place at all sites for 1994–2003. Species richness was calculated for each site using fish species that made up ≥10% of predator diet in at least 1 year. For SST indices and the predominant prey at each site, we used linear and quadratic regression to infer trends between years. Time series were tested for first-order effects of serial autocorrelation (Prais–Winsten regression for small sample sizes). No autocorrelation coefficients were significant (all $p > 0.5$). Series were detrended if necessary by taking residuals. We then used Spearman's rank correlations to examine spatio-temporal concordance of ocean conditions and take of primary forage fish species at each location.

Results

Spatio-temporal SST variability

Relative to latitude, SST anomalies are thought to be greatest in the tropical Pacific (Chavez et al. 2002; Mantua and Hare 2002). In this study, we focused on extratropical regions and found the largest SST anomaly values at lower latitudes (Fig. 2). For a given time period, however, relative anomalies were sometimes higher in northern latitudes. For example, positive SST anomalies during the 1992–1993 ENSO were strongest in the lower latitudes of the eastern Pacific, the positive signal in 1997–1998 was strong at all latitudes, whereas positive anomalies in 2003 were stronger in the northeastern sites.

In general, and particularly between 1994 and 2003 (Table 1) when fish data were also available at all sites, changes in SST were similar in the eastern boundary currents and predominantly inversely related between east and west. This supports the inverse spatial pattern shown by the

PDO (Mantua and Hare 2002). Inverse east–west relationships were always observed during ENSO events. Between 1985 and 1989, however, some positive east–west relationships were observed.

In 1994–2003, correspondence between the Gulf of Alaska and California Current decreased from winter to summer, presumably owing to effects of insolation. SST between eastern and western Pacific sites covaried negatively in winter and more weakly in summer. In spring, relationships were positive even though none were significant. Conditions around TEI in the Sea of Japan were subarctic in the winter (3–9 °C), changing to subtropical in summer (12–23 °C) as the Tsushima Current moved northward. The inverse east–west relationship was strongest relative to the Gulf of Alaska sites in winter (5–9 °C, subarctic system) and to the California Current sites in summer (11–18 °C, relatively subtropical) as the Gulf of Alaska and California Current shifted out of phase and the Tsushima Current moved northward through the Sea of Japan. We found no temporal trends in SST from 1994 to 2003 (linear regressions: $R^2 \leq 0.29$, $p \geq 0.13$).

Forage fish communities

Seabird diets reflect different forage fish communities around the North Pacific Rim, but transitions from one region to another showed largely the loss of one or two species that were replaced by others. In other words, communities appeared as a continuum in species composition, with species replacements occurring incrementally along latitudinal–longitudinal gradients. Forage species included both small schooling fishes and 0-age classes of juvenile predatory fishes (Fig. 3). The small schooling fishes con-

Fig. 3. Rhinoceros auklet (*Cerorhinca monocerata*) take of forage species for 1976–2003 at (*a*) Middleton Island (MI) in the northern and (*b*) St. Lazaria Island (SLI) in the southern Gulf of Alaska, (*c*) Triangle Island (TRI) in the Eastern Coastal Transition Zone, (*d*) Southeast Farallon Island (SFI) and (*e*) Año Nuevo Island (ANI) in the California Current, and (*f*) Teuri Island (TEI) in the Sea of Japan.

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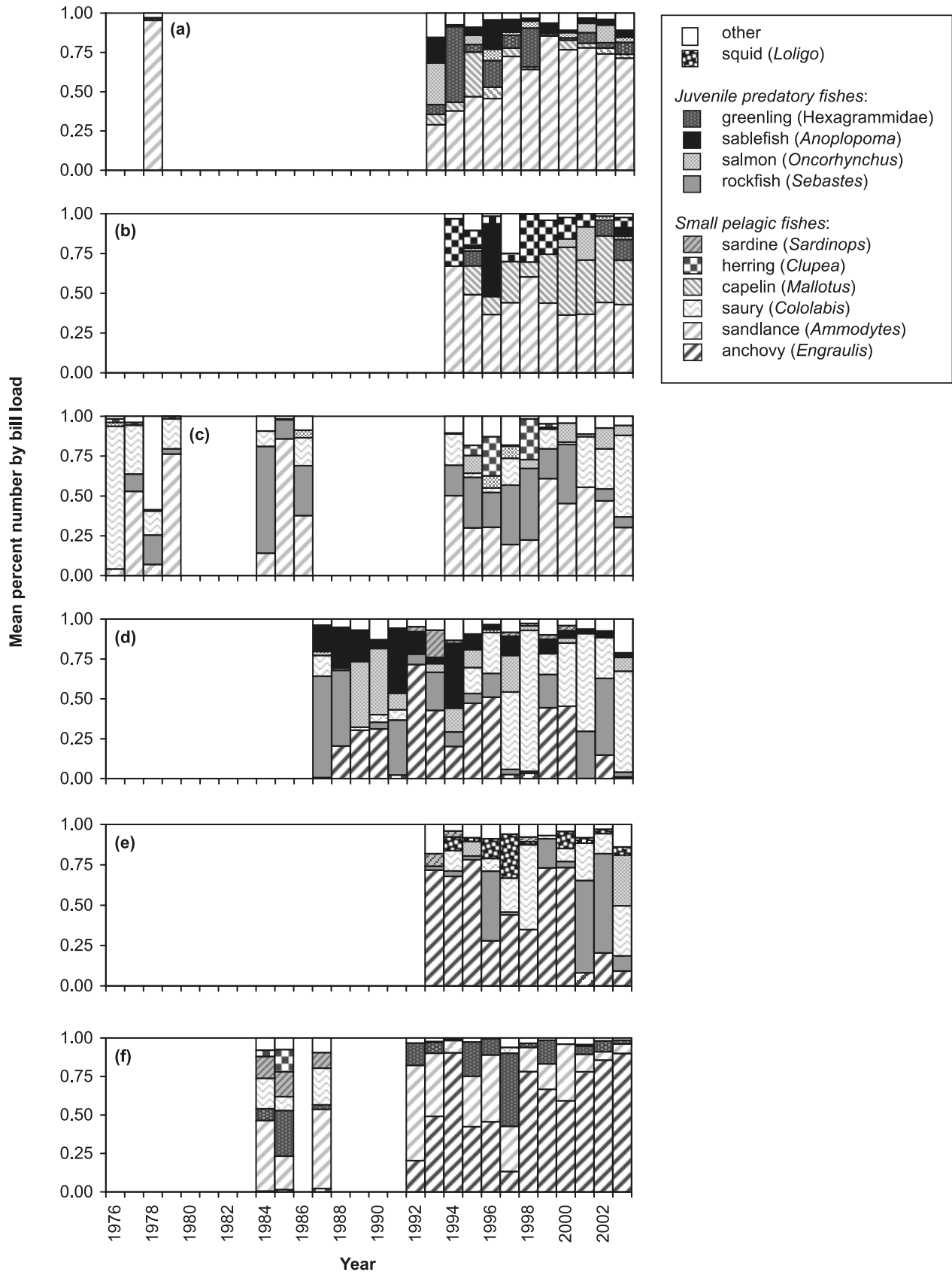Can. J. Fish. Aquat. Sci. Vol. 65, 2008

Table 2. Temporal trends (R^2 values) for take of primary forage fish at each sampling location, 1994–2003.

Latitude (°N)	Site	Species	Trend
59	MI	Sandlance	0.56**
56	SLI	Capelin	0.51**
50	TRI	Sandlance	0.06
44	TEI	Anchovy	0.47 (quad)*
37	SFI	Rockfish	0.01
37	ANI	Rockfish	0.20

Note: Trends are positive linear regression slopes (unless specified as quadratic (quad). MI, Middleton Island; SLI, St. Lazaria Island; TRI, Triangle Island; TEI, Teuri Island; SFI, Southeast Farallon Island; ANI, Año Nuevo Island; *, $p \leq 0.10$; **, $p \leq 0.05$.

sisted largely of anchovy (*Engraulis mordax* in the east, *Engraulis japonicus* in the west), sandlance (*Ammodytes hexapterus* in the east, *Ammodytes personatus* in the west), Pacific saury (*Cololabis saira*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*) and Pacific sardine (*Sardinops sagax*). Juvenile predatory fishes included rockfish (*Sebastes* spp.), salmon (*Oncorhynchus* spp.), sablefish (*Anoplopoma fimbria*) and greenling (*Hexagrammos* spp. in the east, *Pleurogrammus azonus* in the west). California market squid (*Loligo opalescens*) were also present in the diet.

Subarctic species at mid- to high latitudes included capelin and sandlance, while saury, sardine, and anchovy dominated in mid-latitudes. Herring, greenling, salmon, rockfish, and squid were sampled at all locations, but herring and greenling were more prevalent at northern sites. Salmon were eaten more often at eastern sites, while rockfish and squid were most prevalent at southern sites. Sablefish were observed in eastern Pacific samples only. The northern Sea of Japan forage community consisted of anchovy, sandlance, saury, and juvenile greenling. Gulf of Alaska fishes included sandlance, capelin, herring, juvenile greenling, sablefish, and salmon. Sandlance, saury, herring, juvenile rockfish, salmon, and sablefish were present in the Eastern Coastal Transition Zone. California Current forage species included anchovy, saury, squid, juvenile rockfish, sablefish, and salmon. Overall, species richness in the diet was higher in the eastern Pacific (three–seven species each year) versus the western Pacific (two–four species).

Low-frequency variability

The most striking change in community composition occurred in the northern Sea of Japan (see also Deguchi et al. 2004). In 1984, 1985, and 1987, sardine, herring, and saury each comprised up to 15%–25% of birds' diet. However, these species virtually disappeared from the diet in the 1990s, while anchovy increased in 1992–1997, becoming the dominant prey after 1998 (Fig. 3).

Variations in the California Current were more complicated. While shifts in the Sea of Japan involved primarily coastal pelagic species, community changes in the California Current were due to both small pelagic and juvenile predatory fishes. Prior to 1989, juvenile rockfish were abundant (Ralston and Howard 1995; Miller and Sydeman 2004), as

also indicated by SFI data here. Take of anchovy was high between 1989 and 1996, but as rockfish increased again after the 1997–1998 ENSO, saury also increased. This was especially evident at SFI, where saury replaced juvenile predatory species sablefish and salmon.

At TRI in the Eastern Coastal Transition Zone, saury replaced rockfish and herring in 2001–2003, while the presence of salmon remained relatively unchanged. Yet data from the late 1970s also show a large amount of saury, especially during the 1976 ENSO.

In the Gulf of Alaska, juvenile sablefish, salmon, and greenling declined at MI after 1998, while sandlance increased. Capelin, a small pelagic fish, increased at SLI, but there were no visible shifts in take of other species at that location.

We quantified trends in the take of primary prey species at each sampling location from 1994–2003. There were significant linear increases in take of sandlance at MI and capelin at SLI (Table 2). There was a U-shaped quadratic trend in anchovy at TEI.

Interannual covariation between sites

We found some evidence for interannual synchrony among main forage species across sites (Table 3). The take of rockfish at both SFI and ANI was positively correlated with that of sandlance at TRI. Correlations were also found between capelin at SLI and sandlance at MI and between capelin at SLI and rockfish at ANI. Rockfish covaried strongly between the two sampling sites in the California Current; however, no significant east–west relationships were observed.

Ocean conditions and forage species

During the 1992 ENSO event, SFI exhibited a reduction in primary forage species, with fewer rockfish during anomalously high temperatures in the eastern Pacific (Figs. 2, 3). Changes at TEI in the western Pacific were less clear because of a gap in data prior to 1992. During the 1997–1998 ENSO, high SST signals appeared at all latitudes, yet noticeable changes in main forage species occurred mainly at lower latitudes. Rockfish were practically nonexistent in the California Current, fewer sandlance were taken in the Eastern Coastal Transition Zone, and anchovy were extremely low at TEI in 1997. During the 2003 ENSO, when the SST signal was actually higher in the subarctic than in the subtropics, the most definitive changes in forage species were nevertheless recorded in the California Current.

In 1994–2003 in the southern Gulf of Alaska, take of capelin at inshore SLI was inversely correlated with local SST in winter (Fig. 4). In the northern Gulf of Alaska, however, capelin was not as abundant in samples from offshore MI. Rather, sandlance dominated the diet at MI and was inversely correlated with SST in spring (Fig. 4). At TRI in the Eastern Coastal Transition Zone, take of sandlance was most negatively correlated with summer SST (Fig. 4), but also with spring SST (Spearman's rho = –0.66, $p = 0.038$). Rockfish take in the California Current was also inversely related to SST. Relationships were strongest in summer (Fig. 4), but were also significant in spring at ANI (rho = –0.64, $p = 0.048$). In the western Pacific, we expected anchovy take at TEI in the northern Sea of Japan

Table 3. Covariation (Spearman's rho value) in take of primary forage fish between sites.

| Latitude (°N) | Species, location | Western Pacific (Anchovy, TEI) | Eastern Pacific | | | |
			Sandlance, MI	Capelin, SLI	Sandlance, TRI	Rockfish, SFI
59	Sandlance, MI	–0.12				
56	Capelin, SLI	–0.09	0.84**			
50	Sandlance, TRI	0.48	0.48	0.41		
37	Rockfish, SFI	0.14	0.22	0.18	0.59*	
37	Rockfish, ANI	0.24	0.41	0.56*	0.67**	0.76**

Note: TEI, Teuri Island; MI, Middleton Island; SLI, St. Lazaria Island; TRI, Triangle Island, SFI, Southeast Farallon Island; ANI, Año Nuevo Island; *, $p \leq 0.10$; **, $p \leq 0.05$.

to be positively correlated with SST. A positive relationship was observed with summer SST, yet it was not significant (Fig. 4).

Discussion

We used a piscivorous seabird to sample forage fish around the North Pacific Rim. The use of seabird diet as an indicator of prey is not a new idea (Cairns 1987; Barrett 2002; Mills et al. 2007), but this is the first study to use a single seabird species to sample multiple locations over an entire ocean basin. We found that forage species at many sites responded to marine conditions on interannual scales, although indications of lower-frequency change were strongest in the Sea of Japan. There was spatial synchrony (i.e., similarities) in the relationships between SST and certain forage fish species in seabird diet in the northeast Pacific.

Seabirds as indicators of forage fish

As indicators, "puffins" such as the rhinoceros auklet are especially useful in that they are abundant, widely distributed, and samples of forage fish are easily obtained by catching the birds as they return to colonies to feed dependent offspring. In a single feeding episode, puffins may also bring multiple forage fish to the nestlings. While predator-based sampling avoids certain problems inherent in studies of forage fish (e.g., patchy distributions), this technique also presents some difficult interpretive challenges given prey age or size classes and general prey preferences. If independent measures of prey abundance are available, these are valuable to calibrate predator diets. However, once preferences are well established, predator diet may be used to track dynamics of forage species (Reid et al. 1996, 2005).

Prey preferences have been examined at several of our study sites. Auklet take of juvenile rockfish in the California Current has been correlated with midwater trawl surveys for juvenile rockfish over many years (Thayer and Sydeman 2007); auklets in this region preferentially prey on rockfish when they are abundant in the ecosystem. In the Sea of Japan, auklet harvest of anchovy has been linked to annual stock size estimates (1996–2001; Deguchi et al. 2004). In both situations, the take of preferred prey was correlated with increased bird productivity (Takahashi et al. 2001; Thayer and Sydeman 2007). Unfortunately, there were no independent measures of prey availability in the environment that were available for other regions. However, in the Eastern Coastal Transition Zone (British Columbia, Canada), auklet take of sandlance has been related to the take of

sandlance by other predators in the system (groundfish; Bertram and Kaiser 1993) as well as to high offspring survival (Hedd et al. 2006). Ongoing studies in the Gulf of Alaska indicate an increase in capelin since the mid-1990s (Brown 2002), similar to the trend in auklet take of capelin in this study.

Other high-lipid forage fish, though perhaps not known to be "preferred" as described above, may be taken opportunistically by the birds (e.g., sardine, juvenile salmon and sablefish). The appearance of such prey in the diet indicates their presence in the fish community at any given time. Thus, we interpret marine bird diet as useful for examining fish community composition in addition to its potential value as an indicator of dynamics of primary prey relative abundance in the environment. In conjunction with fisheries-independent data, an eventual goal is to use one or more marine birds and possibly other predators at multiple locations to provide a more complete picture of long-term fish community changes.

Forage species' response to interannual marine variability

Relationships of primary forage fishes with SST were observed in the California Current (rockfish), Eastern Coastal Transition Zone (sandlance), and southern (capelin) and northern Gulf of Alaska (sandlance). A mechanistic explanation for these relationships may be related to changes in food availability and larval fish survival. In the California Current, upwelling and cooler SST favors production (Chavez et al. 2002). Changes in the prey base for rockfish that affect adult fecundity or timing of parturition and (or) juvenile survival are likely explanations for the SST–rockfish relationship observed at multiple sites (Miller and Sydeman 2004). Rhinoceros auklets consume multiple age classes of forage fishes, but all of the rockfish taken in the California Current were classified as young of the year, which supports this explanation.

In the Eastern Coastal Transition Zone, Hedd et al. (2006) suggest linkages among 0-age class sandlance survival, copepod abundance, and spring SST rather than temperature-induced distributional shifts in sandlance. As sandlance feed primarily on copepods, cool years would provide favorable feeding conditions for young fish and thus contribute to strong recruitment. Indeed, we observed a strong relationship between spring SST and sandlance in this region. Both 0-age and 1+ age class sandlance were taken by the birds in our study, although 0-age fish were predominant.

Studies in the northern Gulf of Alaska, eastern Bering

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Fig. 4. Relationships of forage fish indices with mean local sea surface temperature (SST) values between 1994 and 2003 at (*a*) Middleton Island (MI), (*b*) St. Lazaria Island (SLI), (*c*) Teuri Island (TEI), (*d*) Triangle Island (TRI), (*e*) Southeast Farallon Island (SFI), and (*f*) Año Nuevo Island (ANI). Trend lines reflect Spearman rank correlations at *p* ≤ 0.10. Series are detrended if necessary. Outlying years are labeled.
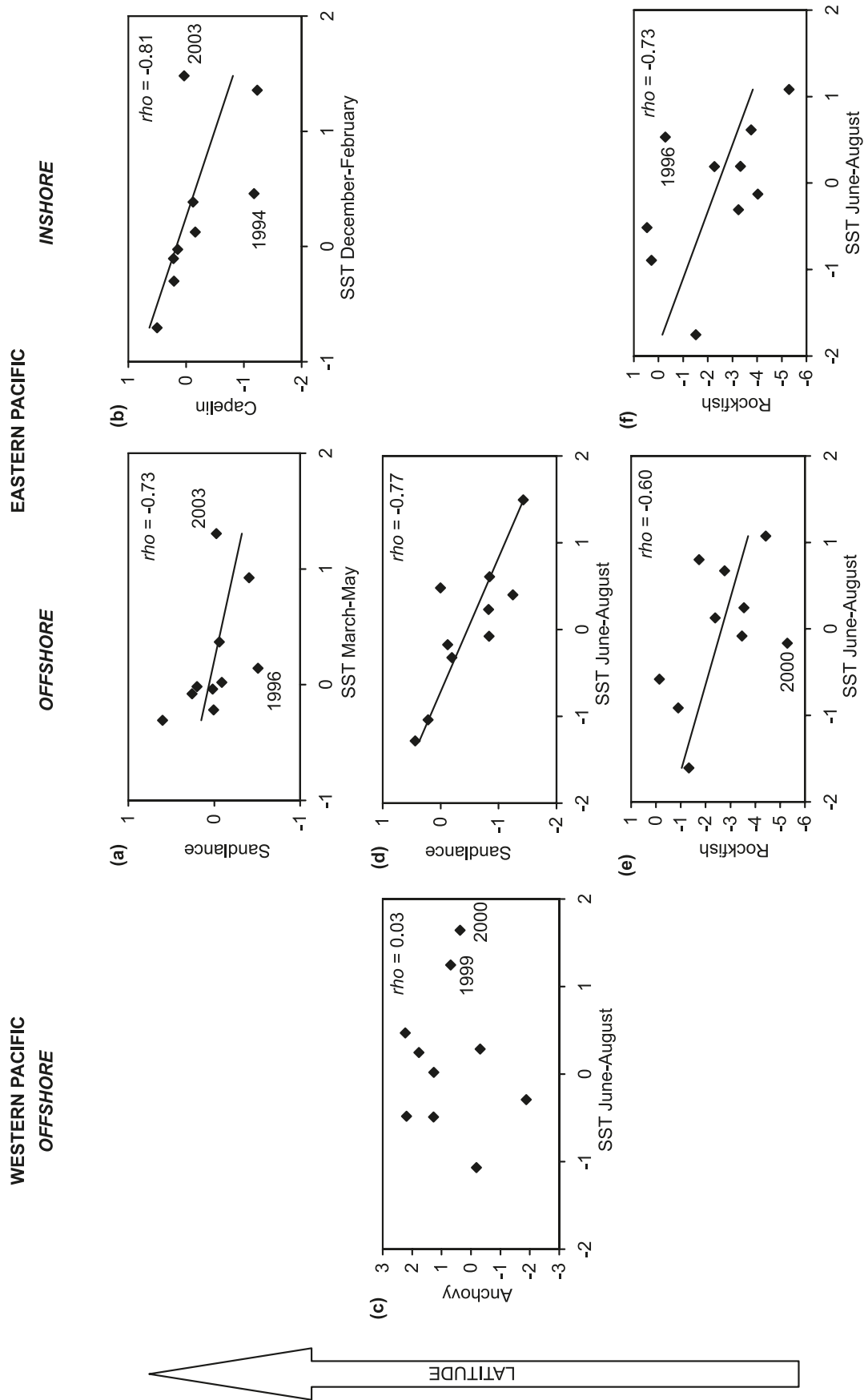
Sea, and Barents Sea indicate that capelin prefer colder waters and that they are found over a wider range in cooler years (Methven and Piatt 1991; Brodeur et al. 1999; Hollowed et al. 2007). Capelin feed on euphausiids and copepods (Hart 1973), and the abundance of these species was higher at lower temperatures in the Gulf of Alaska (Wang and Foy 2006). Therefore, cooler conditions could promote capelin survival. The negative correlation of capelin with winter SSTs in the Gulf of Alaska may be related to food availability and survival prior to reaching age class 1, the age at which they are taken by auklets. This explanation is more probable than one related to direct influence of SST on spawning distribution and behavior. Capelin come inshore to spawn in late spring and early summer (Naumenko 2002), but the relationship we observed with SST occurred during winter. Most importantly, capelin do not mature before ages 2 or 3 (Brown 2002), yet our samples consisted of almost exclusively 1+ age class fish.

In the northern Gulf of Alaska, both 0 and 1+ age class sandlance were harvested by the birds, and we found a strong relationship of sandlance with spring SST. In this region, wind mixing, topographic steering, and periodic upwelling introduce nutrients into surface layers in spring (Okkonen et al. 2001; Stabeno et al. 2004), promoting zooplankton blooms and positively influencing sandlance recruitment (Robards et al. 2002; Hedd et al. 2006).

Pan-Pacific comparisons

SST indices covaried negatively between the eastern and western Pacific Rim and positively within the eastern regions. While we did not find evidence of inverse east–west relationships in take of forage fishes, there was regional synchrony in the take of primary prey in the east. Forage fish take covaried more strongly between sites in proximity to each other and in adjacent ecosystems. We interpret this synchrony as suggestive of bottom-up processes across the entire eastern North Pacific.

In the west, we found no relationships between SST and forage fish. We expected a positive relationship between anchovy in the diet and SST, because the mechanism (advection of fish with intensification of the warm Tsushima Current) has been well described previously (Deguchi et al. 2004). Moreover, Deguchi et al. (2004) observed a correlation between June SST and anchovy in seabird diet between 1992 and 2001. Differences in the SST measurements used for analyses may explain this discrepancy. We used a 50 km radius around TEI based on AVHRR-derived SST, while Deguchi et al. (2004) used shipboard conductivity–temperature–depth (CTD) measurements covering a much larger area. Insolation can cause variation between ocean surface and subsurface temperature measurements (see Appendix A), increasing disparity between satellite and shipboard data. There were also slight differences in the time series. The relationship between June SST from the shipboard surveys and our satellite-derived index was extremely weak during the years of temporal overlap (1994–2001; $R^2_{June} = 0.25$, $p = 0.21$), suggesting that the scale of observation explains these differences. The radius of our measurements may have affected our results, since SST in the Sea of Japan can change drastically along a latitudinal gradient,

depending on the location of the frontal zone between the Tsushima Current and subarctic waters to the north.

Temporal mismatch may have also obscured a temperature – forage fish relationship in the Sea of Japan. If the warm-water front of the Tsushima Current moved northward much earlier or later than average, a temporal mismatch may have occurred between auklet breeding and the anchovy prey around TEI (Takahashi et al. 2001; Deguchi et al. 2004). Auklets will adjust their timing of breeding to match prey availability as much as possible, but auklets may not be able to match extreme phenological and (or) distributional shifts in prey (Takahashi et al. 2001).

Long-term change

Our data sets were too sparse to adequately evaluate decadal changes in forage fish, but indications of shifts in the Sea of Japan and the California Current do support changes reported in the literature. In the California Current, a reduction of rockfish after the climate regime shift in 1989 and an increase after 1997–1998 were suggested by our data at SFI and supported by other studies (Ralston and Howard 1995; Miller and Sydeman 2004). In the Sea of Japan, Tian et al. (2006) showed stronger evidence for decadal versus interannual variations of fish community structure with ocean climate. Shifts in anchovy, sardine, saury, and herring stocks in 1988–1989 and (or) 1992–1993 were aligned with our observations of changes of these species at TEI. Furthermore, we found a significant relationship between anchovy at TEI and the PDO (1994–2003; $rho_{June-August} = -0.72$, $p = 0.02$), supporting evidence of influence by large-scale, low-frequency climatic changes.

In conclusion, based on the diet of a piscivorous seabird, we found regional synchrony in changes in forage fish communities throughout the northeastern coastal Pacific Ocean. Many other studies of synchrony or covariance in fish population dynamics have found relationships with long-term, temporal, environmental variability (Klyashtorin 1998; Hare et al. 1999, although see Hollowed et al. 2001 for shorter periodicities related to ENSO), whereas we observed synchrony on an interannual time scale. This study demonstrates the potential utility of predator-sampled data for obtaining a basin-wide perspective on mid-trophic-level forage species of key importance in food web dynamics. Coupling these data with other sources of forage fish data may be a valuable comparative tool. In the future, longer time series of predator diet will allow examination of forage species dynamics in relation to lower-frequency climate variability.

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Appendix A

Advanced Very High Resolution Radiometer (AVHRR) data were fairly complete within the 50 km radius around most North Pacific sites in most months. In the California Current, >70% of cells contained data in all months in all years. However, data were patchier in the Gulf of Alaska and Sea of Japan – Tsushima Current in winter owing to cloud cover. While there was a minimum of 60% of cells with data at most sites in most months, sea surface temperature (SST) values were obtained at TRI for 5% and 28% of cells in December 2002 and 2003, respectively. Around MI, 45% of cells contained data in January 2003. At SLI, SST was available from 36% of cells in February 1997. Coverage at TEI averaged 44% in the month of January. Since SST values in adjacent cells were highly correlated, we maintained that averaging available values to obtain an SST value for the entire 50 km radius was appropriate for our purposes.

Satellite-derived SST data may be biased somewhat by insolation compared with subsurface measurements, so we compared AVHRR data with in situ measurements of temperature at up to 1 m depth where such data were available near three of our study sites. Satellite SST around SFI was correlated with in situ data, but more so before intense spring–summer solar heating began (linear regression: 1985–2003: $R^2_{\mathrm{December–February}} = 0.93$, $R^2_{\mathrm{March–May}} = 0.88$, $R^2_{\mathrm{June–August}} = 0.74$; $p_{\mathrm{all}} < 0.001$).

In situ measurements in the Eastern Coastal Transition Zone were available at both Kains Island (50°16′N, 128°1′W) at the northwestern edge of Vancouver Island, and Pine Island (50°35′N, 127°26′W) located further inshore towards mainland Canada. An average of SST at these locations was used as a proxy for comparing in situ data with a satellite-derived SST index around TRI. Correlations were significant ($R^2_{\mathrm{December–February}} = 0.78$, $R^2_{\mathrm{March–May}} = 0.88$, $R^2_{\mathrm{June–August}} = 0.74$; $p_{\mathrm{all}} < 0.001$).

In the Tsushima Current, SST measurements for all years were available at Yoichi (Hokkaido Fisheries Experimental Station; 43°12′N, 141°48′E), ∼150 km south of TEI. These in situ measurements were significantly correlated with satellite-derived SST at TEI ($R^2_{\mathrm{December–February}} = 0.53$, $R^2_{\mathrm{March–May}} = 0.69$, $R^2_{\mathrm{June–August}} = 0.73$; $p_{\mathrm{all}} < 0.001$), but not as highly linked in December–May prior to the northward warm-water influx in summer, likely due to the latitudinal distance between sites.

Appendix B

Table B1 appears on the following page.

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Table B1. Sample sizes (number of rhinoceros auklet (*Cerorhinca monocerata*) prey loads) at each study location, 1994–2003.

Site	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
MI	180	124	68	110	305	99	106	116	95	97
SLI	38	45	32	37	77	31	46	76	54	67
TRI	85	117	107	90	88	86	83	93	110	96
SFI	61	58	59	46	70	60	33	93	53	38
ANI	25	22	26	19	24	24	34	52	46	33
TEI	88	88	66	117	112	109	109	99	78	127

Note: MI, Middleton Island; SLI, St. Lazaria Island; TRI, Triangle Island; SFI, Southeast Farallon Island; ANI, Año Nuevo Island; TEI, Teuri Island.