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Oceanography and ecology of the Aleutian Archipelago: spatial and temporal variation

GEORGE L. HUNT, JR[1],[*] AND PHYLLIS J. STABENO[2]

[1]*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA*
[2]*National Oceanic and Atmospheric Administration, Pacific Marine Environmental Laboratory, 7600 Sand Point Way, NE, Seattle, WA 98115, USA*

ABSTRACT

This compilation of new information and summaries of earlier work emphasizes variability within marine waters of the Aleutian Archipelago. From the Alaska Peninsula to Near Strait, net flow through the passes is northward, with four passes (Amukta, Amchitka, Buldir, and Near Strait) contributing most of the flow. East of Samalga Pass (169°W), waters derived from the Alaska Coastal Current predominate, whereas west of Samalga Pass, waters of the Alaskan Stream predominate. The pattern of storm tracks creates a climatological (interannual and long term) transition zone in weather features (e.g. surface air temperature) near 170°W. The marine ecosystem of the Aleutian Archipelago also has a strong discontinuity at Samalga Pass, where cold-water corals, zooplankton, fish, marine mammals and foraging seabirds show a step change in species composition. Diets of ground fish, Steller sea lions (*Eumetopias jubatus*) and some seabirds also change there. Lower growth rates of some fish species and stable isotope data indicate that productivity declines westward along the archipelago. The available data demonstrate considerable ecosystem variability over time scales of decades to millennia. Abrupt changes in composition of fish communities at several of the major passes suggest that Samalga Pass may mark only one of several ecological divisions of Aleutian waters. This spatial and temporal heterogeneity provides an important context within which to view recent declines in populations of Steller sea lions and other species, and has important implications for the management of regional marine resources. We conclude that the marine waters of the Aleutian Archipelago are divided into at least two different ecological regions, with potential for a concomitant separation of some fishery resources.

INTRODUCTION

Although the Aleutians are a site of important fisheries and the center of distribution of the endangered western stock of Steller sea lions (*Eumetopias jubatus*), their remoteness has limited oceanographic investigation. Nevertheless, it has been known for some time that there were spatial discontinuities in the diets and population trajectories of Steller sea lions (York *et al.*, 1996; Sinclair and Zeppelin, 2002) that suggested possible underlying spatial heterogeneity in Aleutian marine ecosystems. Additionally, among marine ornithologists, the shallow, narrow passes of the Aleutian Islands are renowned for their immense aggregations of foraging seabirds, whereas many of the larger, deeper passes were thought to support few foraging birds. Thus, ecologically important spatial heterogeneity was known to exist at a variety of scales. These patterns of variation gave rise to questions about the causal basis of the observed patterns, and their implications for the structure and function of the Aleutian marine ecosystem. When funding became available to investigate potential bottom-up and top-down impacts on Steller sea lions in the Aleutians in 2001 and 2002, there were a number of scientific questions of broad, general interest that helped direct the resulting field study (the Aleutian Passes Project). As a result, research cruises were organized in 2001 and 2002 to investigate spatial patterns in ecosystem properties at a variety of scales from that of frontal systems within passes to large blocks of the archipelago, and at levels of organization from ocean physics and chemistry to the distribution, abundance and foraging ecology of marine birds and mammals.

In assembling this volume, it was felt that it was important to include recent work by investigators working in the Aleutian Archipelago in addition to those who took part in cruises in 2001 and 2002. Thus, the papers in this supplemental volume of *Fisheries Oceanography* have been motivated by a variety of interests, including fisheries management (Heifetz *et al.*, 2005; Logerwell *et al.*, 2005; McDermott *et al.*, 2005), the biology and ecology of sea lions (Call and Loughlin, 2005; Fadely *et al.*, 2005; Sinclair *et al.*, 2005), an interest in the spatial patterns of variability in the ocean environment occupied by the sea lions and other top predators (Byrd *et al.*, 2005; Coyle, 2005; Jahncke *et al.*, 2005; Ladd *et al.*, 2005a,b; Mordy *et al.*, 2005; Rodionov *et al.*, 2005; Stabeno *et al.*, 2005; Vlietstra *et al.*, 2005), understanding change, over time scales of millennia, in human occupation and ecology in the Aleutians (Causey *et al.*, 2005), and sustaining the services that this ecosystem provides (Schumacher and Kruse, 2005). In this overview, we provide a synthesis of recent and past studies to update current knowledge of the spatial and temporal variability of the marine ecosystems of the Aleutian Archipelago. We also identify some of the questions that remain.

PHYSICAL SETTING

The Aleutian Archipelago stretches westward over 2000 km from the Alaska Peninsula in North America to the Commander Islands off the Kamchatka Peninsula in eastern Asia (Fig. 1). From its northernmost point in Alaska at False Pass to its southernmost islands in the Delarof group at 179°10′W, the Aleutian Archipelago spans over four degrees of latitude (425 km). This long, narrow chain of volcanic mountaintops separates the waters of the sub-arctic North Pacific Ocean from the Bering Sea. Recognizing the importance of the region for wildlife, the Aleutians are a designated UNESCO International Biosphere Reserve and most of the islands are within the Alaska Maritime National Wildlife Refuge. The Aleutians form the southern boundary of two Large Marine Ecosystems, the Eastern and the Western Bering Sea (e.g. http://www.edc.uri.edu/lme/, May 2005).

The passes between the islands vary from narrow, shallow channels between large islands, to wide, deep passages bordered by small islands perched on narrow surrounding shelves (Table 1) (Favorite, 1974). The passes, particularly the deep passes, allow transfer of water between the North Pacific Ocean and the Bering Sea (Stabeno *et al.*, 2005). The passes also provide habitat for a vast array of species. The eastern Aleutians, as far west as Samalga Pass, are characterized by shallow, generally narrow passes, and a mixture of large and small islands. The shelf (200 m depth contour) around these eastern islands is narrow on the north side (<10 km), but to the south, it starts off wide
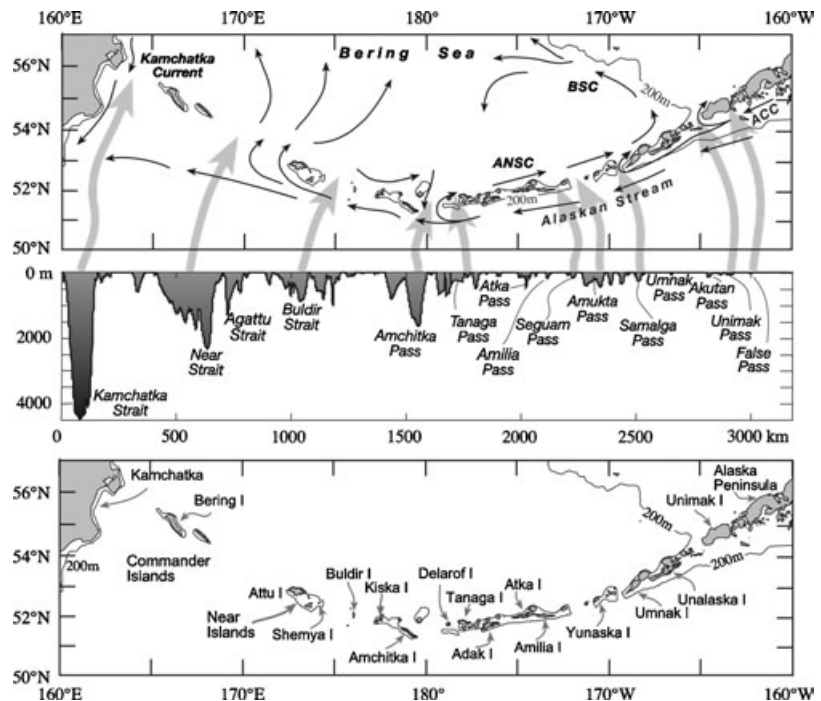
Figure 1. Map of the Aleutian Islands showing 200-m isobath and place names mentioned in the text. ACC, Alaska Coastal current; ANSC, Aleutians North Slope Current; BSC, Bering Slope Current.

Table 1. Depth and area of major passes in the Aleutian-Commander island arc (after Favorite, 1974; Ladd *et al.*, 2005a). Flow from Arsen'ev (1967) in Favorite (1974), and Stabeno *et al.* (2004).

Region	Pass/strait	Depth (m)	Cross-sectional area (km^2)	Flow into Bering Sea (10^6 m^3 s^{-1})
Eastern Aleutians	Unimak	52	1.0	0.1
	Akutan	30	0.1	0.1
	Umnak	7	1.6	??
	Regional total		3.9	~0.2
Central Aleutians	Samalga	200	3.9	??
	Chuginadak	210	1.0	??
	Herbert	275	4.8	??
	Yunaska	457	6.6	??
	Amukta	430	19.3	4.0
	Seguam	165	2.1	0.4
	Tanaga*	235	3.6	
	Amchitka*	1155	45.7	
	Regional total		87.0	>8.8
Western Aleutians	Kiska	110	6.8	
	Buldir	640	28.0	
	Semichi	105	1.7	
	Regional total		36.5	0.7
Commander-Near Straits	Near	2000	239	
	Commander	105	3.5	
	Regional total		242.5	14.4
Kamchatka Strait[†]		4420	335.3	2.6

*Favorite gives the combined flow for Tanaga Pass and Amchitka Pass as 4.4 Sv.
[†]Below 3000 m.

(~100 km) near the Alaska Peninsula and narrows to <25 km by Samalga Pass. The central Aleutians, from Samalga Pass to Amchitka Pass, are a combination of small to medium-sized islands perched on narrow shelves (e.g. Amukta, Yunaska Islands) and deep, wide passes (e.g. Amukta, Tanaga, Amchitka) (Fig. 1). There are also narrow, shallow passes (e.g. Amilia Pass) where water rushes past clusters of islands that, in aggregate, create a large landmass (Fig. 1). Westward from Amchitka Island, much of the Rat Island group (Amchitka, Kiska, and islands in between) in the Aleutian Archipelago is characterized as having small islands and wide passes, some of which contain deep canyons (e.g. Murray Canyon, west of Kiska Island) (Fig. 1). In contrast, the Near Islands (e.g. Agattu and Attu) are situated on a comparatively broad, shallow shelf. Between Attu and the Commander Islands, Near Strait provides a deep passage for exchange of water between the North Pacific Ocean and the Bering Sea.

The Aleutian Islands have a cool, wet and windy maritime climate. The region is frequented by storms, and the Aleutian Low is an index of where storms, on average, reach their lowest pressure. The Aleutian Low is strongest in winter, and practically disappears in summer (Rodionov *et al.*, 2005). The Aleutian Low is the statistical combination of two patterns, one a region of low pressure centered east of 180°, and the other a split between a low-pressure centre east of Kamchatka Peninsula and a second center in the Gulf of Alaska. Typically, storms originate east of Japan and move northeastward along the Aleutian Archipelago to the Gulf of Alaska; less frequently, they originate in the Gulf itself (Rodionov *et al.*, 2005). In the region of cyclogenesis off Japan, storm tracks show considerable consistency in direction; storm tracks originating in the Gulf of Alaska are more variable. Sea level pressure variability reaches its maximum in the gap between these two areas of high storm frequency (170–150°W, south of the Alaska Peninsula) (Rodionov *et al.*, 2005).

Although the seasonal signal in surface air temperatures is similar throughout the Aleutian Islands, interannual and interdecadal variations in surface air temperatures differ substantially in the western and eastern portions of the Aleutian Archipelago, with the dividing line between the two regions in the vicinity of 170°W (Rodionov *et al.*, 2005). In the eastern

Aleutians, there was a shift in 1977 toward a warmer climate, whereas in the western Aleutians there has been a slow, steady decrease in winter surface air temperatures since the 1950s (Rodionov *et al.*, 2005). Variance in winter surface temperatures in the western Aleutians doubled in the period 1986–2002 when compared with 1965–85, resulting in a doubling of the seasonal cooling rate since the 1950s. On a comparative note, in southeast Alaska, the variance of surface air temperature decreased by a factor of 2 (Rodionov *et al.*, 2005). The palaeoenvironmental record indicates that during the Medieval Warm Period of Europe (*c.* AD 900–1350), temperatures on Bering and Shemya Islands were elevated, whereas in the eastern Aleutian Islands and Gulf of Alaska, temperatures were depressed (Heusser *et al.*, 1985; Savinetsky *et al.*, 2004; Causey *et al.*, 2005). Thus, there may be a long-standing split in climate between the eastern and western extremes of the Aleutian Archipelago.

Three currents (Fig. 1) supply the waters bathing the eastern and central Aleutian Islands: the Alaska Coastal Current (Schumacher and Reed, 1986; Reed, 1987) and the Alaskan Stream (Favorite, 1967; Favorite *et al.*, 1976; Onishi and Ohtani, 1999) flow westward along the south side of the archipelago, and the Aleutian North Slope Current flows eastward along the north side from Amchitka Pass (Stabeno and Reed, 1994, 2004; Reed and Stabeno, 1999). The Alaska Coastal Current begins along the coast of southeastern Alaska and flows ∼1000 km along the coast of Alaska to Samalga Pass. It is forced by winds and modified by coastal freshwater discharge in the Gulf of Alaska (Royer, 1979; Royer *et al.*, 1979; Stabeno *et al.*, 2004). There is a strong seasonal signal in transport in response to local wind forcing, and in salinity in response to freshwater discharges in the Gulf of Alaska (Schumacher and Reed, 1980, 1986; Stabeno *et al.*, 2004). In contrast, the Alaskan Stream, a western boundary current of the North Pacific subarctic gyre (Thomson, 1972; Reed, 1984), forms southeast of Kodiak Island and follows the shelf break as a narrow, high-speed current to Amchitka Pass. At Amchitka (∼180°W), the archipelago turns northwestward and the stream broadens and separates from the slope. Thus, west of Amchitka Pass, meanders and eddies exist in theoretical, model and observational studies (Thomson, 1972; Favorite *et al.*, 1976; Overland *et al.*, 1994; Stabeno and Reed, 1994). This portion of the Alaskan Stream remains the predominate source of water bathing the western Aleutians (Stabeno and Reed, 1992).

Prior to the present work, the western extent of the Alaska Coastal Current was assumed to be Unimak Pass, through which it enters the southeastern Bering Sea (Stabeno *et al.*, 2002; Ladd *et al.*, 2005a). However, Ladd *et al.* (2005a) show that while the freshest, inshore portion of the Alaska Coastal Current enters Unimak Pass, the saltier, offshore portion flows westward to Samalga Pass, where it turns northward on the east side of the pass to join the Aleutian North Slope Current. Thus, from False Pass to Samalga Pass, the Alaska Coastal Current is the primary source of northward flowing water in the passes. West of Samalga Pass, as far as Near Strait, the Alaskan Stream and its extension are the major source of water entering the passes from the North Pacific (Reed and Stabeno, 1993; Stabeno *et al.*, 2002). The trajectories of drifters released in the Gulf of Alaska support these results (Ladd *et al.*, 2005a).

The differences in source water along the southern side of the eastern and central Aleutian Islands result in strikingly different physical and chemical properties in the passes. The waters of the Alaska Coastal Current are warmer and fresher than those of the Alaskan Stream, and this results in a front as the last of the Alaska Coastal Current turns northward at Samalga Pass (Fig. 2) (Ladd *et al.*, 2005a). A front also occurs to the north of Samalga Pass with much fresher water occurring to the east of the pass, suggesting that fluxes through the eastern passes freshen the surface waters of the Aleutian North Slope Current (Fig. 2).

The macronutrient levels also differ between the Alaska Coastal Current and the Alaskan Stream. Surface nitrate levels are higher west of Samalga Pass than to the east of it (Ladd *et al.*, 2005a), and Mordy *et al.* (2005) show that this is largely the result of deep tidal mixing within the passes. In May and June of 2001 and 2002, chlorophyll concentrations were high in waters east of Samalga Pass and low between Samalga Pass and Seguam Pass (Mordy *et al.*, 2005). Primary production was relatively low between Unimak and Tanaga Passes, except for the north end of Seguam Pass and the shelf edge in the southeastern Bering Sea where nutrients, mixed upward from deeper layers by tidal action in the passes, were trapped above the pycnocline north of the Aleutians (Mordy *et al.*, 2005).

Flow in the passes of the Aleutian Archipelago is dominated by the tides (Stabeno *et al.*, 2005). Strong tidal currents mix the water column top to bottom over the shallow sills (e.g. to 80 m in Akutan and 140 m in Seguam Pass). In passes that are wider than the internal Rossby radius (e.g. Amukta Pass), flow is bi-directional, resulting in northward flow on the east side and southward flow on the west side (Ladd *et al.*, 2005a; Stabeno *et al.*, 2005). Except in Kamchatka
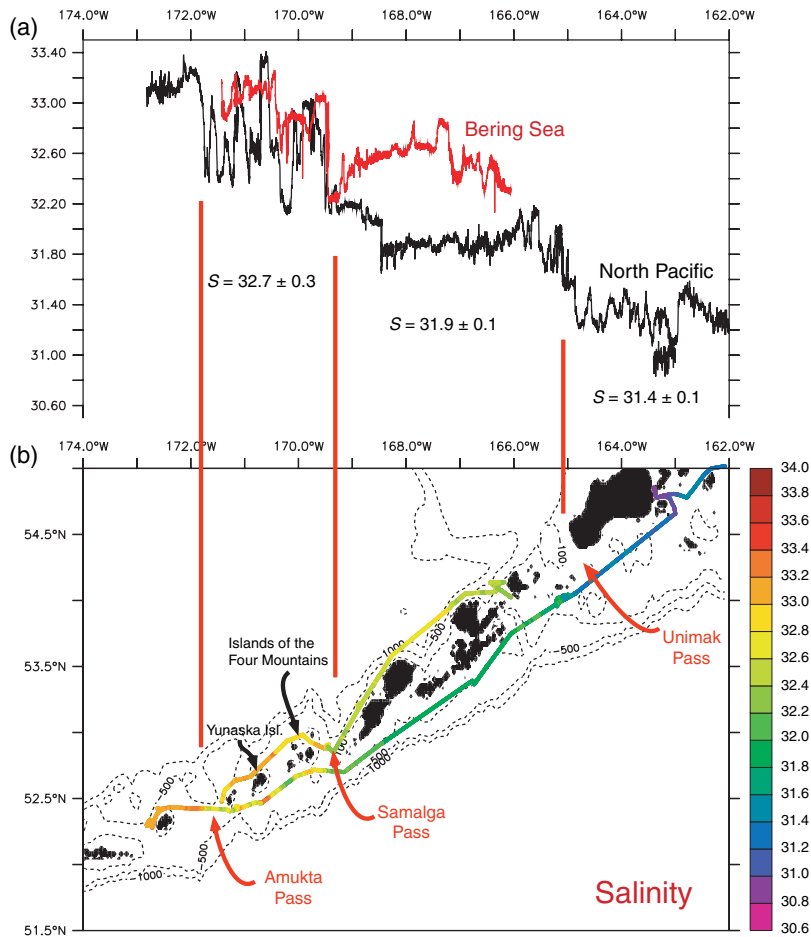
Figure 2. Sea surface salinity (psu) measured underway on the 2001 cruise (from Ladd *et al.*, 2005a). (a) Salinity plotted against latitude south of the Aleutian Islands (black) and north of the islands (red). (b) Average along-track salinity by region, including the region east of Unimak Pass, between Unimak and Samalga Passes, and between Samalga and Amukta Passes.

Strait where flow is southward from the Bering Sea, net flow has been to the north in all passes where it has been measured to date. The northward transport is a source of nutrients for the Bering Sea. Monthly and long-term variability in transport through Amukta Pass is related to the position and strength of the Alaskan Stream (Stabeno *et al.*, 2005).

SPATIAL VARIABILITY AND BIOGEOGRAPHIC PATTERNS

A number of taxa have distribution patterns in the Aleutian Archipelago that suggest responses to habitat variables, including the change in water properties and chemistry at Samalga Pass. For example, the species diversity of cold-water corals increases sharply west of Samalga Pass (Heifetz *et al.*, 2005). East of Samalga Pass, 96% of bottom trawls containing corals had but one or two taxa present, whereas west of Samalga Pass, 33% of hauls contained more than two taxa. Sea whips (35% of species) and sea pens (20.5% of species) predominated in the east, whereas gorgonian (nine

species), cup (four species) and hydrocorals (17 species) predominated to the west of Samalga Pass (Heifetz, 2002; Heifetz *et al.*, 2005). Although research into these cold-water corals is in a preliminary stage, it is already clear that the waters of the central and western Aleutian Archipelago support remarkably high concentrations and diversity of these poorly known taxa. In contrast, the coral populations found in the waters of the eastern Aleutians differ little from those found across the shelf and upper slope of the Gulf of Alaska (Heifetz, 2002; Heifetz *et al.*, 2005).

Within the water column, zooplankton species composition east of Samalga Pass is typical of a neritic community and includes species such as *Calanus marshallae*, *Pseudocalanus* spp., *Acartia* spp., and *Thysanoessa inermis*, all characteristic inhabitants of shelf ecosystems. In contrast, the waters between Samalga and Tanaga Passes are dominated by oceanic species of zooplankton such as *Neocalanus* spp., *Eucalanus bungii* and *Euphausia pacifica* (Hunt *et al.*, 1998; Coyle, 2005). Coyle (2005) found that up to 50% of the observed variance in zooplankton abundance

between Unimak and Tanaga Passes could be accounted for by salinity and temperature. The abundances of *C. marshallae* and *T. inermis* were positively correlated with temperature and negatively with salinity, whereas the abundances of *E. pacifica* and *N. cristatus* showed negative correlations with temperature and positive correlations with salinity. Likewise, in spring the biomass of near-surface meso-zooplankton near Kiska Island, western Aleutian Islands, was dominated by oceanic species of copepods (Coyle and Hunt, 2000).

Demersal fish also show strong longitudinal patterns in faunal affinities, species distribution and abundance, diets, and growth rates (Logerwell *et al.*, 2005). Moving westward from the Alaska Peninsula, species richness drops sharply at Samalga Pass (38%), whereas there is little decline between Samalga and Amchitka Passes (4%). There is a further decline of 20% west of Buldir Island. Of the 36 Aleutian demersal fish species associated with the Oregonian zoogeographic province (Allen and Smith, 1988), there is a 30% decline in species richness between Unimak and Samalga Pass, a 54% drop between Samalga and Amukta Passes and a further drop from nine species to two species between Amchitka Pass and Buldir Island (Logerwell *et al.*, 2005). As Logerwell *et al.* (2005) point out, the larvae of many of these fish species are pelagic, and their distributions are likely to be strongly influenced by water mass origins and movements. Additionally, the deep passes may be potential barriers to dispersal (Logerwell *et al.*, 2005). Abundance patterns of widespread species show longitudinal shifts in numbers (Atka mackerel, *Pleurogrammus monoterygius*, are more abundant west of Samalga Pass; walleye pollock, *Theragra chalcogramma*, are less abundant west of Buldir Island) or depth preferences (Pacific cod, *Gadus macrocephalus*; walleye pollock). At smaller spatial scales, several of the passes (Samalga, Seguam, and Tanaga) appear to support unusually high biomasses of fish such as Atka mackerel and Pacific ocean perch (*Sebastes alutus*).

Diets of some demersal fish species vary with location along the Aleutian Archipelago. Euphausiids constituted 50–90% of the diets of walleye pollock, Atka mackerel and Pacific ocean perch east of Samalga Pass, and <50% of the diets of these fish to the west of this pass, where copepods and myctophid fishes were more important prey (Logerwell *et al.*, 2005). Pacific ocean perch also showed a further increase in their consumption of myctophids west of Buldir Island. Pacific cod diets shifted at Samalga Pass, with walleye pollock predominating to the east of the pass and Atka mackerel to the west.

Growth rates of some fish species show a decline from east to west. Length-at-age for northern rockfish and Atka mackerel decreased from east to west through the Aleutians (Logerwell *et al.*, 2005). Growth rates of Pacific ocean perch also declined from east to west, but the differences were not as striking as those in Atka mackerel and northern rockfish. These patterns suggest that prey biomass may be less plentiful in the western Aleutian Islands than in the eastern portion of the archipelago.

At least 26 species of seabirds nest in the Aleutian Archipelago (Byrd *et al.*, 2005). Their nesting and foraging distributions reflect habitat and prey needs, as well as the influence of terrestrial predators such as introduced foxes and rats (Byrd *et al.*, 2005). Samalga Pass does not seem to be a break point in the distribution of breeding seabirds based on a species by species evaluation (Byrd *et al.*, 2005). Nevertheless, if species are aggregated by foraging guild, there are apparent large-scale patterns (Table 2). In particular, about 68% of the 1.7 million piscivorous seabirds nesting in the Aleutian Islands occur to the east of Samalga Pass. In contrast, 92.5% of the 7.9 million planktivorous seabirds nest to the west of Samalga (U.S. Fish and Wildlife Service, 2000). These species include auklets (least *Aethia pusilla*, crested *A. cristatella*, whiskered *A. pygmaea* and parakeet *A. psittacula* auklets) that forage on zooplankton (e.g. large copepods – *Neocalanus plumbcrus*, *N. cristatus*, and euphausiids – *Thysanoessa raschii*, *T. inermis*, and larval fish) and nest predominately on islands between Tanaga and Buldir Passes (Jones *et al.*, 2001; Byrd *et al.*, 2005). These birds forage in and around passes, where tidal currents result in concentrations of prey (Day and Byrd, 1989; Hunt *et al.*, 1998; Byrd *et al.*, 2005).

Marine bird species that are inshore foragers, such as cormorants, glaucous-winged gulls (*Larus glaucescens*) and pigeon guillemots (*Cepphus columba*), nest predominately on large islands, which typically have a larger area of shallow shelf (Byrd *et al.*, 2005). Interestingly, about 31% of inshore-foraging seabirds nest in the eastern Aleutians and about 31% nest in the Near Islands, at the far western extreme of the Aleutian Archipelago. These two regions hold in common an unusually wide extent of shallow shelf waters, appropriate foraging habitat for inshore-foraging seabirds (Springer, 1991; Springer *et al.*, 1996). In recent years, cormorants in the Near Islands have suffered major population declines, possibly as a result of the destruction of kelp forests subsequent to the decline in sea otters (*Enhydra leutris*) (Doroff *et al.*, 2003; Byrd *et al.*, 2005). Overall, there is no indication of a spatial pattern in either reproductive success or population

Table 2. Distribution and abundance (individuals) of marine birds breeding on the Aleutian Islands (data source: U.S. Fish and Wildlife Service, 2000).

Species or species group	Far West 'Near Islands'	West Amchitka to Buldir Pass	Central Samalga to Amchitka Pass	Eastern Unimak to Samalga Pass
Piscivores				
Red-legged kittiwake	0	12 680	28	700
Black-legged kittiwake	14 518	30 726	10 073	6221
Murres (both species)	23 268	19 574	61 743	54 578
Ancient murrelet	0	12 240	16 542	25 581
Puffins (both species)	53 915	101 756	164 403	1 047 768
Total piscivores	91 701	176 976	252 789	1 130 848
Planktivores				
Northern fulmar	0	1360	509 100	10
Storm-petrels (both species)	2500	3 003 500	1 256 000	576 198
Small auklets (all species)	54	2 549 515	778 699	13 480
Total planktivores	2554	5 554 375	1 765 878	589 688
Inshore foragers				
Cormorants (all species)	21 133	5679	3853	9386
Glaucous-winged gull	12 537	10 893	10 709	20 418
Pigeon guillemot	336	2084	8349	4034
Total inshore foragers	34 006	18 656	22 911	33 838

trends for seabirds nesting in the Aleutian Islands that would suggest a response to lower primary productivity west of Samalga Pass (Mordy *et al.*, 2005). In fact, both murre and kittiwake populations at Buldir Island are increasing (Byrd *et al.*, 2005).

Limited at-sea surveys of migrant and resident marine birds in 2001 and 2002 reinforce the notion that the ecosystems of the eastern Aleutian Islands differ significantly from those of the central region. East of Samalga Pass birds seen at sea were dominated by piscivorous tufted puffins (*Fratercula cirrhata*) and planktivorous short-tailed shearwaters (*Puffinus tenui-rostris*), a migratory species that breeds in the southern hemisphere (Jahncke *et al.*, 2005). West of Samalga Pass, small auklets and northern fulmars (*Fulmarus glacialis*), which were observed feeding on large oceanic copepods, dominated the marine avifauna in Tanaga and Seguam Passes, respectively (Hunt *et al.*, 1998; Jahncke *et al.*, 2005). At smaller spatial scales, surface-foraging fulmars and near-surface-foraging shearwaters were concentrated near frontal features in the passes (Ladd *et al.*, 2005b; Vlietstra *et al.*, 2005). Interestingly, in frontal regions in Akutan Pass where euphausiids were highly concentrated near the surface, shearwaters consumed much smaller individuals than they did in regions where they had to dive to capture euphausiids at depth (Vlietstra *et al.*, 2005). These passes are likely prime foraging areas for marine birds because strong tidal currents impinging on the

bathymetry cause the aggregation of vertically migrating or depth-tending zooplankton (Simard *et al.*, 1986; Vermeer *et al.*, 1987; Genin *et al.*, 1988; Coyle *et al.*, 1992; Hunt *et al.*, 1998).

Pinnipeds and cetaceans also show scale-dependent patterns of distribution and abundance in the Aleutian Archipelago. A number of researchers using different statistical techniques and data sets have obtained strikingly similar groupings of Steller sea lion rookeries in the Aleutian Archipelago and western Gulf of Alaska (York *et al.*, 1996; Sinclair and Zeppelin, 2002; Call and Loughlin, 2005; Sinclair *et al.*, 2005). Call and Loughlin (2005), using diets, population trajectories, and habitat within 10 miles of the rookery, were able to discern five distinct classes of Steller sea lion rookeries, including one group from Attu to Amchitka Pass, a second from Amchitka to Samalga Pass, and three other groupings that were to the east of Samalga Pass. Sinclair *et al.* (2005), in an independent analysis, employed an additional 3 yr of diet and population trend data and focused on the 16 Steller sea lion rookeries within the area covered by the 2001 and 2002 cruises to the Aleutian passes. They found that the strong division of diet types and population trends previously identified by Sinclair and Zeppelin (2002) as occurring at Samalga Pass was still present. To the east of Samalga Pass, diets, on average, had a higher diversity of prey species and population trends showed lesser rates of decline than did diets and population

trends to the west of Samalga Pass. At a smaller spatial scale, Sinclair *et al.* (2005) used generalized additive models to examine the relationships among population trends, diet diversity, and the distance to, and characteristics of, the passes investigated in 2001 and 2002 (Unimak, Akutan, Umnak, Samalga, Amukta, Seguam and Tanaga). Sinclair *et al.* (2005) found that the frequency of occurrence of herring and salmon in sea lion diets was important for predicting the steepness in the rate of population decline, and that with these diet constituents included, the population trends were positively related to increasing depth of the nearest of these passes. Why sea lion population declines in rookeries near deep passes are reduced when diets are considered is unclear.

Although there were too few sightings of Steller sea lions or other pinnipeds during the 2001 and 2002 cruises to assess their at-sea habitat preferences from shipboard surveys, the recent use of satellite-linked time depth recorders has yielded a wealth of information on the foraging habits of juvenile Steller sea lions. Fadely *et al.* (2005) extended the work of Loughlin *et al.* (2003) and Raum-Suryan *et al.* (2004), showing that juvenile sea lions consistently conduct most of their foraging dives within 18.5 km of shore in water <100 m deep. Average trip durations for sea lions <10 months old were shorter than those of lactating females tracked by Merrick and Loughlin (1997) and observed by Trites and Porter (2002), consistent with maternal dependency. However, after May of the year following birth, as juveniles aged, many travelled farther and dove in deeper off-shelf waters. Increases in dive ability and trip duration and distance occurred coincident with seasonal oceanographic changes. These results emphasize the need for greater understanding of the determinants of prey abundance in the near-shore waters of the Aleutian Archipelago and its passes, as these small-scale features of the sea lions' environment are likely of considerable importance.

Call and Loughlin (2005) note that Steller sea lion rookeries are spaced, on average, at intervals of 108 km, though many were at distances of 60 km or less from each other. Steller sea lion females typically forage within 20 km of their rookeries during the breeding season (Merrick and Loughlin, 1997). Call and Loughlin (2005) suggest that the spacing of rookeries may reflect past competition between sea lions from neighbouring rookeries when populations were larger; the preference for foraging over shallow shelf waters would exacerbate this competition, particularly in the central and western Aleutians where many of the small islands have very restricted areas of shelf.

During the 2001 and 2002 cruises, several species of cetaceans were seen with sufficient frequency to permit assessment of their habitat preferences. At the scale of the central and eastern Aleutian Archipelago, humpback whales (*Megaptera novaeangliae*) were most common in the region between Samalga and Unimak Island, with only three of 259 individuals seen to the west of Samalga. In contrast, only one of 118 fin whales (*Balaenoptera physalus*) that was seen was west of Unimak Pass (Sinclair *et al.*, 2005). All sperm whales (*Physeter macrocephalus*) that were seen (56 individuals) were encountered to the west of Samalga, and killer (*Orcinus orca*) and minke whales (*B. acutorostrata*) were seen predominantly west of Unimak Pass. These patterns in cetacean distribution mirrored the spatial groupings of Steller sea lion rookeries based on similarity in diet composition and population trends (Sinclair *et al.*, 2005). Killer whales were encountered most frequently on the north side of the Aleutian Islands and in the vicinity of passes. Most killer whales identified to ecotype were of the resident, fish-eating type, and the few transient, mammal-eating types seen were in the Unimak Pass region, where grey whales (*Eschrichtius robustus*) and their calves were in migration into the Bering Sea (Sinclair *et al.*, 2005).

TEMPORAL VARIABILITY

Abundant recent evidence indicates that decadal-scale fluctuations in climate have affected zooplankton and fish populations in the northeastern Pacific Ocean and eastern Bering Sea (e.g. Brodeur and Ware, 1992; Piatt and Anderson, 1996; Mantua *et al.*, 1997; Hare and Mantua, 2000; Hollowed *et al.*, 2001; Wilderbuer *et al.*, 2002). Climate variability has impacted North Pacific fish populations for millennia (e.g. Baumgartner *et al.*, 1992; Finney *et al.*, 2002). Evidence is also accumulating that marine birds and mammals respond to these changes with shifts in diet or changes in population dynamics (Decker *et al.*, 1995; Hunt *et al.*, 1996; Springer, 1998; Hunt and Byrd, 1999; Trites *et al.*, 1999).

In the Aleutian Archipelago, Aleut middens dating to 3500 yr before present (yr BP) provide evidence for complex faunal changes over time (Causey *et al.*, 2005). Examination of the bones of marine birds consumed by the Aleuts shows that significant changes in the marine avifauna coincided with shifts in climatic conditions. Approximately 1800–2100 yr BP, during a period of cooling, piscivorous birds that feed offshore, such as kittiwakes and murres, increased in abundance, whereas between 650 and 1100 yr BP, a period of warming and increased precipitation,

near-shore foragers such as cormorants and parakeet auklets increased in abundance. Over three millennia, marine bird populations were negatively correlated with temperature and positively correlated with precipitation (Causey et al., 2005). Since the prehistoric period, there have been considerable changes in marine bird populations in the Aleutian Islands, with some species increasing locally whereas others have decreased (Causey et al., 2005).

Dramatic changes in the marine fauna of the Aleutian Archipelago were also recorded during historic times. Pacific cod and Atka mackerel were apparently rarely encountered at Attu Island prior to 1873, but were abundant there in 1878–81 (Turner, 1886). At Attu Island, capelin were said to be very abundant every third year, as may have been the case at Atka Island. At Atka Island, capelin were also abundant when Turner visited (1878–81), and 'dead fish [capelin, post-spawning] were so thick on the beach that it was impossible to walk without stepping on hundreds of them' (Turner, 1886, p. 102). Temporal variability in capelin abundance has also been inferred in the Bering Sea through examination of predator diets (Kajimura, 1984; Sinclair et al., 1994; Decker et al., 1995; Hunt et al., 1996). Capelin were once common at Unalaska Island (Jordan and Gilbert, 1899). In recent decades, capelin have been largely absent from Aleutian Island beaches, though in recent years there are some reports from the eastern Aleutian Islands of their returning in low numbers (G.V. Byrd, personal communication).

During historic times, there have been striking changes in the populations of marine mammals in the Aleutian Archipelago. Steller sea lion populations have gone through a series of declines. In the 1870s, Turner (1886, p. 98) noted that: 'The natives also assert that the coming of these fish [Atka mackerel in the 1870s] was coincident with the disappearance of the sea lion.' In recent years, sea lions have declined precipitously, with considerable controversy remaining as to the cause or causes of the population reduction (Trites et al., 1999, 2005; National Research Council, 2003; Springer et al., 2003; Sinclair et al., 2005). After recovering from near extinction from harvesting by Europeans, sea otters also have recently declined (Doroff et al., 2003; Estes et al., 2005), most likely due to predation by killer whales (Estes et al., 1998).
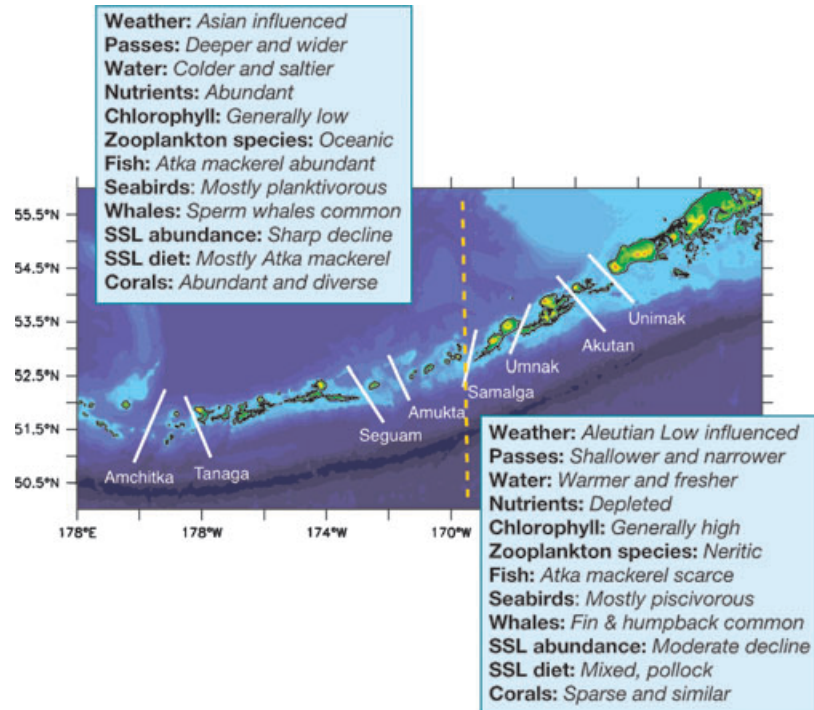
DISCUSSION

The findings reported in this volume support the hypothesis that there is significant spatial variation in the physical and biological properties of marine ecosystems along the Aleutian Archipelago (Fig. 3). These differences include the sources of water in the passes (Ladd et al., 2005a), the nutrient and chlorophyll content of those waters, (Mordy et al., 2005), the species composition of the zooplankton (Coyle, 2005), the distribution patterns and growth rates of fish species (Logerwell et al., 2005), the species composition and foraging ecology of seabird communities (Byrd et al., 2005; Jahncke et al., 2005), the food habits and distribution patterns of pinniped and cetacean species (Call and Loughlin, 2005; Sinclair et al., 2005) and the distribution of cold-water corals (Heifetz et al., 2005). Based on the earlier work of York et al. (1996) and Sinclair and Zeppelin (2002), scientists involved with planning the cruises in 2001 and 2002 to the Aleutian passes had predicted that there would be a difference in the availability of Steller sea lion prey species east and west of the Samalga Pass region. The magnitude of the changes and the number of aspects of the marine ecosystem that differed across Samalga Pass, however, were unexpected. Also unexpected was evidence for a transition in climate that roughly aligned with the ecological boundary at Samalga Pass.

In formulating the field research in 2001 and 2002, there was an expectation that the configuration of passes in the eastern (shallow and narrow) and central (wide and deep) Aleutian Islands might be an important factor in differentiating foraging opportunities for higher trophic level predators. However, the fieldwork failed to test this hypothesis adequately, as the shallow narrow passes investigated were all to the east of Samalga Pass and the wider, deeper passes were in the central Aleutians. The confounding variable of a profound ecosystem change at Samalga Pass had not been anticipated.

At least three hypotheses may explain the abrupt shift in ecosystem properties at Samalga Pass: the differences in width and depth of passes, the origins of water with differing physical and chemical properties in the passes east and west of Samalga Pass, and the shift from large islands on a relatively wide continental shelf in the east to small islands on relatively constrained shelves to the west. These hypotheses are not mutually exclusive, and, at present, we lack the data necessary to rank them in importance as contributors to ecological differentiation between the eastern and central Aleutian Archipelago. Both the source of water and shelf area would be expected to influence water chemistry (Mordy et al., 2005) and zooplankton composition (Coyle, 2005), and the configuration of the passes affects the presence of fronts, eddies, etc. that influence the aggregation of prey and its availability to marine birds and mammals (Fadely et al.,

Weather: *Asian influenced*
Passes: *Deeper and wider*
Water: *Colder and saltier*
Nutrients: *Abundant*
Chlorophyll: *Generally low*
Zooplankton species: *Oceanic*
Fish: *Atka mackerel abundant*
Seabirds: *Mostly planktivorous*
Whales: *Sperm whales common*
SSL abundance: *Sharp decline*
SSL diet: *Mostly Atka mackerel*
Corals: *Abundant and diverse*

Weather: *Aleutian Low influenced*
Passes: *Shallower and narrower*
Water: *Warmer and fresher*
Nutrients: *Depleted*
Chlorophyll: *Generally high*
Zooplankton species: *Neritic*
Fish: *Atka mackerel scarce*
Seabirds: *Mostly piscivorous*
Whales: *Fin & humpback common*
SSL abundance: *Moderate decline*
SSL diet: *Mixed, pollock*
Corals: *Sparse and similar*

Figure 3. Many Aleutian environmental attributes change in the vicinity of Samalga Pass, suggesting that the marine ecosystem of the archipelago may be differentiated into multiple, ecologically distinct regions.

2005; Jahncke *et al.*, 2005; Ladd *et al.*, 2005b; Vlietstra *et al.*, 2005).

Although the fieldwork in 2001 and 2002 on which many of the papers in this volume depend was constrained to the eastern and central Aleutian Archipelago, data from other sources suggest that there may be additional ecological divisions of significance in the archipelago. For example, Logerwell *et al.* (2005) show that there are significant changes in fish species distributions at some of the particularly deep, wide passes, and Springer *et al.* (1996) show that bird species composition and prey use differ at Buldir Island, in an 'oceanic' habitat, and at the Near Islands with a more neritic habitat. Fish species that have restricted movement patterns and tend to remain in a particular locale are likely to be particularly sensitive to ecological divisions (e.g. bottom-tending rockfish; Atka mackerel, MacDermott *et al.*, 2005). The decrease in species richness of fish of the Oregonian biogeographic province is not unexpected. The theory of island biogeography (MacArthur and Wilson, 1967) predicts decreasing species richness with increasing distance from source areas, even when there are habitat 'stepping stones' that diminish isolation (Wilson and Hunt, 1967). The effects of isolation from source areas have been demonstrated experimentally for a variety of marine species requiring 'hard' substrates, including fish and a variety of invertebrates (Schoener, 1974;

Molles, 1978; Hockin, 1982; Osman and Dean, 1987). New field studies, focused on the western portions of the archipelago, are required to resolve the existence and locations of additional ecological transitions in the Aleutians. These features are of significance to fisheries managers, as they may well demark the boundaries of separate stocks of fish or shellfish. Thus, Schumacher and Kruse (2005), who advocate the need to sustain the myriad benefits from the Aleutian Archipelago, suggest the development of an integrated ecosystem services management plan.

Although field measurements of primary production in 2001 and 2002 were insufficient to resolve large-scale geographic patterns in rates of primary production (Mordy *et al.*, 2005), data on sea lion population dynamics (York *et al.*, 1996), fish growth rates (Logerwell *et al.*, 2005) and ratios of stable isotopes of carbon (Schell *et al.*, 1998) suggest a decrease in the productivity of marine ecosystems as one progresses westward in the Aleutian Archipelago (Fig. 4). However, as Schell *et al.* (1998) pointed out, the depleted values of ^{13}C and ^{15}N in zooplankton of the western Aleutian Islands could indicate decreased primary productivity in the waters of the western Aleutian Islands, excess nutrient conditions there, or both. They reported nitrate concentrations in surface waters of the western Aleutians ranging between 14 and 30 μM, and phosphate concentrations of 1.2–2.2 μM

Figure 4. Ratios of the stable isotopes of carbon ^{12}C and ^{13}C expressed as $\delta^{13}C$ in copepods (top) and euphausiids (bottom). Higher values of $\delta^{13}C$ indicate regions with lower rates of primary production and/or plentiful macronutrients (from Schell et al., 1998).
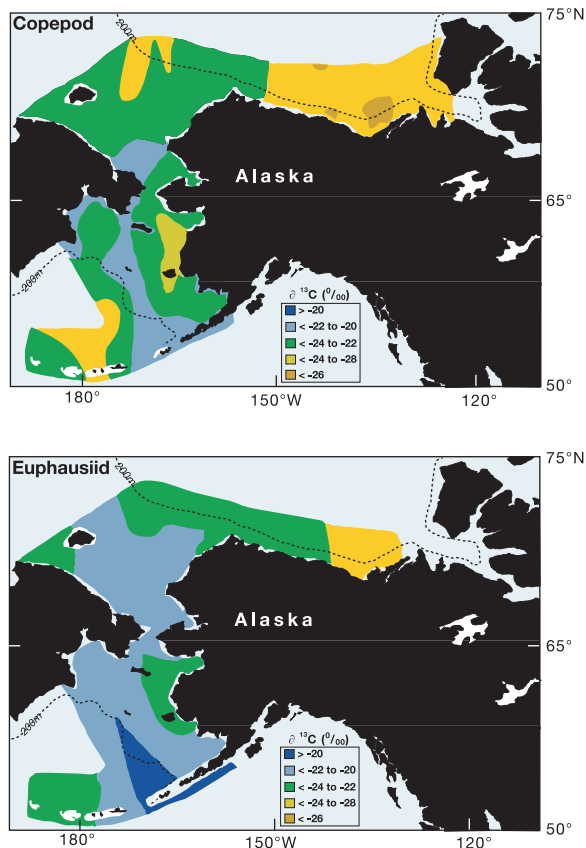
(see also Conkwright et al., 1994). Schell et al. (1998) suggest that a combination of heavy cloud cover and deep mixing in the western Aleutian passes could depress phytoplankton production despite the presence of high concentrations of macronutrients in surface waters. If this explanation is correct, these observations suggest that the great depth and width of many of the passes in the western Aleutian Archipelago have a critical impact on the productivity of the ecosystem. Alternatively, iron limitation in stratified surface waters of the Alaskan Stream could be a factor (Martin et al., 1989), though evidence to this effect is lacking. There remains a need to investigate further the spatial variability in rates of primary production and the underlying causes of this variability.

The abundance of prey and its availability to top predators such as marine birds and mammals varies at time scales as short as tidal cycles (Hunt et al., 1998; Ladd et al., 2005b; Vlietstra et al., 2005) and as long as

centuries and millennia (Finney et al., 2000, 2002; Causey et al., 2005). Of particular interest is the potential for rapid change in the availability of prey in the Aleutian Archipelago. Causey et al. (2005) cite a variety of reports by Turner (1886) of rapid changes in the abundance of Pacific cod and Atka mackerel, among other species, in the western Aleutian Islands. Similarly, in the early 1880s, Veniaminov (1984) reported striking decreases in the abundance of fish of several species, including cod at Unalaska Island. In the winter of 1825, '…cod…were floating half dead on the surface of the sea.' '…They floated on their side or belly-side up and were perfectly immobile. If touched…they would move slightly and sometimes made an effort to get away to the bottom' (Veniaminov, 1984, pp. 39–40).

Although we do not know the causes of these changes at Unalaska in the 1880s, they coincided with a period of exceptionally cold sea surface temperatures (Finney et al., 2000). The distribution of Pacific cod is sensitive to water temperature (http://www.fao.org/figis/servlet/species?fid=3011, May 2005), and cod may have migrated out of shallow coastal waters if water temperatures were exceptionally cold. Atlantic cod (G. moruhua) generally migrate offshore in winter to avoid low water temperatures; those that do stay inshore in sub-zero waters avoid freezing by developing antifreeze glycoproteins in response to low water temperatures (Fletcher et al., 1987; Ruzzante et al., 1996). Rodionov et al. (2005) show that, in recent decades, there has been a decrease in winter temperatures in the western Aleutians, and this may have affected the distribution or abundance of cod there.

Another source of physical forcing that could affect marine productivity is temporal change in the flow through the Aleutian passes and concomitant changes in the availability of nutrient and zooplankton inputs. Reed and Stabeno (1993) documented decreased flow of North Pacific water through the passes of the western Aleutian Islands. Whether these changes were related to climate forcing is not known, but changes in flow through the passes can directly impact the ecosystem by changing the availability of nutrients to primary producers and by affecting the advection and concentration of zooplankton and its availability to higher trophic level predators (Hunt et al., 1998).

An underlying motivation for the shipboard studies in 2001 and 2002 was the need to gain a broader understanding of the potential causes of the spatial and temporal changes in the endangered western population of the Steller sea lion. Steller sea lions show regional patterns in diet composition and population trends among the Aleutian Islands (York et al.,

1996; Sinclair and Zeppelin, 2002; Call and Loughlin, 2005). These patterns support the hypothesis that the Steller sea lions of the Aleutian Archipelago are divided into discrete subpopulations (meta-populations) and that the ecological conditions encountered by these subpopulations differ such that diets and population growth rates also differ. The information on the spatial heterogeneity of the marine ecosystems of the Aleutian Archipelago presented in this volume are concordant with the hypothesis that the difference in spatial patterns in sea lion diets and population dynamics reflect underlying differences in the productivity and abundances of prey species in the waters of the Aleutian Islands.

The material assembled in this volume has less to say about the possibility of temporal changes in the marine environment driving the recent changes in sea lion populations. It is clear that prey populations have varied, sometimes remarkably, in historic times, and that in at least one case, a dramatic decline in sea lion numbers was coincident with such a change (Turner, 1886). While we surmise that the spatial patterns may be related to bottom-up influences via diet (Sinclair *et al.*, 2005), we have no time series that would allow association of recent changes in sea lion populations with bottom-up aspects of the Aleutian marine environment.

The Aleutian Passes Project also collected data for assessing the potential of killer whales to exert top-down control on Steller sea lion populations in the eastern and central Aleutian Islands. Springer *et al.* (2003) hypothesized that with the loss of large whales from the North Pacific and Bering Sea marine ecosystems, transient, mammal-eating killer whales shifted their foraging from the large whales to smaller marine mammals including Steller sea lions. Veniaminov (1984) provided evidence that killer whales ate not only sea lions in the early 1800s, but also frequently attacked all species of large whales, in particular the Pacific right whale (*Eubalaena japonica*). During the 2001 and 2002 cruises, few transient killer whales were seen, and those were in the vicinity of Unimak Pass (Sinclair *et al.*, 2005). However, the lack of transient killer whales west of Unalaska Island cannot be taken as evidence that they were not capable of causing the decline in Steller sea lions there, or of preventing their recovery. Given the extremely low numbers of sea lions (York *et al.*, 1996) and sea otters (Doroff *et al.*, 2003; Estes *et al.*, 2005), little prey remains inshore in the Aleutian Archipelago to reward transient killer whales foraging there. Despite the importance to fisheries managers and the public of resolving the question of the relative importance of bottom-up and top-down determinants of the sea lion collapse, it remains very

difficult to identify the cause(s) of the decline and the subsequent failure of the western population of the Steller sea lion to recover its former numbers.

There is an increasing interest in shifting the focus of management of fishery resources from single species to a more holistic view incorporating a broad ecosystem context. The information assembled in this volume emphasizes the spatial and temporal complexities within which the resources harvested from the marine waters of the Aleutian Archipelago exist. Thus, to sustain the ecosystem services (food, fuel, fibres, spiritual, recreational, educational and other non-material benefits) provided by the marine ecosystem of the Aleutian Archipelago, Schumacher and Kruse (2005) recommend development of an integrated ecosystem services management plan. They emphasize the need to maintain a broad set of ecosystem services objectives rather than the traditional narrow focus on commercial fishery yields. An integrated ecosystem services management plan would require coordination of state and federal regulatory agencies with a broad stakeholder community involving commercial and recreational fishing, subsistence, conservation, oil and gas development, coastal development, shipping, tourism, and other interest groups.

CONCLUDING REMARKS

The Aleutian Passes Project investigated both bottom-up and top-down processes influencing faunal patterns observed along the Aleutian Islands (Byrd *et al.*, 2005; Call and Loughlin, 2005; Coyle, 2005; Fadely *et al.*, 2005; Jahncke *et al.*, 2005; Ladd *et al.*, 2005a,b; Mordy *et al.*, 2005; Sinclair *et al.*, 2005; Stabeno *et al.*, 2005; Vlietstra *et al.*, 2005). These studies, and others reported in this volume (Heifetz *et al.*, 2005; Logerwell *et al.*, 2005; McDermott *et al.*, 2005; Rodionov *et al.*, 2005), revealed unexpected spatial patterns in the physical and biological components of the marine ecosystems of the eastern and central Aleutian Archipelago, and the potential for additional spatial partitioning to exist in the western Aleutians. This spatial heterogeneity and the temporal variability seen in both the biological and human time series (Causey *et al.*, 2005) suggest that the marine environment of the Aleutian Islands is, and has been, far more variable than previously acknowledged. Additionally, there may be a cline in productivity, with lower rates of production in the west. This variability will need to be taken into account in developing ecosystem-based management of the living marine resources of the Aleutian Archipelago. The presence of ecological heterogeneity in marine habitats along the Aleutian

Archipelago raises the possibility that this spatial heterogeneity may also apply to the stock structure of many more species than those investigated here. Additionally, if the apparent cline in primary production is real, this would have important implications for fisheries management and the efforts to recover western Aleutian sea lion populations. Thus, there is an urgent need to understand the causes of this apparent cline in productivity and to learn how it will likely respond to climate change.

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