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Journal

Fisheries Oceanography, 14(s1)

ISSN

1054-6006

Authors

LADD, CAROL
JAHNCKE, JAIME
HUNT, GEORGE L
[et al.](#)

Publication Date

2005-11-01

DOI

10.1111/j.1365-2419.2005.00374.x

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Peer reviewed

Hydrographic features and seabird foraging in Aleutian Passes

CAROL LADD,^{1,*} JAIME JAHNCKE,²
GEORGE L. HUNT, JR.,^{2,†} KENNETH O. COYLE³
AND PHYLLIS J. STABENO¹

¹Joint Institute for the Study of the Atmosphere and Ocean,
University of Washington, Seattle, WA 98195-4235, USA

²Ecology and Evolutionary Biology Department, University of
California Irvine, Irvine, CA 92697-2525, USA

³Institute of Marine Science, University of Alaska Fairbanks,
Fairbanks, AK 99775-7220, USA

ABSTRACT

Strong tidal currents crossing over the abrupt topography of the Aleutian Passes result in regions with high horizontal property gradients. These frontal regions vary with the tidal cycle and form the boundary between vertically mixed and stratified regions. Concentrations of seabirds were associated with convergence zones in the mixed water (MW) and with the front between North Pacific (NP) water and MW. Species that were foraging by picking at prey from the surface were associated with surface convergences that appeared to be associated with Langmuir circulation cells or tidal features (all fulmar aggregations) in the central passes (Samalga, Seguam). In contrast, sub-surface foraging puffins and small alcids were mostly observed in areas of turbulent, well-mixed water near the shallow regions of the passes. Short-tailed shearwater flocks that were plunge-diving for prey were associated with the front between the NP water and MW in the passes. On our transects, we observed no significant aggregations of seabirds associated with Bering Sea water or NP water away from the frontal zones. The interaction of strong currents with bathymetric features results in zones of vertical advection, mixing, and surface convergences that make island passes attractive foraging regions for seabirds. Deep passes lacking these features, such as many of the passes in the western Aleutian Archipelago, are not as likely

to facilitate trophic transfer to top predators as shallow passes, such as those found in the eastern Aleutian Islands.

Key words: Aleutian Islands, Aleutian Passes, convergences, *Fulmarus glacialis*, northern fulmar, *Puffinus tenuirostris*, seabird foraging, short-tailed shearwater, tidal fronts, trophic transfer, zooplankton

INTRODUCTION

The Aleutian Archipelago comprises the boundary between the North Pacific (NP) Ocean and the Bering Sea (BS). This region supports an extremely rich ecosystem including many varieties of fish, marine mammals, and seabirds. The oceanography in the Aleutian Passes is highly dynamic, with intense tidal oscillations superimposed on highly variable, lower frequency currents (Stabeno *et al.*, 2005). The combination of strong, variable currents, abrupt topography, and distinct water masses from two separate ocean basins results in numerous fronts separating mixed and stratified regions.

The physical features inherent in such a dynamic environment (fronts, eddies, tidal rips, etc.) influence seabird prey distributions (e.g. Hunt *et al.*, 1998, 1999). Their zooplankton prey can be concentrated either in the vertical (at the pycnocline in stratified water; Cooney, 1989; Fragopoulou and Lykakis, 1990; Hunt *et al.*, 1990), or as horizontal patches (Hunt *et al.*, 1998). Surface convergences concentrate floating or weakly swimming organisms at the surface (Franks, 1992), and tidal currents interacting with bathymetry result in the upwelling of zooplankton near the bottom (Wolanski and Hamner, 1988). Vertically migrating zooplankton can become concentrated when they swim against currents (Simard *et al.*, 1986; Coyle *et al.*, 1992). Or, prey may be advected into shallower regions to become trapped against the bottom (Genin *et al.*, 1988; Hunt *et al.*, 1996).

Considerable variation in the abundance and species composition of seabirds has been observed in the Aleutian Passes (Jahncke *et al.*, 2005), and seabird distribution within the passes is patchy. The eastern passes (Unimak, Akutan, and Umnak) are narrower and shallower than the central passes (Samalga, Seguam and Tanaga) (Ladd *et al.*, 2005). In addition,

*Correspondence. e-mail: carol.ladd@noaa.gov

†Present address: School of Aquatic and Fishery Sciences, Box 355020 University of Washington, Seattle, WA 98195–5020, USA.

Received 15 December 2003

Revised version accepted 20 August 2004

the eastern and central passes have been shown to have different water properties (eastern: coastal; central: oceanic; Ladd *et al.*, 2005), zooplankton species composition (eastern: neritic; central: oceanic; Coyle, 2005), and seabird species composition and diet (eastern: dominated by shearwaters; central: dominated by fulmars; Jahncke *et al.*, 2005).

In this study, we investigated the hydrographic structure of the water masses and frontal features within the eastern and central Aleutian passes, with focus on Unimak, Akutan, Seguam and Tanaga Passes (Fig. 1). We examined the relationships between physical features and the distribution of aggregations of foraging seabirds. Our analyses focused on the most abundant seabird species that exhibited significant foraging aggregations: short-tailed shearwater (*Puffinus tenuirostris*), northern fulmar (*Fulmarus glacialis*), ancient murrelets (*Synthliboramphus antiquum*), least auklets (*Aethia pusilla*), whiskered auklets (*Aethia pygmaea*), and tufted puffins (*Fraterecula cirrhata*).

METHODS

The eastern and central Aleutian Passes were visited in May and June of 2001 and 2002 (Fig. 1; Table 1). On multiple transects through the passes, we recorded hydrographic structure (salinity and temperature), zooplankton distributions (MOCNESS and CalVET net tows and acoustics), and seabird distributions (systematic seabird surveys).

Conductivity, temperature, and depth (CTD) casts were taken with a Sea-Bird SBE-911 Plus system (Sea-Bird Electronics, Inc., Bellevue, WA, USA). Salinity calibration samples were taken on all casts and analyzed on a laboratory salinometer. Underway surface temperature and salinity were collected with a Sea-Bird Electronics thermosalinograph installed in the ship's seachest. Note that a full transect takes approximately 7–12 h, and, therefore, observations at one end of the transect are taken on a different tidal phase than those

at the other end of the transect. The direction of the tides influences the position of the observed fronts. Tidal phase and time of change on each transect is noted in Table 1. For details on physical measurements, their calibration and analysis, see Ladd *et al.* (2005).

Acoustic data were collected using a Hydroacoustic Technology Inc. (HTI) model 244 split-beam digital system (Hydroacoustic Technology, Inc., Seattle, WA, USA). During 2001, the acoustic data were collected with four transducers: a 420-kHz 6° single beam, and 43-kHz 7°, 120-kHz 6° and 200-kHz 3° split-beam transducers. During 2002, the data were collected with 420-kHz 3°, 120-kHz 6°, and 200-kHz 3° split-beam transducers. The transducers were towed beside the vessel at about 3 m s⁻¹ in a dead-weight tow body about 4 m from the hull and 2 m below the surface. Acoustic transects were run through the passes during the day in the direction of current flow. The system collected 20 log R data for echo integration using 15-s time intervals and 1-m depth intervals resulting in a sample interval of about 45 m. The acoustic data were converted from volume scattering to estimates of acoustically determined zooplankton biomass (ADB) by direct comparison of net data as discussed by Coyle (2005).

Interpretation of acoustic data is complicated by the fact that the density of sound-scattering organisms is a function of both the time of day that the acoustics were collected and the water-column properties. The data from Unimak Pass, for example (not shown), show high concentrations of zooplankton on the north side of the pass because the data were collected when it was starting to get dark. In addition, acoustic determination of biomass in convergence zones is confounded by the entrainment of bubbles, which scatter sound and produce artefacts in the data. An example was observed in Akutan Pass, where flow through the pass was sufficient to generate this artefact. It is therefore necessary to eliminate data from strong convergence zones to avoid misinterpretation of the results. Because of the above complications, simple correlations between

Figure 1. Map of eastern and central Aleutian Islands. Passes discussed in the text are noted by white lines. Currents are noted by black arrows. Water depth is colour coded from light blue (shallow) to dark purple (deep).

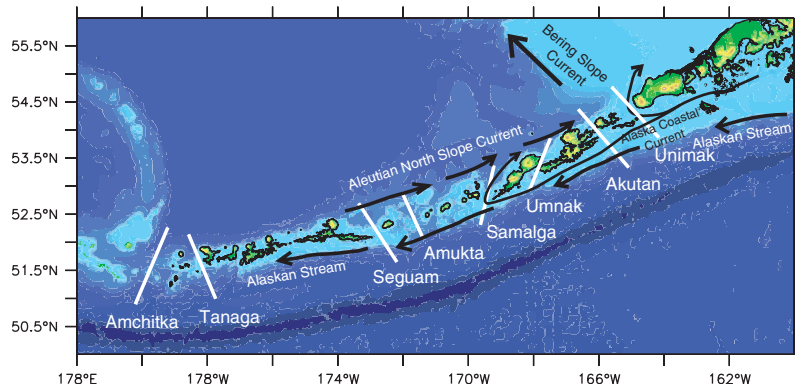


Table 1. List of all transects carried out along passes in 2001 and 2002.

Pass	Transect	Date	Survey	Start of transect			End of transect			Number of foraging seabirds							
				Time [†]	Latitude (°N)	Longitude (°W)	Tide	Change of tide*	Time [†]	Latitude (°N)	Longitude (°W)	Tide	Distance (km)	Shearwater	Fulmar	Puffin	Auklet [‡]
Unimak	UN0101	June 18, 2001	CTD	06:32	54°33.45'	165°47.86'	Ebb	12:15	16:53	54°08.28'	164°15.87'	Flood	110	1539	11	75	9
	UN0102	June 18, 2001	Acoustic	17:14	54°08.25'	164°15.57'	Flood	20:45–22:15	03:38 [§]	54°31.30'	165°39.99'	Flood	100	8	0	25	1
Akutan	AK0103	June 14, 2001	CTD	11:31	54°08.00'	166°26.41'	Flood	13:45	17:46	53°56.30'	165°45.07'	Ebb	50	9510	4	60	1182
	AK0104	June 14, 2001	Acoustic	19:28	53°56.28'	165°44.74'	Flood	NA	23:44	54°08.19'	166°26.87'	Flood	51	41	1	57	222
Amukta	AM0105	June 15, 2001	CTD	06:57	54°09.11'	166°30.71'	Ebb	08:45	14:12	53°54.14'	165°36.74'	Flood	65	5833	17	108	52
	AM0106	June 12, 2001	CTD	07:06	52°37.14'	171°50.15'	Flood	10:15–16:45	19:31	52°02.66'	171°41.94'	Flood	65	0	7	3	6
Seguam	SG0107	June 10, 2001	CTD	08:07	52°21.05'	172°59.06'	Ebb	15:15	20:27	51°54.25'	172°22.73'	Flood	66	1	721	13	37
	SG0108	June 11, 2001	Acoustic	10:38	52°23.17'	173°02.00'	Ebb	16:15	18:39	51°54.07'	172°22.52'	Flood	70	3	934	12	23
Unimak	UN0201	May 20, 2002	Acoustic	07:44	54°31.18'	165°39.60'	Flood	13:53–20:44	23:46	54°00.29'	163°46.79'	Ebb	105	414	8	24	20
	UN0202	May 25, 2002	CTD	09:40	54°33.63'	165°48.19'	Ebb	13:42	22:26	54°04.83'	164°03.40'	Flood	125	15	4	58	76
Akutan	AK0203	June 12, 2002	Acoustic	06:22	54°30.04'	165°35.43'	Flood	07:52	15:00	54°05.97'	164°07.54'	Flood	87	602	3	133	42
	UN0204	June 12, 2002	CTD	15:04	54°05.98'	164°07.64'	Ebb	15:40	23:05	54°30.09'	165°35.44'	Flood	95	120	2	184	18
Akutan	AK0205	May 22, 2002	CTD	07:29	54°09.15'	166°30.62'	Flood	15:53	18:52	53°48.28'	165°16.28'	Ebb	90	0	0	50	39
	AK0206	May 24, 2002	Acoustic	07:29	54°09.19'	166°30.65'	Ebb	NA	11:26	53°58.45'	165°52.35'	Ebb	46	0	0	16	10
Akutan	AK0207	May 26, 2002	Acoustic	07:21	53°48.27'	165°16.18'	Ebb	NA	13:32	53°55.79'	165°43.00'	Ebb	33	0	5	5	1
	AK0208	June 15, 2002	CTD	13:49	54°09.25'	166°30.59'	Ebb	16:52	22:27	53°48.34'	165°15.92'	Flood	90	0	2	166	23
Unimak	UM0209	June 16, 2002	Acoustic	05:00	53°48.14'	165°15.55'	Flood	10:33	13:25	54°09.16'	166°30.68'	Ebb	91	0	31	218	50
	UM0210	June 10, 2002	CTD	10:07	53°38.13'	167°40.88'	Ebb	14:30	15:55	53°07.19'	167°55.94'	Flood	65	0	0	427	136
Samalga	UM0211	June 10, 2002	Acoustic	16:28	53°07.18'	167°55.83'	Flood	NA	20:53	53°33.44'	167°39.94'	Flood	46	0	0	232	145
	SA0212	June 7, 2002	CTD	12:36	53°05.36'	169°16.71'	Flood	NA	16:49	52°49.37'	169°28.17'	Flood	32	0	450	1	0
Amukta	SA0213	June 8, 2002	CTD	09:34	52°28.18'	169°21.83'	Ebb	13:11	15:04	52°49.36'	169°28.08'	Flood	40	2	1827	8	6
	SA0214	June 9, 2002	Acoustic	07:37	52°28.33'	169°21.79'	Ebb	13:51	19:29	53°00.42'	169°22.41'	Flood	46	0	45	6	0
Seguam	AM0215	June 5, 2002	Acoustic	11:44	52°02.66'	171°41.80'	Flood	15:15	19:58	52°45.26'	171°51.96'	Ebb	80	2	11	6	3
	AM0216	June 5, 2002	CTD	21:32	52°45.33'	171°52.02'	Flood	03:15	08:44 [¶]	52°10.65'	171°43.64'	Ebb	65	N	N	N	N
Tanaga	SG0217	June 2, 2002	CTD	12:29	52°27.73'	173°07.48'	Ebb	17:45	22:50	51°52.07'	172°19.87'	Flood	85	0	380	20	6
	SG0218	June 3, 2002	Acoustic	09:18	52°27.20'	173°07.44'	Flood	13:00	17:33	51°52.03'	172°19.88'	Ebb	85	141	3008	53	95
Tanaga	TN0219	May 29, 2002	Acoustic	12:56	51°25.64'	177°44.75'	Ebb	14:57	22:28	52°04.26'	178°29.08'	Flood	100	0	2	8	10 417
	TN0220	May 30, 2002	CTD	09:14	52°03.97'	178°28.81'	Ebb	15:42	21:38	51°26.71'	177°48.74'	Flood	93	0	12	8	1621

NA, not applicable; N, survey conducted at night.

*Change of tide approximated from tidal charts from nearest pass with information.

†Times noted in Hawaii-Aleutian Daylight Time (UTC-9).

‡Total number includes ancient murrelets, least and whiskered auklets.

§Transect finished on June 19, 2001.

¶Transect finished on June 6, 2002.

seabird concentrations and acoustically determined biomass will not necessarily be observed.

Data on the distribution and abundance of seabirds were obtained by counting seabirds from the bridge of the R/V *Alpha Helix* (eye height = 7.7 m above the sea surface) while the ship was underway. Vessel speed varied from 11 to 19 km h⁻¹, depending on whether we were conducting acoustic or CTD surveys. Birds were counted continuously during daylight hours in a 300-m arc from directly ahead of the vessel to 90° off the side with best visibility (i.e. lowest glare) and were logged into a portable computer. Observers switched to a snapshot method of counting when large aggregations of birds (>1000 individuals) were encountered crossing the bow of the vessel (Tasker *et al.*, 1984). Seabird behaviors were recorded as flying, sitting on the water, and feeding. Seabirds sitting on the water were assumed to be about to forage, or to be resting from a previous foraging bout.

We divided the transects through the passes into non-overlapping regions based on hydrographic features such as stratification and frontal structures. In the majority of transects, surface density exhibited three regions with fairly constant surface density separated by two fronts (regions of high horizontal gradients in surface density). We called the northernmost water mass BS water, the water mass in the center of the pass mixed water (MW), and the southern water mass NP water. The NP water is derived from Alaska Coastal Current water in the eastern passes (Unimak, Akutan, Umnak and Samalga) and Alaskan Stream water in the central passes (Seguam and Tanaga) (Ladd *et al.*, 2005). The front separating the BS water from the MW is called the BS/MW front, while the front separating the MW from the NP water is called the NP/MW front. The locations of the frontal regions were calculated as the locations of high horizontal gradient in surface density from the underway system. Where the frontal regions were not well defined, we note that information in Tables 2–5. The width of the frontal regions was extended 1 km to the north and south of each front to include seabirds foraging in the vicinity of the front.

We used the utilization test to examine the significance of seabird use of the different water masses and frontal features (Haney and Solow, 1992). Assuming a uniform distribution of seabirds along each transect, we calculated an expected value for the number of seabirds that should have occurred within each water mass and frontal area. This expected value is based on the total number of seabirds counted along the transect and the amount of survey effort (km surveyed) spent in each area. Observed values were compared with expected values, and 95% confidence intervals

were constructed according to the methods of Neu *et al.* (1974) for the observed proportions of birds for a type I error rate of ± 0.05 . We conducted the analyses separately on each transect surveyed.

We used permutation analysis (Riehle *et al.*, 2001) to determine the location of significant aggregations of seabirds along transects where no clear water masses were identified. We determined the observed density of birds based on a 5-km (50 100-m bins) sliding window that moved through the series of data. The expected density of birds and the confidence intervals were obtained by using a permutation testing procedure. The mean, variance and 95% confidence intervals in density of birds were calculated over 500 random permutations of the order of 500 100-m bins sampled from the remaining length of the transect. Bird aggregations were considered significantly higher when densities within the sliding window were larger than the 95% confidence interval estimated for the remainder of the transect.

RESULTS

Shallow, eastern passes (<100 m deep)

Unimak Pass

Unimak Pass is the first pass encountered by the Alaska Coastal Current as it flows westward along the shelf of the NP. The shallowest part of the pass is <80 m deep and, at its narrowest, it is approximately 20 km wide. On the NP side of Unimak Pass, the shelf is wide, and our surveys did not reach the shelf break. On the BS side of the pass, the depth drops dramatically from approximately 100 m within the pass to >400 m in <10 km (Fig. 2). Six transects through Unimak Pass were sampled (two in 2001 and four in 2002) with three CTD and three acoustic transects (Table 1). The longest transect surveyed in Unimak Pass was approximately 125 km.

North Pacific water, with its warm, low-salinity, low-density signature, was observed on the south side of Unimak Pass while cooler, saltier, denser BS water was observed at the north end of the pass (see Fig. 2 for an example transect). Because of its low density, the NP water intruded into the pass in the top 20–40 m overlying a strong pycnocline. A region of reduced stratification (MW) was often observed near the shallowest part of Unimak Pass. Surface density in the center of the pass was generally higher than the NP surface water and lower than the surface BS water (Fig. 2d). That density structure, along with temperature and salinity properties, suggests that the water in the middle of Unimak Pass was primarily a result of

Table 2. Proportion of shearwaters, expected abundance (in parentheses) and 95% confidence interval on the proportion of birds observed in each identified region along the transect.

Pass	Transect	Seabirds counted	Distance surveyed	Location				
				Bering Sea water	BS/MW front	MW	NP/MW front	NP water
Unimak	UN0101	1539	106	0.01 (0.28)	<0.01 (0.06)	0.03 (0.29)	0.93 (0.15)	0.04 (0.23)
	UN0201	414	121	$0.00 \leq X_i \leq 0.01^*$	$0.00 \leq X_i \leq 0.00^*$	$0.02 \leq X_i \leq 0.04^*$	$0.92 \leq X_i \leq 0.95^\dagger$	$0.02 \leq X_i \leq 0.05^*$
	UN0203	602	97	No identifiable physical features [‡]	Not encountered	0.38 (0.65)	0.62 (0.02)	No birds (0.33)
Akutan	UN0204	120	97	Not encountered	Not encountered	$0.33 \leq X_i \leq 0.43^*$	$0.57 \leq X_i \leq 0.67^\dagger$	$0.00 \leq X_i \leq 0.00^*$
	AK0103	9510	39	No birds (0.14)	No birds (0.09)	0.51 (0.64)	0.49 (0.11)	No birds (0.25)
	AK0105	5833	61	$0.00 \leq X_i \leq 0.00^*$	$0.00 \leq X_i \leq 0.00^*$	$0.40 \leq X_i \leq 0.63^*$	$0.37 \leq X_i \leq 0.6^\dagger$	$0.00 \leq X_i \leq 0.00^*$
Seguam	SG0218	141	84	No birds (0.07)	No birds (0.03)	<0.01 (0.55)	1.00 (0.10)	<0.01 (0.11)
				$0.00 \leq X_i \leq 0.00^*$	$0.00 \leq X_i \leq 0.00^*$	$0.00 \leq X_i \leq 0.00^*$	$1.00 \leq X_i \leq 1.00^\dagger$	$0.00 \leq X_i \leq 0.00^*$
				No birds (0.40)	0.09 (0.03)	0.34 (0.56)	0.63 (0.06)	0.03 (0.25)
				$0.00 \leq X_i \leq 0.00^*$	$0.00 \leq X_i \leq 0.00^*$	$0.32 \leq X_i \leq 0.35^*$	$0.62 \leq X_i \leq 0.65^\dagger$	$0.02 \leq X_i \leq 0.03^*$
				0.19 $\leq X_i \leq 0.39^*$	$0.02 \leq X_i \leq 0.15^{ns}$	0.62 (0.37)	No birds (0.05)	No birds (0.16)
						$0.52 \leq X_i \leq 0.73^\dagger$	$0.00 \leq X_i \leq 0.00^*$	$0.00 \leq X_i \leq 0.00^*$

ns, No significant differences in use.

*Significantly ($P < 0.05$) lower use than expected.

†Significantly greater use than expected.

‡Significantly high densities of shearwaters at the northern end of the transect near 54.5°N, not associated with an evident front.

Table 3. Proportion of ancient murrelets (ANMU), least auklets (LEAU) and whiskered auklets (WHAU), expected abundance (in parentheses) and 95% confidence interval on the proportion of birds observed in each identified region along the transect.

Pass	Transect	Species	Seabirds counted	Distance surveyed	Location				
					Bering Sea water	BS/MW front	MW	NP/MW front	NP water
Unimak	UN0202	ANMU	76	126	No birds (0.30) $0.00 \leq X_i \leq 0.00^*$	No identifiable frontal region No birds (0.09)	0.71 (0.46) $0.58 \leq X_i \leq 0.84^\dagger$	No identifiable frontal region No birds (0.10)	0.29 (0.25) $0.16 \leq X_i \leq 0.42^{ns}$
	AK0103	ANMU	72	39	No birds (0.14) $0.00 \leq X_i \leq 0.00^*$	No birds (0.09) $0.00 \leq X_i \leq 0.00^*$	1.00 (0.55) $1.00 \leq X_i \leq 1.00^\dagger$	No birds (0.11) $0.00 \leq X_i \leq 0.00^*$	
	AK0103	WHAU	1110	39	No birds (0.14) $0.00 \leq X_i \leq 0.00^*$	No birds (0.09) $0.00 \leq X_i \leq 0.00^*$	1.00 (0.55) $1.00 \leq X_i \leq 1.00^\dagger$	No birds (0.11) $0.00 \leq X_i \leq 0.00^*$	
	AK0104	WHAU	206	35	Not encountered	Not encountered	0.82 (0.73) $0.75 \leq X_i \leq 0.89^\dagger$	No birds (0.15) $0.00 \leq X_i \leq 0.00^*$	
Umnak	UM0210	ANMU	134	62	No identifiable physical features [‡]				
	UM0211	ANMU	143	57	No identifiable physical features [§]				
Tanaga	TN0219	LEAU	10384	101	0.11 (0.49) $0.10 \leq X_i \leq 0.11^*$	<0.01 (0.02) $0.00 \leq X_i \leq 0.00^*$	0.89 (0.27) $0.89 \leq X_i \leq 0.90^\dagger$	No birds (0.20) $0.00 \leq X_i \leq 0.00^*$	
	TN0220	LEAU	1593	93	0.10 (0.46) $0.08 \leq X_i \leq 0.12^*$	0.03 (0.06) $0.02 \leq X_i \leq 0.04^*$	0.88 (0.21) $0.85 \leq X_i \leq 0.90^\dagger$	No birds (0.09) $0.00 \leq X_i \leq 0.00^*$	

ns, No significant differences in use.

*Significantly ($P < 0.05$) lower use than expected.

†Significantly greater use than expected.

‡Significantly high densities of ancient murrelets found at the central region of transect in the vicinity of 53.5°N, not associated with evident feature.

§Significantly high densities of ancient murrelets found at the northern and central regions of transect in the vicinity of 53.5 and 53.4°N, likely associated with convergence areas.

Table 4. Proportion of tufted puffins, expected abundance (in parentheses) and 95% confidence interval on the proportion of birds observed in each identified region along the transect.

Pass	Transect	Seabirds counted	Distance surveyed	Location				
				Bering Sea water	BS/MW front	MW	NP/MW front	NP water
Unimak	UN0101	75	106	0.07 (0.28)	No birds (0.06)	No birds (0.29)	0.71 (0.15)	0.23 (0.23)
	UN0202	58	126	$0.00 \leq X_i \leq 0.14^*$ No birds (0.30)	$0.00 \leq X_i \leq 0.00^*$ No identifiable frontal region	$0.00 \leq X_i \leq 0.00^*$ 0.72 (0.46)	$0.57 \leq X_i \leq 0.84^\dagger$ No identifiable frontal region	$0.10 \leq X_i \leq 0.35^{ns}$ 0.28 (0.25)
	UN0203	133	97	$0.00 \leq X_i \leq 0.00^*$ Not encountered	Not encountered	$0.57 \leq X_i \leq 0.87^\dagger$ 0.76 (0.65)	0.08 (0.02)	$0.13 \leq X_i \leq 0.43^{ns}$ 0.16 (0.33)
	UN0204	184	97	Not encountered	Not encountered	$0.66 \leq X_i \leq 0.85^\dagger$ 0.84 (0.64)	$0.02 \leq X_i \leq 0.14^{ns}$ 0.13 (0.11)	$0.08 \leq X_i \leq 0.24^*$ 0.03 (0.25)
Akutan	AK0103	60	39	0.02 (0.14)	0.05 (0.09)	$0.77 \leq X_i \leq 0.91^\dagger$ 0.75 (0.55)	$0.07 \leq X_i \leq 0.19^{ns}$ 0.08 (0.10)	$0.00 \leq X_i \leq 0.07^*$ 0.10 (0.11)
	AK0104	57	35	$0.00 \leq X_i \leq 0.06^*$ Not encountered	$0.00 \leq X_i \leq 0.12^{ns}$ Not encountered	$0.61 \leq X_i \leq 0.89^\dagger$ 0.81 (0.73)	$0.00 \leq X_i \leq 0.18^{ns}$ 0.09 (0.12)	$0.00 \leq X_i \leq 0.20^{ns}$ 0.11 (0.15)
	AK0105	108	61	0.01 (0.07)	0.02 (0.07)	$0.67 \leq X_i \leq 0.94^{ns}$ 0.94 (0.56)	$-0.01 \leq X_i \leq 0.18^{ns}$ 0.03 (0.06)	$0 \leq X_i \leq 0.21^{ns}$ 0.01 (0.25)
	AK0205	50	90	$0.00 \leq X_i \leq 0.03^*$ Not encountered	$0.00 \leq X_i \leq 0.05^*$ Not encountered	$0.87 \leq X_i \leq 1.00^\dagger$ 0.96 (0.59)	$0.00 \leq X_i \leq 0.07^{ns}$ No birds (0.04)	$0.00 \leq X_i \leq 0.03^*$ 0.04 (0.37)
Umnak	AK0208	165	89	0.10 (0.15)	0.18 (0.04)	$0.89 \leq X_i \leq 1.03^\dagger$ 0.69 (0.44)	$0.00 \leq X_i \leq 0.00^*$ No birds (0.06)	$0.00 \leq X_i \leq 0.11^*$ 0.03 (0.30)
	AK0209	218	70	$0.04 \leq X_i \leq 0.16^{ns}$ Not encountered	$0.10 \leq X_i \leq 0.25^\dagger$ Not encountered	$0.60 \leq X_i \leq 0.79^\dagger$ 1.00 (0.84)	$0.00 \leq X_i \leq 0.00^*$ No birds (0.07)	$0.00 \leq X_i \leq 0.06^*$ No birds (0.09)
	UM0210	427	62	No identifiable physical features [†]	physical features [†]	1.00 $\leq X_i \leq 1.00^\dagger$	$0.00 \leq X_i \leq 0.00^*$	$0.00 \leq X_i \leq 0.00^*$
Sequam	UM0211	232	57	No identifiable physical features [§]	physical features [§]	0.68 (0.37)	0.02 (0.05)	0.04 (0.16)
	SC0218	53	84	0.23 (0.40)	0.04 (0.03)	$0.51 \leq X_i \leq 0.84^\dagger$	$0.00 \leq X_i \leq 0.07^{ns}$	$0.00 \leq X_i \leq 0.11^*$

ns, No significant differences in use.

*Significantly ($P < 0.05$) lower use than expected.

†Significantly greater use than expected.

‡Significantly high densities of puffins in the central region of transect in the vicinity of 53.3°N, foraging over a strong tide rip area.

§Significantly high densities of puffins found in the northern region of transect north of 53.4°N, likely associated with convergence areas.

Table 5. Proportion of northern fulmars, expected abundance (in parentheses) and 95% confidence interval on the proportion of birds observed in each identified region along the transect.

Pass	Transect	Seabirds counted	Distance surveyed	Location				
				Bering Sea water	BS/MW front	MW	NP/MW front	NP water
Samalga	SA0212	450	41	No identifiable physical features*				
	SA0213	1827	43	No identifiable physical features†				
	SG0107	721	98	0.01 (0.10)	0.06 (0.08)	0.88 (0.43)	0.03 (0.03)	0.01 (0.35)
Seguam	SG0108	934	70	0.00 ≤ X_i ≤ 0.02‡	0.04 ≤ X_i ≤ 0.08‡	0.85 ≤ X_i ≤ 0.91§	0.02 ≤ X_i ≤ 0.05 ^{ns}	0.00 ≤ X_i ≤ 0.02‡
	SG0217	380	67	0.04 (0.34)	0.28 (0.30)	0.54 (0.17)	0.08 (0.03)	0.06 (0.16)
	SG0218	3008	84	0.02 ≤ X_i ≤ 0.05‡	0.25 ≤ X_i ≤ 0.32 ^{ns}	0.50 ≤ X_i ≤ 0.58§	0.06 ≤ X_i ≤ 0.10§	0.04 ≤ X_i ≤ 0.08‡
				0.01 (0.42)	0.24 (0.03)	0.74 (0.50)	0.02 (0.05)	Not encountered
				0.00 ≤ X_i ≤ 0.02‡	0.18 ≤ X_i ≤ 0.29§	0.68 ≤ X_i ≤ 0.79§	0.00 ≤ X_i ≤ 0.03‡	<0.01 (0.16)
				0.30 (0.40)	0.08 (0.03)	0.62 (0.37)	<0.01 (0.05)	0.00 ≤ X_i ≤ 0.00‡
				0.28 ≤ X_i ≤ 0.32‡	0.07 ≤ X_i ≤ 0.09§	0.6 ≤ X_i ≤ 0.64§	0.00 ≤ X_i ≤ 0.01‡	

^{ns}, No significant differences in use.

*Significantly high densities of fulmars between the northern and central regions of transect near 52.9°N, fulmars were lined up on Langmuir cells.

†Significantly high densities of fulmars at central region of transect in the vicinity of 52.8°N, fulmars were foraging in tight flocks over water slicks.

‡Significantly ($P < 0.05$) lower use than expected.

§Significantly greater use than expected.

lateral mixing between shallow NP and BS waters (Ladd *et al.*, 2005).

Surface density in Unimak Pass often exhibited sharp horizontal gradients (fronts) that were usually apparent in both temperature and salinity. Occasionally, however, fronts were only apparent in the surface salinity, while the surface temperature exhibited no strong gradient. The strength and position of the surface expression of the fronts and the width of the frontal regions varied in time. The fronts sometimes represented the boundaries between two of the three water masses (NP, MW, and BS), but the fronts may have also indicated transient eddies and/or other features. Multiple surface density fronts in Unimak Pass may have been the result of pulses of NP water advecting through the pass on different phases of the tides. These pulses were often too small to be resolved by the CTD station spacing, but were apparent in the surface temperature and salinity measured by the underway system. In Unimak Pass, the NP/MW front was usually stronger and narrower than the BS/MW front.

In Unimak Pass, foraging and sitting shearwaters were significantly concentrated (Utilization test, $P < 0.05$) in the vicinity of the NP/MW front (Table 2). Approximately 1400 shearwaters were found aggregated just on the MW side of the NP/MW front on June 18, 2001 (UN0101; Fig. 2; Table 2). This location also coincided with the shallowest point in the transect. South of the front, the water column was stratified with a warmer, fresher ($>7.5^\circ\text{C}$, <31.7 psu) surface layer approximately 20 m deep (Fig. 2f,g). Surface density in this stratified region exhibited two additional fronts that may have indicated a small (<10 -km diameter), cyclonic eddy (Fig. 2d). No shearwaters were associated with this feature (Fig. 2a). In the MW region, temperature and salinity were well mixed to the bottom (5.7°C , 32.0 psu, 64 m depth).

On another occasion, an aggregation of approximately 375 shearwaters was observed sitting on the water just on the mixed-water side of the NP/MW front (UN0203; Table 2). Six hours later, on a second transect through Unimak Pass (UN0204), an aggregation of approximately 55 shearwaters was observed sitting on the water over the NP/MW front that was approximately 3 km north of its previous location. The northward shift in the location of the front was due to the direction of the tidal currents changing from southward flowing during our observation of the NP/MW frontal region of the first transect to northward flowing during the second.

On May 20, 2002, a significant aggregation (Permutation analysis, $P < 0.05$) of shearwaters (approximately 230 birds) was found at the northern end of the

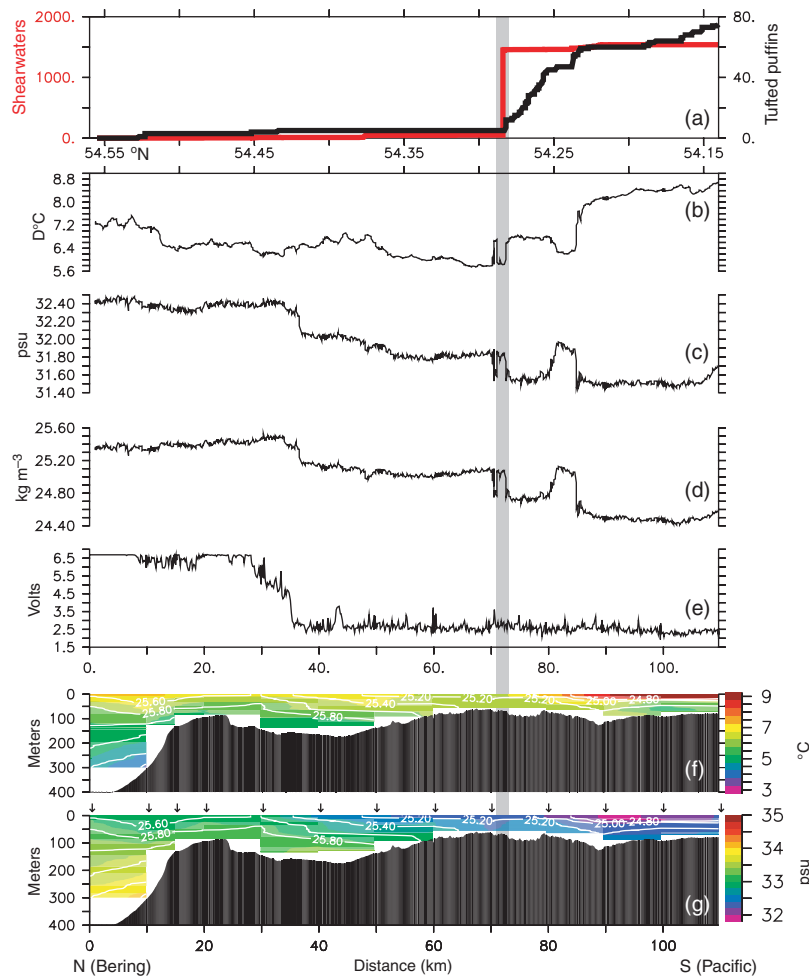


Figure 2. CTD transect through Unimak Pass on June 18, 2001 (UN0101). (a) Accumulated number of seabirds from the northern end of the transect, (b) SST ($^{\circ}\text{C}$) from thermosalinograph, (c) surface salinity from thermosalinograph, (d) surface density (kg m^{-3}), (e) surface fluorescence (volts), (f) CTD temperature (colour scale: $^{\circ}\text{C}$), (g) CTD salinity (colour scale: psu). Arrows show locations of CTD casts. White contours in bottom two plots are σ_t density (kg m^{-3}). Grey shading marks shearwater aggregation and associated physical features.

transect (UN0201; Table 2). The location of the birds coincided with the highest fluorescence in the transect, which may have attracted grazing euphausiids, a principal prey of the shearwaters in this area (Jahncke *et al.*, 2005).

Two species of pursuit-diving seabirds, ancient murrelets, and tufted puffins showed significant aggregations over the MW of Unimak Pass (Tables 2 and 3). Feeding and sitting ancient murrelets were significantly aggregated over the MW in 2002 (UN0202: 54 birds, Table 3), as were tufted puffins (Utilization test, $P < 0.05$, Table 4) in 2001 and 2002. An exception to this pattern was observed in 2001 (UN0101), when tufted puffins were concentrated (approximately 53 birds) at the NP/MW front (Table 4).

Akutan Pass

Akutan Pass is approximately 60 m deep at its shallowest, slightly shallower than Unimak Pass. It is also about half as wide (approximately 10 km) as Unimak. On the BS side of the pass, the depth drops to >800 m in <10 km, even more dramatically than in Unimak

Pass. Three transects were sampled in 2001 (two CTD and one acoustic transect) and five in 2002 (two CTD and three acoustic transects) (Table 1). Two of the transects (AK0206 and AK0207) were aborted before obtaining a full transect through the pass.

In all six full transects, a surface density front (with decreasing density to the south) was apparent in Akutan Pass south of 54°N (see Fig. 3d, for example). This front defined the northern edge of the NP water. The mixed region in the center of the pass was larger and more consistent ($25.4 < \sigma_t < 25.6$) than in Unimak Pass and was separated from the NP waters by well-defined surface density fronts. The division between MW and BS water was illustrated by increasing stratification in the northern part of Akutan Pass. The BS/MW front and the MW/NP front both slant toward the south, with depth with deep BS water underneath MW and MW underneath NP water (Fig. 3). As in Unimak Pass, the temperature, salinity, and density suggest that Akutan Pass MW is a lateral mixture of shallow BS and NP waters.

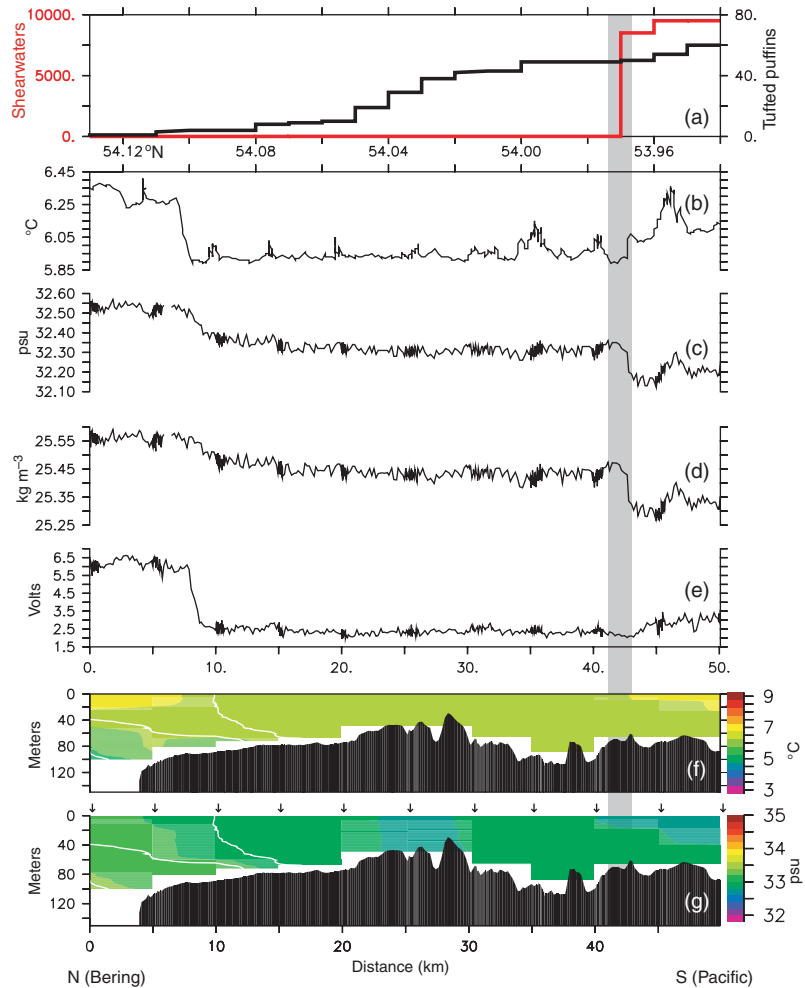


Figure 3. CTD transect through Akutan Pass on June 14, 2001 (AK0103). (a) Accumulated number of seabirds, (b) SST ($^{\circ}\text{C}$) from thermosalinograph, (c) surface salinity from thermosalinograph, (d) surface density (kg m^{-3}), (e) surface fluorescence (volts), (f) CTD temperature (colour scale: $^{\circ}\text{C}$), (g) CTD salinity (colour scale: psu). Arrows show locations of CTD casts. White contours in bottom two plots are σ_t density (kg m^{-3}). Grey shading marks shearwater aggregation and associated physical features.

In Akutan Pass on June 14, 2001 (AK0103), we encountered approximately 9500 shearwaters (approximately 20 000 total birds in flock including birds foraging beyond the 300-m limit) feeding and sitting on the water along the NP/MW front at the southern end of the pass (Utilization test, $P < 0.05$; Fig. 3; Table 2). The northern edge of the aggregation coincided with the location of the greatest horizontal gradient in temperature and salinity. The largest part of the aggregation was over the more stratified NP water. When we returned later that day with an acoustic survey, we found about 40 shearwaters in about the same region (south of the NP/MW front), but no evidence of euphausiids in the upper water column (Fig. 4). A day later (AK0105; Table 2), approximately 3700 shearwaters (approximately 10 000 total birds in the flock including birds foraging beyond the 300-m limit) were associated with the NP/MW front, but just on the mixed-water side of the front. On both days, shearwaters were actively feeding

on euphausiids (primarily *Thysanoessa inermis*), as evidenced by the prey regurgitated by birds leaving the area and prey found in the stomachs of shot birds (Jahncke *et al.*, 2005).

No shearwaters were observed foraging in Akutan Pass in May (three transects) or June (two transects) 2002. We do not know why foraging shearwaters were absent from our transects in this pass in 2002, but dense aggregations of birds (5000–20 000 birds km^{-2}) sitting on the water were found covering the water to the horizon in all directions north and west of Unimak Pass in June 2002 (J. Jahncke, unpublished data). It may be that shearwaters foraging in the vicinity of Akutan and Unimak passes move between the passes and adjacent shelf areas depending on the availability of near-surface aggregations of euphausiids. Based on many past visits to the region, there are almost always large flocks of foraging shearwaters present, but their exact location with respect to the two passes is highly variable and their use of frontal regions may in part

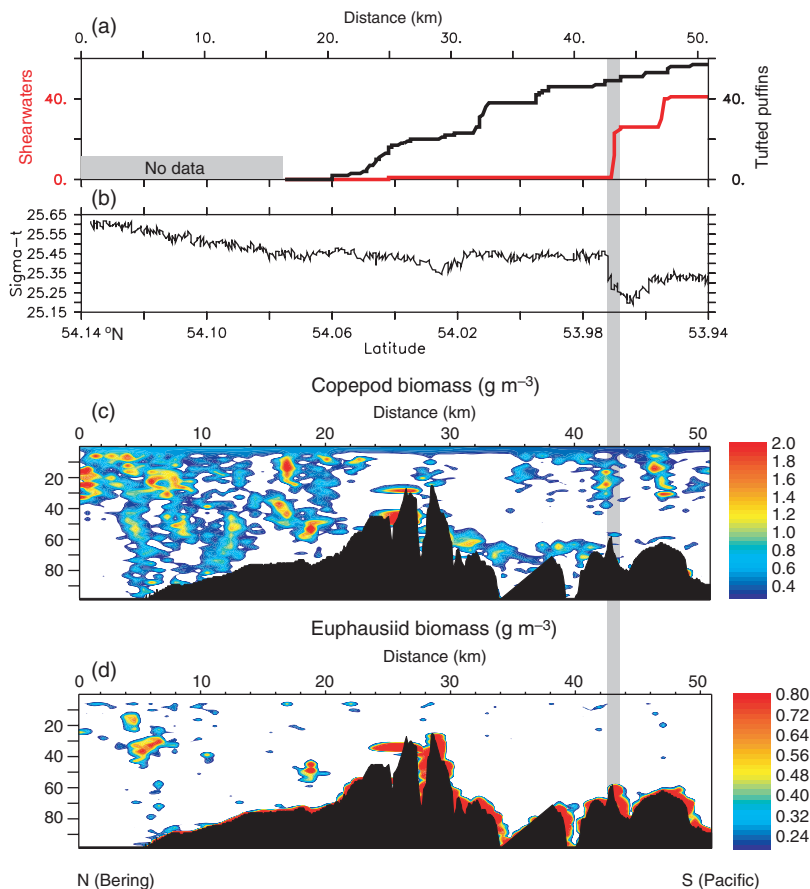


Figure 4. Acoustic transect through Akutan Pass on June 14, 2001 (AK0104). (a) Accumulated number of seabirds, (b) surface density (kg m^{-3}), (c) copepod biomass (g m^{-3}), (d) euphausiid biomass (g m^{-3}).

reflect their use of subadult euphausiids (Vlietstra *et al.*, 2005; G.L. Hunt, personal observations).

Three species of pursuit-diving seabirds, ancient murrelets, whiskered auklets, and tufted puffins were found foraging in significant aggregations in Akutan Pass (Tables 3 and 4). Ancient murrelets aggregated over the MW region in 2001 (AK0103: 71 birds, Table 3), as did whiskered auklets in 2001 (AK0103: 1110 birds; AK0104: 169 birds). Similarly, we found significantly more tufted puffins than expected by chance (Utilization test, $P < 0.05$, Table 4) feeding and sitting on the water over the MW region of Akutan Pass in both 2001 and 2002.

Umnak Pass

Umnak Pass is shallow (approximately 25 m at its shallowest) and narrow (approximately 5 km wide). Umnak was sampled on two transects, both in 2002. Surface waters were colder and saltier at the north end than at the south end of the pass during both sections. However, the three water masses and accompanying fronts exhibited by other passes were not so apparent in Umnak. Instead, the mixed region in the centre of the pass exhibited many small-scale surface fronts, and

it was difficult to distinguish three distinct water masses.

We found significant aggregations (Permutation analysis, $P < 0.05$) of ancient murrelets (UM0210: 134 birds; UM0211: 143 birds; Table 3) and tufted puffins (UM0210: 290 birds; UM0211: 190 birds; Table 4) feeding and sitting on the water over the central and northern regions of Umnak Pass in 2002. CTD data for this pass showed no clear water masses; however, our observations suggest that the ancient murrelets were associated with tide rips and convergences. The tufted puffins in this pass were foraging over an area of strong tide rips during our first survey, and were foraging north of the strongest tide rip, likely associated with a strong convergence, during our second survey of the pass.

Central passes of intermediate depth (100–500 m deep)

Samalga Pass

Samalga Pass (depth approximately 200 m; width approximately 29 km) marks a transition between the eastern passes which are dominated by Alaska Coastal Current (ACC) water and a neritic or shelf ecosystem, and the central passes which are dominated by

Alaskan Stream water and an oceanic ecosystem (Coyle, 2005; Ladd *et al.*, 2005). Our CTD survey of the length of Samalga Pass was disrupted by bad weather, and thus our physical description of this pass is incomplete. Nevertheless, water throughout the pass was fairly well stratified, although there was evidence of strong vertical displacements in the isopycnals (Ladd *et al.*, 2005). A transverse CTD line showed that the eastern side of the pass was dominated by relatively fresh water of ACC origin whereas the western side of the pass was dominated by saltier Alaskan Stream and/or BS water.

In Samalga Pass, we found significant aggregations (Permutation analysis, $P < 0.05$) of northern fulmars in 2002 (SA0212: 334 birds; SA0213: 1572 birds; Table 5) near the middle of the transects. On June 7 (SA0212), fulmars in this area were lined up on what appeared to be Langmuir cells, and on June 8 (SA0213) they were foraging in tight flocks over slicks associated with convergences.

Seguam Pass

Seguam Pass is deeper and wider than the eastern passes (35 km wide, 100 m deep). The minimum depth in Seguam Pass is approximately 100 m with an average depth of approximately 150 m over the approximately 50-km long pass. The shallowest part of the pass is only approximately 20–30 km long. Four transects through Seguam Pass were sampled (one CTD and one acoustic transect in each year). Each of the transects exhibited well-defined surface density fronts separating the MW in the center of the pass from the NP water in the south and the BS water in the north (Fig. 5). The MW was denser than either the BS surface water or the NP surface water, reflecting the influence of deeper water mixed to the surface (vertical mixing as opposed to the lateral mixing that dominates in the eastern passes; Ladd *et al.*, 2005). This vertical mixing is due to a combination of factors including the shorter along-pass distance and higher current speeds in Seguam relative to the eastern passes (Stabeno *et al.*, 2005). Salinity levels

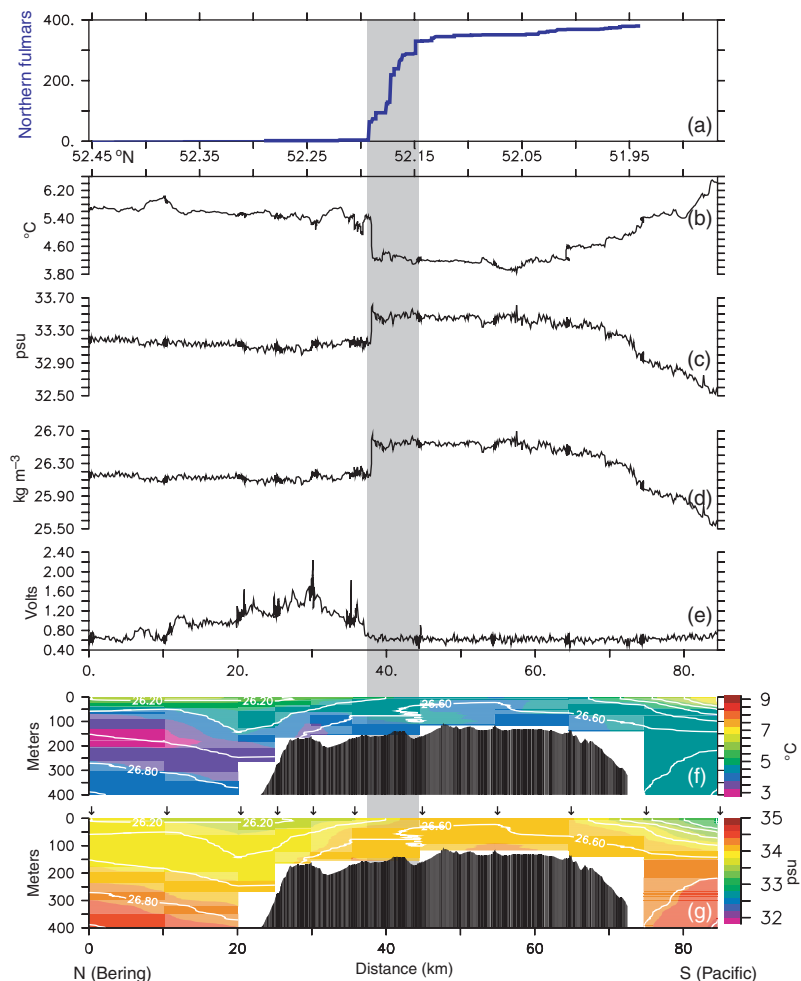


Figure 5. CTD transect through Seguam Pass on June 2, 2002 (SG0217). (a) Accumulated number of seabirds, (b) SST (°C) from thermosalinograph, (c) surface salinity from thermosalinograph, (d) surface density (kg m^{-3}), (e) surface fluorescence (volts), (f) CTD temperature (colour scale: °C), (g) CTD salinity (colour scale: psu). Arrows show locations of CTD casts. White contours in bottom two plots are σ_t density (kg m^{-3}).

in the MW of the central passes were much higher than in the eastern passes, reflecting the influence of both vertical mixing and the higher salinity of the source waters (Alaskan Stream as opposed to ACC). The position of the fronts appears to be tied to the topographic break at either end of the pass with the surface expression of the front advected north or south of the topographic break depending on the phase of the tide. This frontal structure is particularly apparent in the relatively simple geometry of Seguam Pass (Fig. 6).

In Seguam Pass, significantly more shearwaters than expected by chance (Utilization test, $P < 0.05$) were found feeding and sitting on the water over the MW at the middle of the pass in 2002 (Utilization test, $P < 0.05$, Table 2). Approximately 72 birds were observed feeding in tight groups over slicks or loosely spread out over frontal structures (SG0218; Fig. 7). Although the cause of these slicks was not resolved by either the CTD transects or the continuous underway sea surface property measurements, observations from the ship's bridge suggest that these slicks were related to convergence zones and tidally driven eddies. Convergence is also suggested by the large biomass of copepods and euphausiids distributed vertically to almost 100-m depth. The largest aggregation of

shearwaters was co-located with this vertical distribution of biomass (Fig. 7). The shearwaters were actively foraging on euphausiids (primarily *Thysanoessa longipes*), as evidenced by regurgitates and stomach analysis (Jahncke *et al.*, 2005).

Approximately 650 fulmars were observed foraging in scattered groups over areas of slick water on June 10, 2001 (SG0107: Table 5). The majority of these were observed over the northern end of the MW region, south of the BS/MW front. A day later (SG0108), we found approximately 500 birds scattered along slicks parallel to the ship's course; the distribution had shifted approximately 15 km southward along with the BS/MW front. Both transects were taken on the ebb (southward) flowing tide. Fulmars on June 11 (SG0108) were distributed over the entire MW region with very few birds observed north of the BS/MW front or south of the NP/MW front. An aggregation of approximately 350 fulmars were observed sitting on the water over approximately 7 km of trackline just south of the BS/MW front in June 2002 (SG0217; Table 5). One day later (SG0218), approximately 1865 fulmars were observed actively feeding in lines together with shearwaters over slick areas parallel to the wind, possibly the result of Langmuir circulation cells. Birds over the slick areas were in tight lines or groups pecking at the surface. Birds over fronts were loosely spread out (Fig. 7). The northern edge of the distribution was just north of the BS/MW front, with the majority of the birds observed over the MW south of the front. The aggregation did not reach as far south as the NP/MW front.

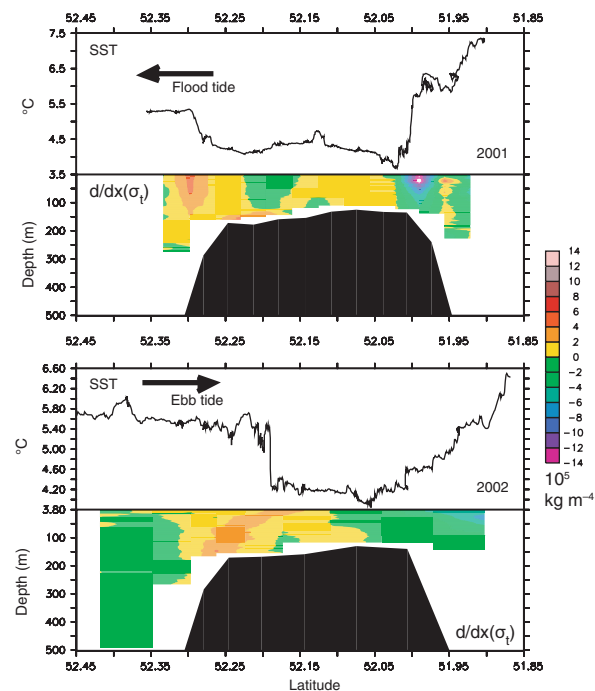
In both 2001 and 2002 at Seguam Pass, we found foraging and sitting tufted puffins concentrated on the water over the MW region (Utilization test, $P < 0.05$; Table 4).

Tanaga Pass

The minimum depth in Tanaga Pass is approximately 160 m with an average depth of approximately 350 m over the approximately 20 km-long pass. One CTD transect and one acoustic transect were sampled in Tanaga Pass in late May 2002 (Table 1). As in Seguam Pass, the MW in Tanaga is denser and higher in salinity than the surface waters either the north or the south (Fig. 8), reflecting the influence of deeper water mixed to the surface.

Least auklets (*Aethia pusilla*), feeding and sitting on the water, were significantly more abundant than expected by chance over the MW region in Tanaga Pass in 2002 (TN0219: 9242 birds; TN0220: 1401 birds, Table 3; Fig. 8). The aggregation of actively foraging least auklets occurred in an area of boils and

Figure 6. Frontal structure in Seguam Pass during two different tidal phases. (a) SST and (b) horizontal derivative of density during June 10, 2001 transect (SG0107) during a flood tide, (c) SST and (d) horizontal derivative of density during June 2, 2002 transect (SG0217) during an ebb tide.



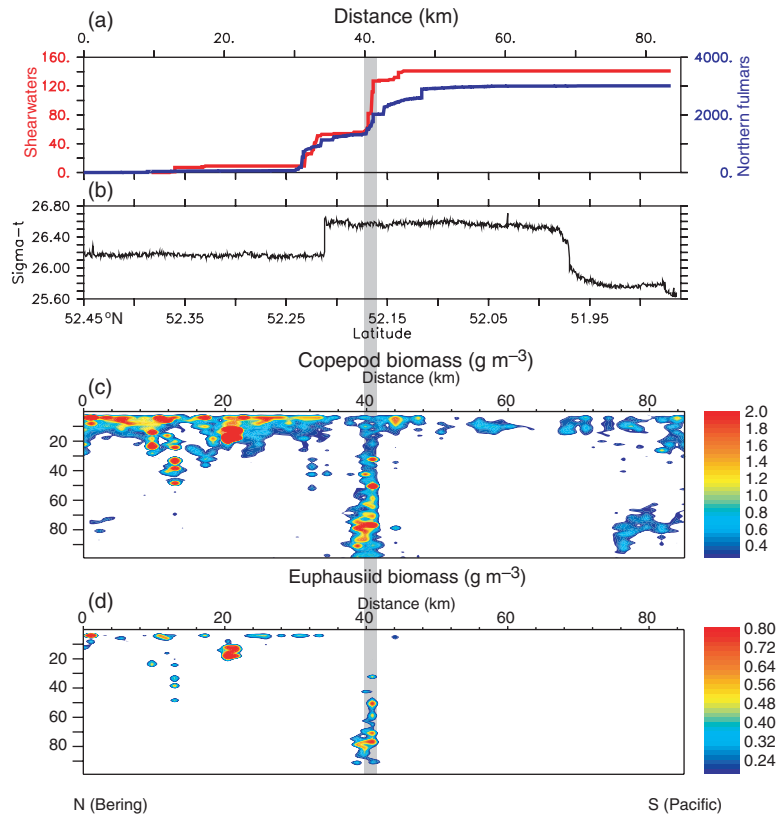


Figure 7. Acoustic transect through Seguam Pass on June 3, 2002 (SG0218). (a) Accumulated number of seabirds, (b) surface density (kg m^{-3}), (c) copepod biomass (g m^{-3}), (d) euphausiid biomass (g m^{-3}).

convergences resulting from the interaction between a northward tidal flow and the shallow bathymetry of a submerged mountain (51.6°N, 178.2°W, 80 m deep; not seen in Fig. 8, but recorded by the ship's depth sounder). Our observations suggest zooplankton was physically forced to the surface and aggregated in this area as evidenced by the copepod prey (*Neocalanus plumchrus-flemmingeri*) found in the stomachs of shot birds (Jahncke *et al.*, 2005).

DISCUSSION

North Pacific water, with its warm, low-salinity, low-density signature, was observed on the south side of the passes. In each pass, a front separates the NP water from the MW observed in the center of the pass. A second front separates the MW from the BS water at the north end of the pass (Fig. 9). Note that the schematic showing three water types in Fig. 9 is simplistic. In reality, there are often numerous fronts of varying strength (as opposed to the two shown in the schematic).

Eastern versus central passes

Generally, in the eastern passes, the surface density of the BS surface water is denser than the MW,

which in turn is denser than the NP surface water (Fig. 9). Comparing temperature and salinity properties of the three water types shows that, in the eastern passes, the MW is formed via (primarily lateral) mixing between shallow NP and BS waters. The northern front (separating BS water from MW) often appears to tilt to the south with depth such that the BS water undercuts the MW. The movement of BS water into the pass at depth may be dependent on the phase of the tidal cycle, with denser BS water observed at depth in the passes most frequently on the ebb (southward flowing) tide.

The central passes are generally shorter, deeper, and wider than the eastern passes. This topography allows for higher current speeds and larger transports (Stabeno *et al.*, 2005). The sill depth in Seguam Pass (Tanaga Pass) is approximately 100 m (160 m) with an average depth of approximately 150 m (350 m) over the approximately 50-km (20-km) long pass. In Seguam and Tanaga Passes, the MW is denser than either the BS surface water or the NP surface water reflecting the influence of deeper water mixed to the surface (vertical mixing as opposed to the lateral mixing that dominates in the eastern passes).

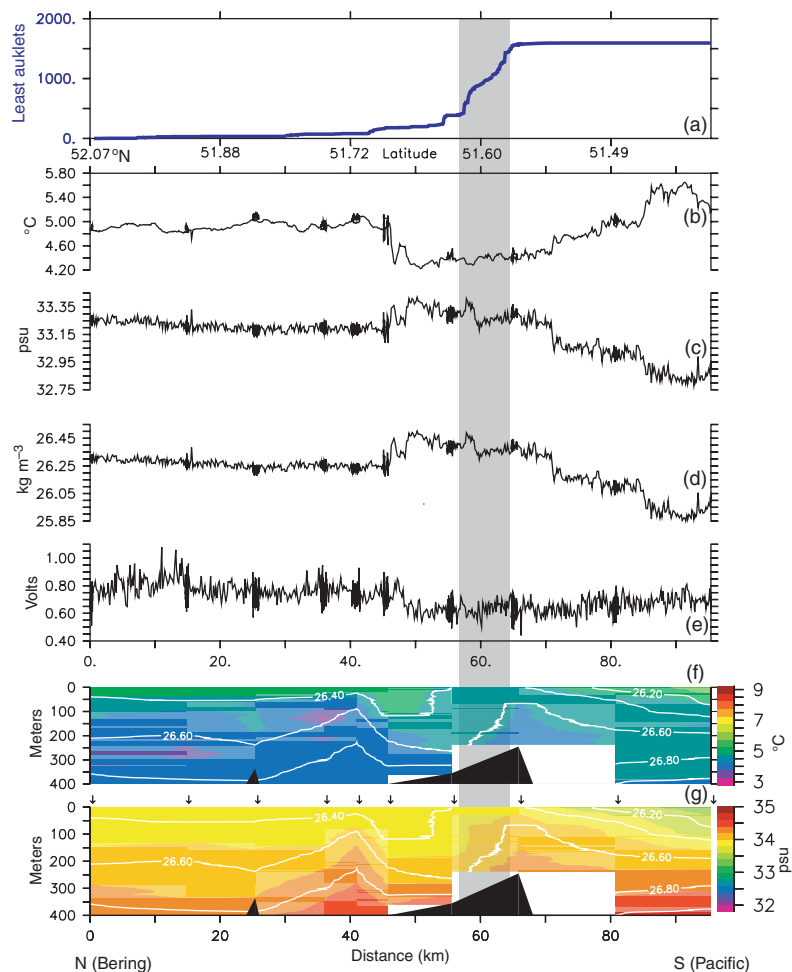


Figure 8. CTD transect through Tanaga Pass on May 30, 2002 (TN0220). (a) Accumulated number of seabirds, (b) SST ($^{\circ}\text{C}$) from thermosalinograph, (c) surface salinity from thermosalinograph, (d) surface density (kg m^{-3}), (e) surface fluorescence (volts), (f) CTD temperature (colour scale: $^{\circ}\text{C}$), (g) CTD salinity (colour scale: psu). Arrows show locations of CTD casts. White contours in bottom three plots are σ_t density (kg m^{-3}).

Marine bird uses of the passes

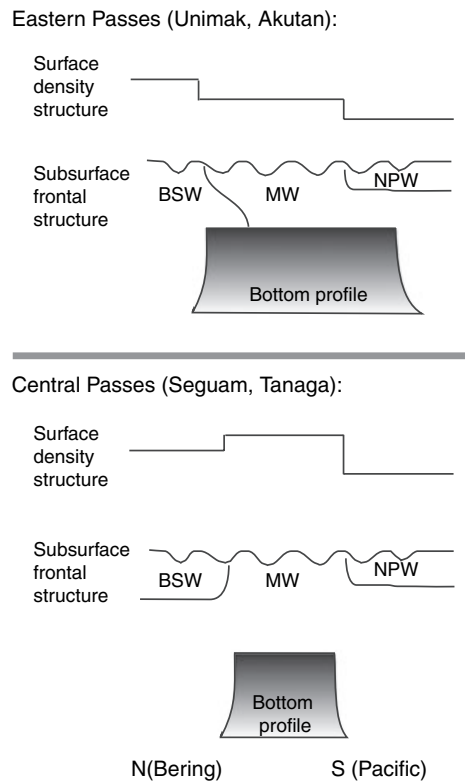
In the shallow eastern passes (Unimak, Akutan, and Umnak), short-tailed shearwaters and tufted puffins were most common (Jahncke *et al.*, 2005). In Samalga and Seguam, central Aleutian Archipelago Passes, northern fulmars were most common, although shearwaters were also observed (Jahncke *et al.*, 2005). Least auklets were the most common seabird observed in Tanaga Pass (Table 1).

Although most (21/28) transects through the passes encountered at least 50 individuals of one of the six seabird species on which we focused, any one species was present in numbers ≥ 50 on a minority of the transects through the eastern and central passes. Short-tailed shearwaters were present in numbers ≥ 50 on 7/28 transects, northern fulmars on 6/28 transects, tufted puffins on 13/28 transects, and three species of small alcids combined on 10/28 transects. One reason that a given species was abundant on a small proportion of

the transects was a result of the large-scale distribution of species; shearwaters were present in large numbers in only three of six passes (Unimak, Akutan, and Seguam), fulmars were present in only two (Samalga and Seguam), and tufted puffins were numerous in four passes (Unimak, Akutan, Umnak, and Seguam) (Jahncke *et al.*, 2005). Of the small alcids, ancient murrelets had significant aggregations in three passes (Unimak, Akutan and Umnak), Whiskered auklets had aggregations in one pass (Akutan), and least auklets had significant aggregations only in Tanaga Pass. In the central passes (Seguam and Tanaga), only the least auklet had significant aggregations, although small numbers of small alcids were also present in Seguam Pass. Amukta Pass, a wide (68 km), deep (430 m) central pass, had no significant seabird aggregations on three separate transects (one in 2001 and two in 2002).

There was considerable variation in the distribution of seabird aggregations between visits to passes within

Figure 9. Schematic comparing the surface density structure and subsurface frontal structure in the eastern and central passes.



a year, and from one year to another. Part of this variation was undoubtedly related to the phase of the tide during our transects, but other factors, such as seasonal differences and patchiness in the availability of zooplankton (Coyle, 2005) must have been important as well.

Within these passes, if ≥ 50 birds of a species were present, then they were likely to be in statistically significant aggregations: seven significant aggregations of shearwaters were observed within seven transects, 9/6 for fulmars, 12/13 for tufted puffins, and 8/10 for small alcids. These aggregations were not evenly distributed among the water masses and hydrographic features within the passes (Table 6). Aggregations of foraging seabirds were generally not associated with stratified waters and high concentrations of chlorophyll. Rather, concentrations of seabirds were found to be associated with convergence zones in the MW and with the front between NP water and MW. The MW in the center of the passes appeared to be the most attractive to fulmars and small alcids, while the NP/MW front was most attractive to the shearwaters. Over the 2 yr of the study, no signi-

Table 6. Summary of hydrographic features at which significant concentrations of seabirds occurred in Aleutian Passes. Data are ratios of significant aggregations to number of encounters with the hydrographic feature in passes where a species was present.

	Bering Sea Water	BS/MW front	MW	NP/MW front	NP water
Northern Fulmar	0/4	2/4	4/4	1/4	0/3
Short-tailed Shearwater	0/4	0/4	1/6	5/6	0/6
Small Alcids	0/5	0/4	6/6	0/5	0/6
Tufted Puffin	0/6	1/5	9/11	1/10	0/11

ficant aggregations were found in either BS or NP waters.

Species (all fulmar aggregations) that were foraging by picking at prey from the surface were associated with surface convergences that appeared to be associated with Langmuir circulation cells or tidal features in the central passes (Samalga, Seguam); whereas subsurface foraging puffins and small alcids were mostly observed in areas of turbulent, well-mixed water near the shallow regions of the passes (15 of 17 aggregations).

In contrast, short-tailed shearwater flocks that were plunge-diving for prey were associated with the front between the NP water and MW in the passes (5/6 transects). When plunge-diving, they can dive to depths of up to 40 m or more to catch prey (adult euphausiids, small forage fish) (Hunt *et al.*, 1996). Thus, prey patches located between the surface and 40 m are available to shearwaters (Vlietstra *et al.*, 2005 and references therein).

Northern fulmars forage for prey (primarily copepods) at the surface. During the Aleutian Pass surveys of 2001 and 2002, these birds were only observed in significant numbers in Seguam and Samalga Passes. In contrast to shearwaters, fulmar aggregations were often spread out over the pass, implying that the mechanisms concentrating their prey at the surface must be of fairly small spatial scale.

Captive tufted puffins have been shown to feed near the bottom more than other puffins and murres (Duffy *et al.*, 1987). Tufted puffins can dive up to 100 m in pursuit of prey, but most search dives are probably in the upper 60 m of the water column (Piatt and Kitaysky, 2002). They were observed in both years in all of the eastern and central passes in which we had observations, with the exception of Tanaga and Amukta. Distributions of puffins were spread out and were observed over

the MW region in the center of the passes with fewer distributed over the BS or NP waters.

Least auklets were observed in significant numbers only in Tanaga Pass in 2002. Auklets obtain their food by pursuit-diving (Ashmole and Ashmole, 1967) and least auklets can dive to depths of approximately 15 m (Obst *et al.*, 1995). Hunt *et al.* (1998) found that, in the Delarof Islands west of Tanaga Pass, thousands of least auklets congregated on the water downstream of a sill, usually between boils and sometimes around the edges of boils. These auklets were feeding primarily on copepods. Our present results suggest a similar affinity for topographically generated boils and convergences. However, least auklets also forage on near-surface patches of copepods, particularly when they are concentrated at a shallow pycnocline (Hunt *et al.*, 1990). In past cruises north of Kiska Island and northeast of Amchitka Pass, least auklets were observed foraging on near-surface patches of copepods (G.L. Hunt and K.O. Coyle, unpublished observations), but in the present study, we did not have the opportunity to see if similar foraging aggregations existed over stratified water to the north of Tanaga Pass.

The interaction of strong currents with bathymetric features creates zones of vertical advection, mixing, and surface convergences that make island passes attractive foraging regions for seabirds. Deep passes lacking these features, such as Amukta Pass (Jahncke *et al.*, 2005; Ladd *et al.*, 2005) and many of the passes in the western Aleutian Archipelago, are not as likely to facilitate trophic transfer to top predators as shallow passes such as those found in the eastern Aleutian Islands. Thus, not only may there be less primary production in the central Aleutian Passes (as observed in the sparse primary production data collected during 2001 and 2002; Mordy *et al.*, 2005), but the transfer of that production to higher trophic levels may be constrained by the lack of the physical processes required to create predictable regions of enhanced foraging opportunities in the deeper passes.

Most studies of seabirds in relation to physics emphasize the use of fronts or other structures that concentrate prey in the horizontal plane (Hunt *et al.*, 1999). Less frequently, there have been observations of birds using prey concentrated in the vertical plane, i.e. on the pycnocline (Hunt *et al.*, 1990). In coastal regions, marine birds forage in areas where currents interact with bathymetry to force prey toward the surface (Coyle *et al.*, 1992; Hunt *et al.*, 1998). They are also frequently found foraging in tide rips where clear frontal structures are absent (Safina and Burger, 1985, 1989; Zamon, 2003). However, within these areas of MW, there may be small-scale convergences

forced by tidal currents that can concentrate prey. These areas are often marked by the aggregation of flotsam or by the presence of foraging seabirds. In the present study, the presence of lines of birds foraging at the surface coincided with areas of convergence within regions of well-mixed water. These convergences were identified by accumulations of flotsam at the surface and the presence of slicks or dimpled surface waters. The present paper contributes to our understanding of seabird foraging by demonstrating the importance of physical concentrating mechanisms within areas of well-mixed water that do not fit the definition of frontal structures.

ACKNOWLEDGEMENTS

We thank the captain and crew of the R/V *Alpha Helix* for their support during this project. R.L. Pitman, L. de Souza, L.S. Vlietstra, and S.W. Webb provided assistance during seabird observations. We thank A.D. Long and M.M. Riehle for modifying the RiehleTRON. J. Jahncke was supported by a Graduate Assistance in Areas of National Need (GAANN) Fellowship while working on this paper. This research was sponsored by CIFAR and NOAA's Steller Sea Lion Research Program and its contribution FOCI-L486 to Fisheries-Oceanography Coordinated Investigations and PMEL contribution number 2655. This publication was also funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA17RJ1232, Contribution no. 1039.

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