

Characterising meso-marine ecosystems of the North Pacific

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Abstract

To delineate mesoscale variability in marine ecosystems of the subarctic North Pacific and identify “hotspots” of biological activity, we conducted contemporaneous surveys of plankton and avifaunal communities in 2000–2003. Plankton samples were collected with a continuous plankton recorder (CPR) towed by a commercial vessel while a trained observer recorded marine bird distributions using strip-transect techniques. Near- and sub-surface physical oceanographic properties and productivity patterns were measured using a temperature data logger and satellite-derived chlorophyll *a* concentrations. We identified 10 distinct biological communities across the North Pacific, which we refer to as ‘meso-marine ecosystems’ (MME). We examined the characteristics of MME over multiple years to assess temporal persistence. MME were associated with different bathymetric domains and current systems. MME differed in the overall abundance and species composition of their fauna and, therefore, almost certainly in productivity. Regular monitoring of the spatial and temporal variability of MME will enhance our ability to detect and understand coupled climate-ecosystem responses, and, in turn, help guide ecosystem-based fisheries and wildlife management.

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1. Introduction

Increasingly, living marine resource management and ocean conservation are moving toward ecosystem-level approaches (Botsford et al., 1997; Crowder and Murawski, 1998; Sherman and Duda, 1999). As such, ‘ecosystem status reports’ have proliferated (e.g. Venrick et al., 2003; Edwards

et al., 2003; DFO, 2003; PICES, 2004). Yet, while ecosystem-based management is currently emphasized, our ability to identify, characterize, and monitor ‘ecosystems’ remains limited. Moreover, the conceptual and operational scales considered by ‘ecosystem-level’ studies are highly variable, ranging from single habitat ‘hot-spots’ (e.g., a seamount or frontal system) to an entire sea or biogeographic domain.

At the largest scale lies the large marine ecosystem (LME) concept. LMEs are large regions, on the order of 200,000 km², characterized by

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distinct bathymetry, hydrography, productivity, and trophic dependencies (<http://www.edc.uri.edu/lme/intro.htm>). LMEs, while providing an overall framework for conservation and management, often lack key information on meso-scale (10–100 km) variability in oceanographic processes and productivity—including delineation of ‘hot-spots’ of biological activity (Haury et al., 1978; Hunt and Schneider, 1987). Thus, smaller-scale approaches, possibly nested within the larger LME framework, are required to reconcile the critical meso-scale variability that often drives ecosystem dynamics (Gould and Piatt, 1993; Vinogradov et al., 1997; Longhurst, 1998). For example, the California Current LME has been subdivided by the US GLOBEC program into four sub-regions with distinct hydrographic and biological characteristics (GLOBEC, 1992, 1996). Similarly, the Gulf of Alaska may be subdivided by physical and biological properties into different oceanographic domains (Ware, 1989; Wahl et al., 1989). Water depth may structure distinct meso-scale ecosystems on continental shelf–slope regions (<2000 m), due to onshore–offshore gradients in stratification, productivity, and trophic interactions. Similarly, transition zones (ecotomes) between oceanographic domains may represent important zones of differentiation in marine communities.

Upper-trophic-level predators and fisheries resources should be managed via an understanding of the meso-scale ecosystems they inhabit, but initially such systems need to be identified and characterized. Examining meso-scale community structure, physical variability, and productivity patterns represents an important first step towards establishing functional spatial subdivisions of existing LMEs in the North Pacific. Until recently, replicate basin-scale biological surveys, effort required to define and delineate meso-scale marine ecosystems (hereafter MME) at the scale of the North Pacific Ocean, did not exist. Indeed, previous descriptions of North Pacific ‘domains’ were based on either physical oceanography (e.g. water mass characteristics) or lower trophic-level constituents (e.g. primary producers). Favorite et al. (1976), for example, described mean conditions of provinces of the North Pacific based on 10 years of oceanographic records. Longhurst (1998) described five biomes for the subarctic North Pacific based on ocean colour. More recently, Wong et al. (2002) divided the North Pacific into 12 major provinces, based on sea surface temperature (SST), surface nitrate gradients and, in

near-shore regions, surface salinity. These studies suggest that there are strong linkages in physical and biological properties of the North Pacific Ocean, but are limited to one or two trophic levels.

Herein, we provide a synoptic perspective of oceanographic and biological domains of the North Pacific. We test the hypothesis that functional MME can be derived on the basis of biological characteristics. We examine meso-scale biological variability (plankton and seabirds) along a survey transect through the Gulf of Alaska, southern Bering Sea, and Oyashio/Kuroshio current regions of the western North Pacific Ocean. To delineate MME, we use clustering of biological communities to define distinct geographic regions of the North Pacific. We tested the persistence of MME delineations by comparing biological observations collected in different years (2000–2003), and consider how physical oceanographic characteristics account for the observed biological clusters.

2. Methods

The Continuous Plankton Recorder-Marine Bird and Mammal (CPR-MBM) transect sampled waters to the north of the subarctic transition zone of the North Pacific; the 7500 km survey crossed both the eastern and western subarctic gyres, and ventured into the southern Bering Sea and the eastern (Alaskan Current) and western (Kuroshio) boundary currents of the North Pacific (Fig. 1). Our analyses are based upon data collected in June 2002, the first survey we made with a full suite of concurrent physical and biological measurements. To evaluate the year-to-year persistence of the MME defined by the June 2002 data, we use additional June observations from plankton-only surveys in 2000 and 2001, and seabird-only surveys in 2003.

2.1. Biological data

2.1.1. Plankton distribution and abundance

Plankton samples were collected using a continuous plankton recorder (CPR) towed behind the bulk-cargo carrier ‘*M/V Skaubryn*’ in June 2000, 2001 and 2002. Depth of tow was ~7 m and ship speed averaged ~12 knots. Batten et al. (2003) describe the CPR sampling device. The position and time of deployment, recovery, and course changes logged by the ship were used to divide the continuous sample into discrete samples, each

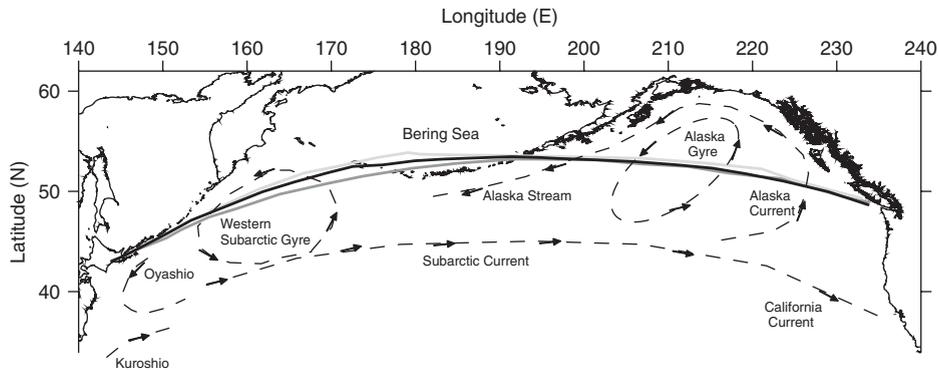


Fig. 1. The survey transect in June 2002 (black), June 2001 (dark grey) and June 2000 (light grey), together with the general circulation patterns referred to in the text.

representing 18.5 km of tow. We analysed every fourth sample (separated by a spacing of about 55 km) microscopically and enumerated the abundance of phytoplankton and zooplankton taxa. A mechanical problem owing to fouling of the CPR by floating debris inhibited sampling between 155° E and 165° E in June 2002, and in June 2000 the transect extended east only as far as 155° E.

Taxonomic resolution varied among taxa (Batten et al., 2003), but was consistent for each sample. Copepods and most hard-shelled dinoflagellates were identified to species, while euphausiids and chaetognaths were identified to family. The CPR sampling mechanism and preservative only adequately preserves hard-shelled forms. Because coelenterates and athecate dinoflagellates are not evident in the samples, the CPR does not sample the whole plankton community. Phytoplankton taxon abundance was recorded as presence/absence in 20 fields of view across the sample, while zooplankton were counted in categories of abundance from either a subsample or the whole sample depending on their size (smaller taxa, <2 mm, are usually more numerous and can be adequately enumerated in a subsample). While these quantitative data were used to estimate zooplankton abundance and biomass, the community composition analyses were restricted to the presence/absence data to allow the concurrent analysis of the phytoplankton and zooplankton communities. The data set was further restricted to day-time samples (collected between local sunrise and local sunset) since diel vertical migration by some zooplankton influences their presence in the surface waters sampled by the CPR. Moreover, seabird surveys were conducted only during daylight. Notably, in

June at these high latitudes, night is short so many more day-time samples were available.

Separate analyses were carried out for each year. The presence/absence of each taxon in each sample was used to calculate the Bray–Curtis similarity of all possible pair-wise combinations of samples (Bray and Curtis, 1957), resulting in a matrix of similarity values ranging from 0 (samples with no taxa in common) to 1 (samples with all taxa in common). This matrix was subjected to hierarchical clustering (Euclidean distance, average linkage) and multi-dimensional scaling (MDS) using SystatTM. Hierarchical clustering and MDS provide complementary perspectives, since these methods are better suited for communities characterized by distinct species assemblages and a continuum in species composition. By combining these approaches we obtained more robust MME delineations.

Mesozooplankton biomass was estimated by multiplying the abundance of each taxon by its taxon-specific dry weight, and summing these values for each sample. The dry weight values were derived from empirical measurements of individual organism's length and dry weight (Planque and Batten, 2000). If measurements were not available for a particular taxon, dry weights were calculated from the published length of the organism and the empirical length to weight ratio for the closest taxonomically available organism.

2.1.2. Marine bird distribution and abundance

Marine birds were primarily surveyed from the flying bridge, and occasionally the foc'sle deck, of the 'M/V Skaubryn' at an eye height of 28 m and 10 m above the sea surface, respectively. One observer (MH) surveyed seabirds continuously

during daylight hours while the vessel cruised at speeds of 4.0–14.0 knots ($7.4\text{--}25.9\text{ km h}^{-1}$), following standardized strip-transect methods, modified to fit this platform of opportunity (Tasker et al., 1984; Hyrenbach et al., in preparation). All seabirds sighted within a 400-m strip transect to the one side of the vessel with best visibility (e.g., least sun glare) were identified to the lowest taxonomic level possible, and summed in 5-min survey bins ($\sim 1.85\text{ km}$ at 12 knot sailing speed). Behaviour (e.g., sitting vs. flying) was noted for each sighting; ship-following birds were recorded when they were first encountered and ignored thereafter. Due to poor visibility (fog), no bird surveys were undertaken between 155° and 165° E in June 2002; this corresponds to the region also not sampled by the CPR in June 2002. To obtain seabird observations at the same scale as the CPR samples ($\sim 18.5\text{ km}$), we combined sequential 5 min surveys to produce contiguous bins of 15–25 km in length (this variability is due to breaks in the sampling structure). For each bin, density (birds km^{-2}) of each species was calculated by dividing the number recorded by the area surveyed ($400\text{ m} \times \text{trackline length}$). We used seabird density as the response variable in cluster and MDS analyses.

2.2. Environmental data

2.2.1. Bathymetry

Water depth along the CPR-MBM transect was obtained from NOAA's (National Oceanic and Atmospheric Administration) National Geophysical Data Center ETOPO 5-min gridded elevation dataset (NGDC, 1998).

2.2.2. Water temperature

We obtained near-surface temperature data from a VemcoTM mini-logger attached to the CPR in June 2002. This device logged water temperature at the near surface every 15 min; no salinity data were obtained. We obtained temperature profiles to 800 m using expendable bathythermograph (XBT); six XBTs were deployed along the transect in June 2002. XBT and mini-logger temperature records were similar (mean difference 0.59°C , $n = 6$), suggesting an appropriate calibration of the mini-logger.

2.2.3. Chlorophyll *a* concentration

Chlorophyll *a* concentrations for each seabird survey bin were derived from monthly composites

of sea-viewing wide field-of-view sensor (SeaWiFS) imagery, with a spatial resolution of $9 \times 9\text{ km}$ (<http://seawifs.gsfc.nasa.gov/SEAWIFS.html>). SeaWiFS estimates are within 35% of in situ chlorophyll *a* concentrations within the range of $0.05\text{--}50\text{ mg m}^{-3}$. Thus, we discarded unreasonably high chlorophyll *a* concentrations beyond the range of SeaWiFS validation ($> 50\text{ mg m}^{-3}$) (Hooker and McClain, 2000).

3. Results and discussion

3.1. Plankton community structure

Several distinct plankton communities were revealed by cluster and MDS analyses (Fig. 2). Groupings which contained fewer than four samples were not considered significant clusters. Clusters were assigned a symbol and plotted along the transect (Fig. 2A). MDS results were plotted using these same symbols so clusters of samples could be easily identified; pair-wise similarity between samples is represented by their distance in a two-dimensional plot (Fig. 2B). The stress value was 0.24, suggesting that the two-dimensional representation was an adequate portrayal of community structure (confirmed by clustering). Taxonomic resolution is an obstacle to the interpretation of these results. For example, euphausiids were not identified below family level; therefore, coastal samples from opposite ends of the survey line may cluster together even though they did not have any species in common.

Cluster analyses showed a gradient in plankton community structure across the GoA rather than abrupt boundaries, with overlap in some of the six clusters documented for this region. For instance, cluster \blacklozenge predominates in the eastern GoA (and the west-central Bering Sea), while the central GoA is occupied by cluster \times , and the western GoA contains predominantly cluster \bullet samples. These three groups of symbols appear on the right-hand side of the MDS plot. We observed a transition to the $+$ cluster at the continental slope of the Aleutian Island chain (moving from east to west), and an abrupt change in Unimak Pass in the Aleutian Islands to the \blacktriangle cluster. These two clusters are distinct in the MDS analysis. The \blacksquare cluster is most numerous in the western Pacific, although there are also outlying samples that did not belong to a specific cluster (depicted by the small dots). The region nearest to Japan contains almost exclusively \bullet samples—which

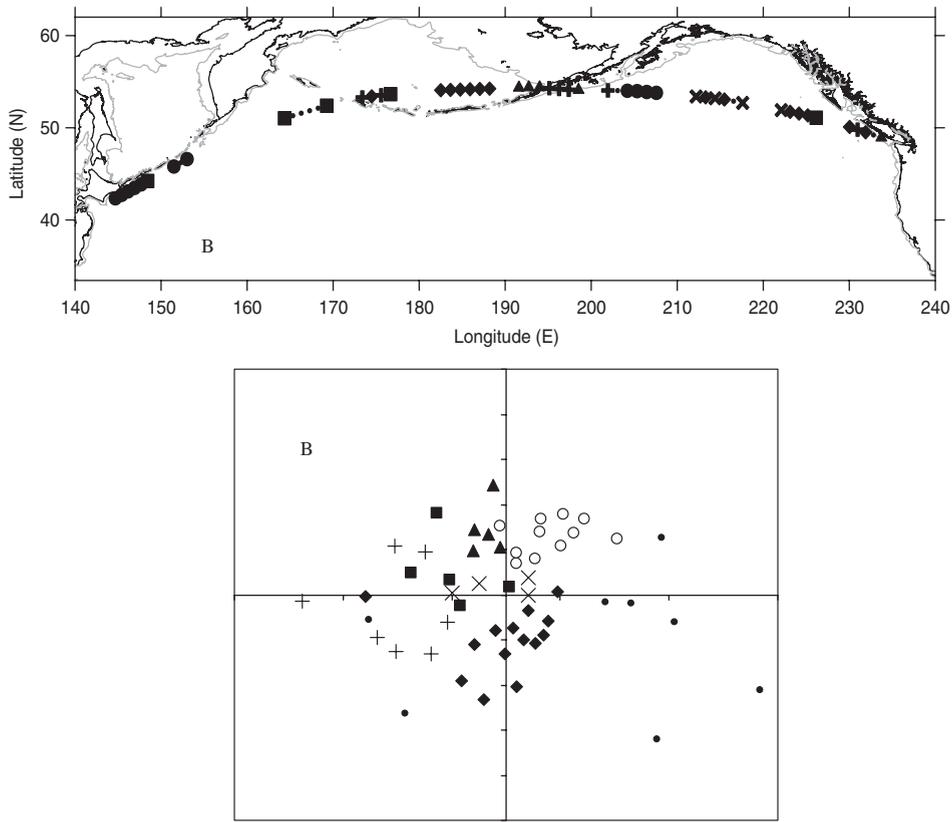


Fig. 2. Plankton community composition analysis for June 2002. (A) Results from hierarchical clustering. Separate clusters identified by symbols, plotted according to sample location (gaps indicate where night-time samples occurred that were excluded from the analyses). (B) Results from MDS analysis, the same symbol used for each sample as in Panel A. The 1000 m isobath is also shown.

are also found in the western GoA. The MDS plot also shows a gradient in plankton community composition across the Pacific (Fig. 2B).

3.2. Plankton taxonomic groups comprising clusters

Clusters were discriminated based upon commonality in presence/absence of taxa in the samples. Cluster-specific importance of each taxon was determined by calculating the proportion of samples in each cluster that contained each taxon. Based on their importance, the taxa were then grouped as follows (Table 1):

1. Ubiquitous taxa—occurred in at least one sample from each cluster and were thus not important in discriminating clusters. In several cases these ‘cosmopolitan’ taxa were not discriminated to a fine taxonomic level (e.g. euphausiids).
2. Common taxa—those that occurred in at least four (i.e. >50%) of the clusters.

3. Uncommon taxa—those that occurred in three or fewer clusters, but were found in more than 50% of the samples from any particular cluster and thus were quite important in defining clusters.
4. Rare taxa—those that occurred in less than four clusters, and in all cases in less than 50% of the samples within any given cluster. These taxa were not important in discriminating the clusters.

Cluster ▲: Occurred principally on the shelf to the west of the Aleutian Islands, with one sample on the eastern Aleutian shelf and one sample on the shelf west of Vancouver Island, British Columbia. Phytoplankton were common, with all of the taxa listed in Table 1 under ‘Ubiquitous’ and ‘Common’ occurring in at least 60% of the samples (except *Rhizosolenia styliformis* and *Coscinodiscus concinnus*) and additionally, *R. hebetata semispina*. Oceanic microzooplankton were absent as were the younger stages of *Neocalanus plumchrus* and

Table 1
Plankton taxa recorded from CPR samples in June 2002 and used in the cluster/MDS analyses

Ubiquitous taxa	Common taxa	Uncommon taxa	Rare taxa	
<i>Chaetoceros</i> spp. (Phaeoceros)	<i>Ceratium pentagonum</i>	<i>Ceratium longipes</i>	<i>Actiniscus pentasterias</i>	<i>Ditylum brightwellii</i>
<i>Corethron criophilum</i>	<i>Chaetoceros</i> spp. (Hyalochaetes)	<i>Pseudonitzschia seriata</i>	<i>Blepharocysta paulsenii</i>	<i>Exuviaella</i> spp.
<i>Coscinodiscus</i> spp.	<i>Coscinodiscus concinnus</i>	<i>Proboscia alata</i>	<i>Ceratium arcticum</i>	<i>Fragilaria</i> spp.
<i>Neodenticula seminae</i>	<i>Protoperdinium</i> spp.	<i>Proboscia inermis</i>	<i>Ceratium furca</i>	<i>Gonyaulax</i> spp.
<i>Rhizosolenia styliformis</i>	<i>Rhizosolenia hebetata</i> <i>semispina</i> Silicoflagellatae <i>Thalassiosira</i> spp. <i>Thalassiothrix</i> <i>longissima</i>		<i>Ceratium fusus</i> <i>Ceratium horridum</i> <i>Ceratium lineatum</i> <i>Ceratium massiliense</i> Coccolithaceae <i>Cylindrotheca</i> <i>closterium</i> <i>Dinophysis</i> spp.	<i>Halosphaera</i> spp. <i>Navicula</i> spp. <i>Pseudonitzschia</i> <i>delicatissima</i> <i>Rhizosolenia alata</i> <i>curvirostris</i> <i>Guinardia delicatula</i>
Foraminifera	<i>Parafavella gigantean</i>		<i>Ptychocyclus</i> spp.	
<i>Calanus</i> spp. I–V	<i>Acartia</i> spp.	<i>Calanus marshallae</i> V+	<i>Acartia longiremis</i>	Euphausiacea calyptopis
Euphausiacea	Chaetognatha adult	<i>Calanus pacificus</i> V+	<i>Acartia tumida</i>	Euphausiacea eggs
Hyperiid	Chaetognatha juvenile	<i>Clione limacina</i>	<i>Centropages abdominalis</i>	Fish eggs
<i>Limacina helicina</i>	Larvacea	Decapoda larvae	cirripede larva	Fish larvae
<i>Neocalanus plumchrus</i> IV	<i>Metridia pacifica</i>	<i>Neocalanus cristatus</i> V+	<i>Clausocalanus</i> spp.	<i>Metridia</i> spp. I–V
<i>Neocalanus plumchrus</i> V	<i>Neocalanus plumchrus</i> II		<i>Clione limacina</i>	<i>Nannocalanus minor</i>
<i>Oithona</i> spp.	<i>Neocalanus plumchrus</i> III		Coelenterata	<i>Neocalanus cristatus</i> I–V
	<i>Neocalanus</i> sp. (small) prob.			
<i>Pseudocalanus</i> spp. V+	<i>flemingeri</i>		Echinoderm larvae <i>Eucalanus bungii</i>	<i>Pontella pulvinata</i> Sergestidae

In each column, phytoplankton are listed first, followed by microzooplankton (only a few taxa) and then mesozooplankton. See text for explanation of column headings.

N. flemingeri (stages II and III). Decapod larvae occurred in 80% of the samples (but only otherwise occurred in cluster +). The ubiquitous taxa (euphausiids, hyperiids, *Pseudocalanus* spp. and *Limacina helicina*) were important as were the juvenile stages of calanid copepods. The diversity of phytoplankton taxa, including the coastal forms of *Chaetoceros* (hyalochaetes; Cupp, 1943), the absence of oceanic microzooplankton, and the presence of decapod larvae are characteristic of plankton from a continental shelf.

Cluster +: Was composed of shelf and near-shelf samples, predominantly to the east of Unimak Pass (through the Aleutians), to the east of the exit from the Bering Sea (also in shallow waters), and west of the British Columbia shelf. There were no important phytoplankton in this cluster, and many of the ‘Common’ phytoplankton taxa were absent. Some

ubiquitous zooplankton, including *Pseudocalanus* spp., euphausiids and hyperiids, were important in this cluster. Moreover, the shelf copepod *Calanus marshallae* was a discriminating species, occurring in more than 50% of the samples. This species also occurred in a few of the samples in cluster ▲, but probably not sufficiently to define that cluster. Although cluster + consisted of predominantly shelf samples (as did cluster ▲) *C. marshallae* was the only important shelf species. The samples from clusters + and ▲ occurred on the Aleutian shelf and were separated by Unimak Pass: cluster ▲ (rich in phytoplankton taxa) to the west and cluster + (poor in phytoplankton taxa) to the east.

Cluster ◆: Contained a large number of samples from the Bering Sea and the eastern GoA. Older stages of *N. flemingeri*, and the ubiquitous phytoplankton taxa, except *R. styliformis*, were

important; a pattern suggestive of productive oceanic waters.

Cluster ■: Was predominantly found in the western Pacific, although one sample occurred in the eastern GoA. Older stages of *N. cristatus* were a distinction of this cluster, and the pteropod *Clione limacina* was also more important here than in the other clusters where it was present, being found in 60% of the samples. *Oithona* spp. and foraminifera, which are indicative of subarctic oceanic waters, were important to this cluster (but not to clusters ▲, ◆, and +).

Cluster x. Was confined to the central GoA, although there was some overlap with cluster ◆. The samples contained a diversity of taxa of all three planktonic trophic groups (phyto-, microzoo- and mesozoo-). *Calanus pacificus* was a distinguishing species, which occurred in all samples (and only on one additional sample outside of this cluster, the single cluster ■ sample in the GoA). This is a species indicative of warmer water. Oceanic microzooplankton (foraminifera and the tintinnid *Parafavella gigantea*) were important as were several ‘uncommon’ phytoplankton species; *Pseudonitschia seriata*, *Proboscia inermis* and *Ceratium longipes*.

Cluster o. Contained samples from two distinct, widely separated regions; the western GoA and the western Pacific, off the Kuriles Islands and north-east Japan. Eight phytoplankton taxa from the ‘ubiquitous’ and ‘common’ groups and one mesozooplankton taxon (the copepod *Oithona*) were important in this cluster. Because all other zooplankton were absent, or almost absent, from the samples in this cluster, this cluster is defined by the lack of “cosmopolitan” and “common” taxa.

3.3. Seabird community structure

Seabird observations yielded more ‘samples’ (109) than the CPR (54), since surveys were almost continuous during daylight hours and all observations were included in the analysis (while only every fourth plankton sample was processed). Clusters have been plotted in three sections to reduce overlap of the symbols (Fig. 3A). Most of the seabirds were identified to species, and all to genus, so more distinct clustering results would be expected than those for the plankton data. A large number (49.9%) of the birds were recorded as ‘dark shearwaters’, a code routinely used to refer to two closely related *Puffinus* shearwaters that are very difficult to identify at sea. ‘Dark shearwaters’ were omitted from analyses.

The stress value for the MDS analysis was 0.20, suggesting that a two-dimensional plot was an adequate representation of community structure. The seabird and plankton community composition results are similar. Samples off British Columbia revealed a mixed avifauna. The o cluster became dominant farther west, followed by the ◆ and x clusters in the eastern and central GoA, respectively. The avifauna along the western GoA was also mixed, but these samples clustered together on the MDS plot (Fig. 3B). Similar to the plankton, the eastern and western coastal Aleutians were represented by distinct clusters (+ to the east and ▲ to the west) separated by Unimak Pass. These two clusters were widely separated at the top and bottom of the MDS plot, highlighting the very different composition of the bird communities between these two adjacent regions. The central/southern Bering Sea and the western Pacific formed a large cluster (□), with the western Bering Sea samples apparent as a sub-group (△) in the MDS plot. The ★ cluster occurred in a region off eastern Japan that was not sampled by the CPR due to the numerous port calls along the Japanese coast. On the MDS plot these samples resemble those from the eastern Aleutian Islands. Overall, a longitudinal gradient in the seabird community composition across the Pacific is evident on the MDS plot, with the eastern Pacific to the left, the western Pacific to the top right, and the eastern Aleutian/eastern Japan sections intermingling at the bottom.

3.4. Seabird species comprising clusters

The occurrence of different bird species was used to discriminate clusters. Based on their importance, the taxa were grouped as follows (Table 2):

1. Ubiquitous species—those that were found in almost all clusters (≥ 7), usually with a high relative abundance.
2. Common species—those that were found in 50% or more clusters and were important in at least one cluster (occurring on $> 50\%$ of the sections within that cluster).
3. Uncommon species—those that occurred on $< 50\%$ of the sections of any cluster (and were therefore not very important in distinguishing clusters).
4. Rare species—those occurring in only one or two clusters. Some of these species were found to be important to that cluster.

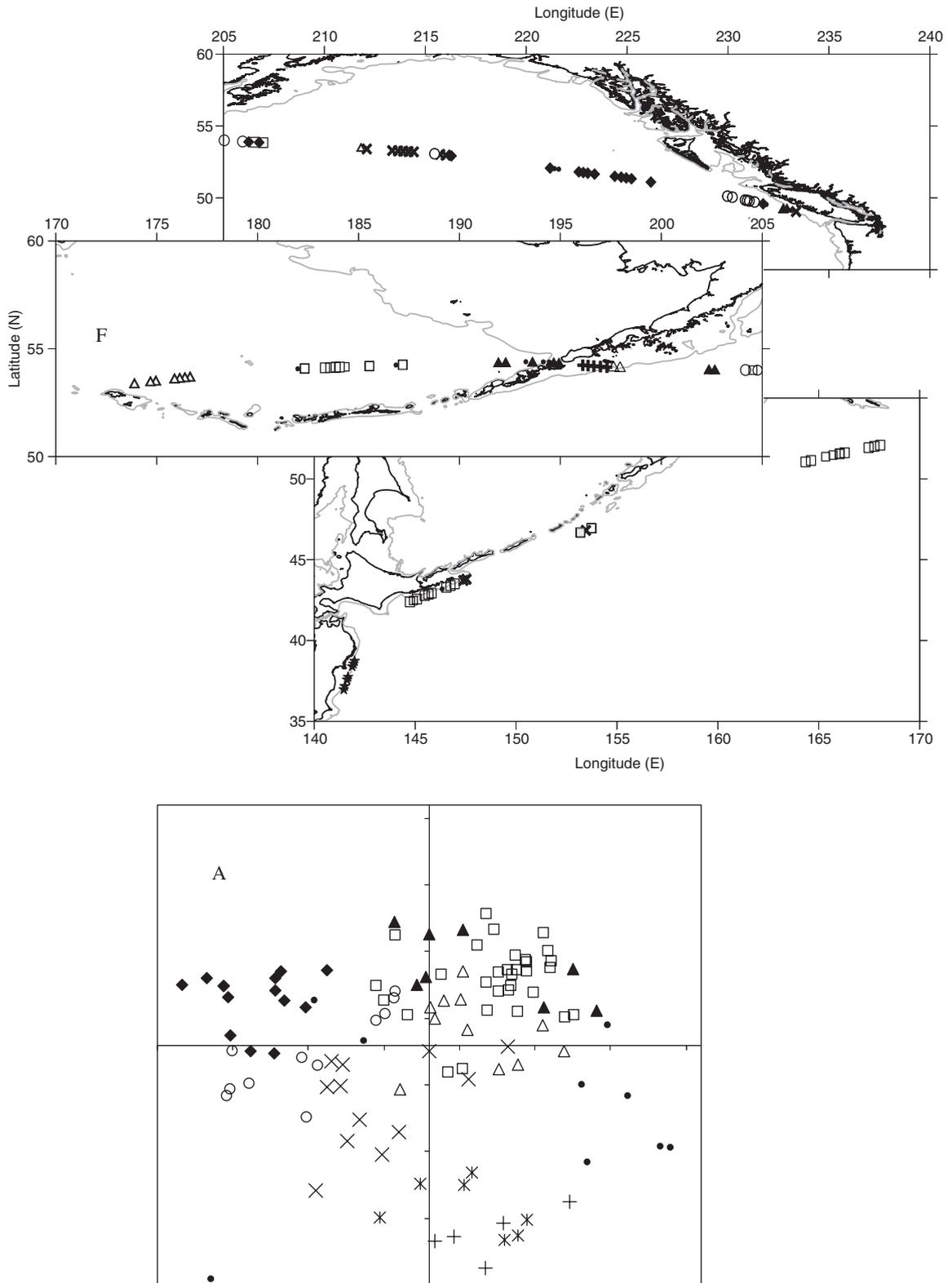


Fig. 3. Seabird community composition analysis for June 2002. (A) Results from hierarchical clustering, broken into three longitudinal sections for clarity. Separate clusters identified by symbols, plotted according to sample location (gaps indicate where night-time samples occurred that were excluded from the analyses). (B) Results from MDS analysis, the same symbol used for each sample as in Panel A. The 1000m isobath is also shown.

Table 2
Bird species recorded in June 2002 (see text for explanation of column headings)

Ubiquitous species	Common species	Uncommon species	Rare species
Black-footed Albatross	Ancient Murrelet	Alcid spp.	Parasitic Jaeger
Fork-tailed Storm-Petrel	Common Murre	Black-legged Kittiwake	Pelagic Cormorant
Leach's Storm-Petrel	Dark Shearwater sp.	Cassin's Auklet	Petrel spp.
Northern Fulmar	Glaucous-winged Gull	Common Tern	Phalarope spp.
Sooty shearwater	Laysan Albatross	Crested Auklet	Pink-footed shearwater
	Mottled Petrel	Flesh-footed shearwater	Red Phalarope
	Parakeet Auklet	Gull spp.	Red-breasted Merganser
	Short-tailed Shearwater	Herring Gull	Red-legged Kittiwake
	Thick-billed Murre	Horned Puffin	Rhinoceros Auklet
	Tufted Puffin	Jaeger sp.	Sabine's Gull
		Least Auklet	Slaty-backed Gull
		Long-tailed Jaeger	South Polar Skua
		Murphy's Petrel	Storm-Petrel spp.

Cluster o: Widespread along the eastern and western rim of the eastern subarctic gyre in the GoA in waters where the continental slope (3000 m > depth > 1000 m) meets the abyssal plain (depth > 3000 m) and at one location in the central GoA. The Leach's Storm-Petrel (*Oceanodroma leucorhoa*) was the only species to be found in all the sections in this cluster. Otherwise a suite of 12 species occurred, each on less than 50% of the sections. No Laysan Albatross (*Phoebastria immutabilis*) were recorded at these localities.

Cluster ◆: Occurred in the eastern open GoA with one section just off the British Columbia shelf and two sections further west. The bird community was not diverse, with only nine species recorded on these sections and most were 'ubiquitous' or 'common' species. Leach's Storm-Petrels were found in all sections. No Tufted Puffins (*Fratercula cirrhata*) or Laysan Albatrosses were recorded in this cluster, though both species were common elsewhere.

Cluster x: Principally restricted to the central open GoA, although two sections occurred off the Kurile Islands in the western Pacific and one section occurred on the shelf of British Columbia. Sooty Shearwaters were found in all sections, and three pelagic species (Fork-tailed Shearwaters *O. furcata*, Leach's Storm-Petrels and Mottled Petrels *Pterodroma inexpectata*) were also common.

Cluster +: Confined to the Aleutian shelf east of Unimak Pass. According to the MDS analysis, this cluster was very different to all others, except cluster ★. Tufted Puffins and dark shearwaters (spp.) occurred in all the sections of this cluster, and two subarctic alcid species not numerically abundant in any other cluster (Ancient Murrelet *Synthliboram-*

plus antiquus and Common Murre *Uria aalge*) were recorded in 80% of the bins. Two other alcid species (Thick-billed Murre *U. lomvia* and Parakeet Auklet *Aethia psittacula*) were also common in these sections, occurring 60% of the time. Notably, the Leach's Storm-Petrel, a wide-spread pelagic species, was not found in these sections but occurred in all other clusters.

Cluster ▲: Found principally on the shelf to the west of Unimak Pass with one bin at the shelf-break off Vancouver Island and two sections near the shelf-break of the eastern Aleutians. The ubiquitous Northern Fulmar (*Fulmarus glacialis*) and Fork-tailed Storm-Petrel were common in these sections as well as the Tufted Puffin. Glaucous-winged Gulls (*Larus glaucescens*) were also important (but were not important in any other cluster). Black-footed Albatross (*P. nigripes*) were not observed in this cluster, and yet they occurred in every other cluster.

Cluster △: Found in the western Bering Sea, with two sections in the western GoA. The seabird communities of these regions were quite diverse and included all of the 'ubiquitous' and 'common' species. Most important were Fork-tailed Storm-Petrels (100% of the sections), Northern Fulmars (91%), Tufted Puffins, Short-tailed Shearwaters and Laysan Albatross (82% of sections).

Cluster □: Widely distributed throughout the western Pacific and central Bering Sea, with a few sections in the western GoA. Again, this was a cluster rich in species containing all of the 'ubiquitous' and 'common' species. However, the only species that occurred in most of the sections were Northern Fulmars, Short-tailed Shearwaters and Fork-tailed Storm-Petrels. The MDS analysis shows

cluster \triangle as occurring as a group within cluster \square with both groups including very similar species. Subtle differences such as fewer occurrences of Laysan Albatross and Tufted Puffin in cluster \square , as well as different relative species abundances, are probably responsible for the observed pattern.

Cluster \star : Confined to the extreme western side of the Pacific, off Japan. Streaked Shearwaters (*Calonectris leucomelas*) and Black-tailed Gulls (*L. crassirostris*) were important species in this area, and not found in any other cluster. Similarly, no Fork-tailed Storm-Petrels or Tufted Puffins, common elsewhere, occurred in this region.

3.5. Defining MME

While both lower- and upper-trophic-level data define similar sub-regions of the North Pacific, the avifauna provides sharper faunal boundaries than the plankton data. The plankton data suggest an overlap between eastern and central GoA communities, while the bird data suggest a sharp divide at $\sim 220^\circ$ E. Nonetheless, these data highlight several abrupt transitions in community structure, which delineate distinct biological regions. A particularly fine faunal boundary was apparent at Unimak Pass, where the surveys revealed a sharp discontinuity in the plankton and seabird communities. However, identifying the precise locations of these biogeographic

boundaries was complicated by the lack of sampling at night. Thus, the boundaries we present here should be interpreted with caution, and deserve further finer-scale analyses (Fig. 4).

MME boundaries often coincided with bathymetry (Fig. 4). Both the eastern and western shelf regions (off British Columbia and the Kuril Islands) differed from adjacent oceanic regions. Similarly the boundary between the bird and plankton clusters in the western GoA and the eastern Aleutian shelf coincided with the transition from the abyssal plain to the continental slope. Faunal shifts from the Aleutian Basin to the western Bering Sea coincided with the location of Bower's Ridge. However, the biological divisions of the GoA did not coincide with bathymetry. The most likely explanation for this biogeographic discontinuity is the influence of the current systems of the eastern North Pacific. The surface circulation of the GoA derived from Argo float data for 15 May (Fig. 5) matches closely with our biological division of the eastern and central GoA regions. Our central GoA region corresponds to the eastern (northeast-ward moving) part of the Alaska Gyre and our western GoA region matches the position of the western (southwest-ward moving) part of the Alaska Gyre. Similarly, the divide at Unimak Pass is also likely related to hydrography (Stabeno et al., 2002; Ladd et al., 2005). For more details see Appendix A.

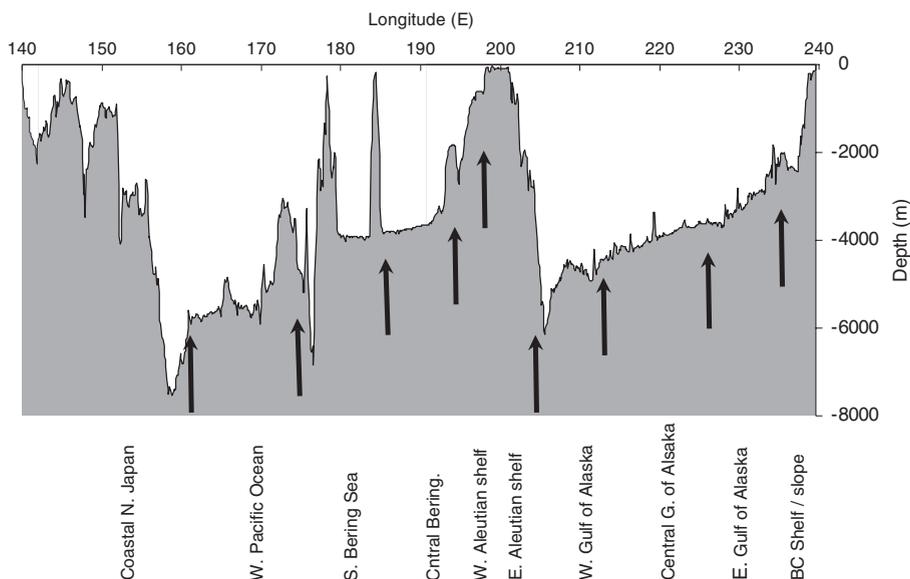


Fig. 4. Bathymetry along the survey line, extracted from the ETOPO five gridded elevation dataset. The arrows indicate the position of MME boundaries from the biological analyses.

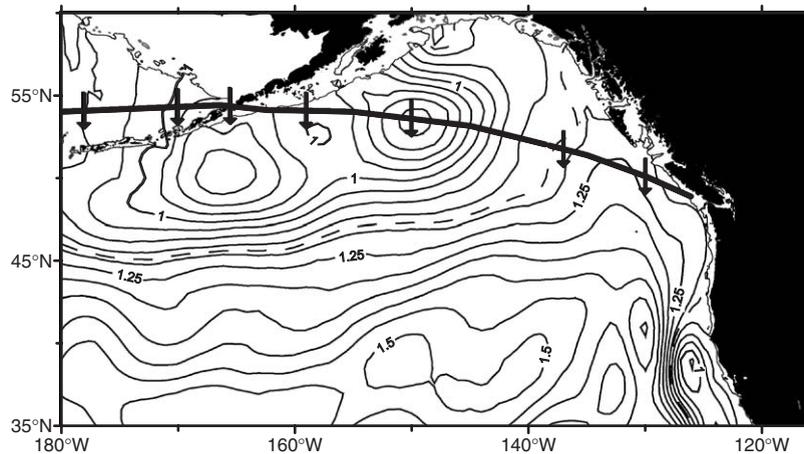


Fig. 5. Surface circulation in the Gulf of Alaska for 15 May 2002 derived from Argo float data. The dashed line represents the dividing streamline separating water that ultimately flows into the Alaska Gyre from that flowing into the California Current. The survey line is shown as a solid line and arrows indicate the position of MME boundaries. The 200 m isobath is also shown.

Table 3

Characteristics of the meso-marine ecosystems of the North Pacific, showing the mean (\pm SD) of physical and biological characteristics

MME	Depth (m)	SST ($^{\circ}$ C, from logger at \sim 7 m)	Chl <i>a</i> (mg m^{-3} , from SeaWiifs)	\sim Thermocline depth (m, from XBTs)	Mesozooplankton Biomass ($\text{mg dry weight sample}^{-1}$)	Seabird density ($\# \text{ km}^{-2}$)
BC shelf/slope	1550 (777)	10.18 (0.41)	1.62 (0.62)	10	88.92 (83.94)	4.06 (3.96)
Eastern GoA	3280 (525)	9.00 (0.46)	0.44 (0.36)	38	112.50 (63.75)	1.00 (1.06)
Central GoA	3911 (250)	8.49 (0.21)	0.30 (0.05)		39.31 (28.48)	6.34 (9.71)
Western GoA	4894 (379)	8.16 (0.25)	0.68 (0.51)	24	24.38 (39.10)	3.06 (1.32)
E. Aleutian shelf	69 (44)	7.45 (1.07)	1.42 (0.55)		71.14 (43.60)	323.40 (487.34)
W. Aleutian shelf	803 (419)	6.61 (0.41)	2.81 (2.02)		128.10 (94.54)	107.45 (156.64)
Aleutian Basin	3733 (61)	5.98 (0.28)	0.55 (0.08)	20	60.67 (33.53)	30.32 (51.88)
W. Bering Sea	3918 (43)	4.80 (0.22)	0.43 (0.08)		46.52 (21.13)	32.94 (31.00)
W. open Pacific	4686 (730)	4.79 (0.34)	0.34 (0.05)	40	3.22 (5.90)	6.70 (1.70)
Coastal N. Japan	1428 (1173)	4.76 (1.36)	5.17 (3.29)	<10	9.13 (6.93)	29.59 (72.94)

3.6. Biomass correlations in MME

Between MME, SST and phytoplankton abundance was not correlated (Table 3, Spearman $\rho = -0.079$, $p = 0.829$, $n = 10$). However, SST was correlated with mesozooplankton biomass ($\rho = 0.564$, $p = 0.089$) and seabird densities ($\rho = -0.539$, $p = 0.108$). Chlorophyll *a* concentrations were weakly correlated with mesozooplankton biomass ($\rho = 0.309$, $p = 0.385$) nor seabird densities ($\rho = 0.261$, $p = 0.467$). Mesozooplankton biomass and seabird density were not correlated ($\rho = 0.139$, $p = 0.701$). Nonetheless, the two MME with the highest mesozooplankton biomass (Aleutian coastal and southern Bering Sea), also showed high chlorophyll *a* concentrations and supported the highest seabird densities.

Mesozooplankton biomass was significantly different between most ($\frac{2}{9}$ pairwise tests) pairs of adjacent MMEs (Mann–Whitney U-tests; $p < 0.05$ for all comparisons). Exceptions were between the British Columbia shelf and the eastern GoA, and between the central and western southern Bering Sea. Additionally, there were insufficient samples ($n = 3$) from the western Aleutian shelf for a significance test. However, the mean biomass was higher than for both the eastern Aleutian shelf and central Bering Sea regions to either side. These results highlight that the MMEs we documented using mesozooplankton community structure also differ in their plankton standing stocks.

The density of seabirds was significantly different only between adjacent shelf and oceanic areas ($\frac{2}{9}$ pairwise tests): coastal British Columbia/the

eastern GoA, western GoA/Aleutians, and the western Pacific/western Bering Sea. This result suggests that the MME divisions were mostly caused by changes in species composition along the transect, rather than by shifts in overall abundance. However, seabird densities (birds km⁻²) in the western North Pacific (6.7, SD = 1.70) were higher than densities in the eastern (1.0, SD = 1.06), central (6.3, SD = 9.7) and western (3.1, SD = 1.32) GoA, underscoring pronounced differences in productivity between the eastern and western North Pacific.

3.7. Interannual persistence of MME

Although the full suite of variables was not available for other years, two preceding June transects (2000, 2001) surveyed plankton distributions and one subsequent June transect (2003) surveyed seabird distributions. We used these transects to examine the year-to-year persistence of the MMEs. The same community analyses described above were carried out using these data, and showed that patterns of community structure are consistent from year to year, especially in the GoA and eastern Bering Sea where coverage in all years was good (Figs. 6 and 7). MDS analyses are not shown but confirm the cluster analysis. Stress

values for June 2000 (plankton = 0.19), June 2001 (plankton = 0.25) and June 2003 (bird = 0.22) are similar to those noted for 2002. These analyses show only that changes in community structure occur in the same localities in multiple years.

The GoA plankton communities are, in fact, more clearly divided into eastern, western and central regions in 2000 and 2001 than they were in 2002, but there is no evidence for a boundary at Unimak Pass in 2001 (and insufficient sampling in 2000). The southern Bering Sea and the region southeast of Kamchatka also show some separation in 2001, and in 2000 the western Pacific (including the Bering Sea) shows overlapping of clusters. The transect was also shorter in 2000 so there are no data for the Kurile Islands/north east Japan region.

The timing of the ship's departure in June 2003 was such that the periods of day occurred in almost the exact locations where night had occurred in June 2002, so that the bird observations were made in different locations in each year. The transect crossed the GoA about 2° further north than in 2002 but the change from eastern to central GoA is clear at about 224° E and from central to western GoA occurs at about 212° E. These positions agree with the boundary positions determined for 2002 (Fig. 4). In 2003, the ship went through Unimak Pass at

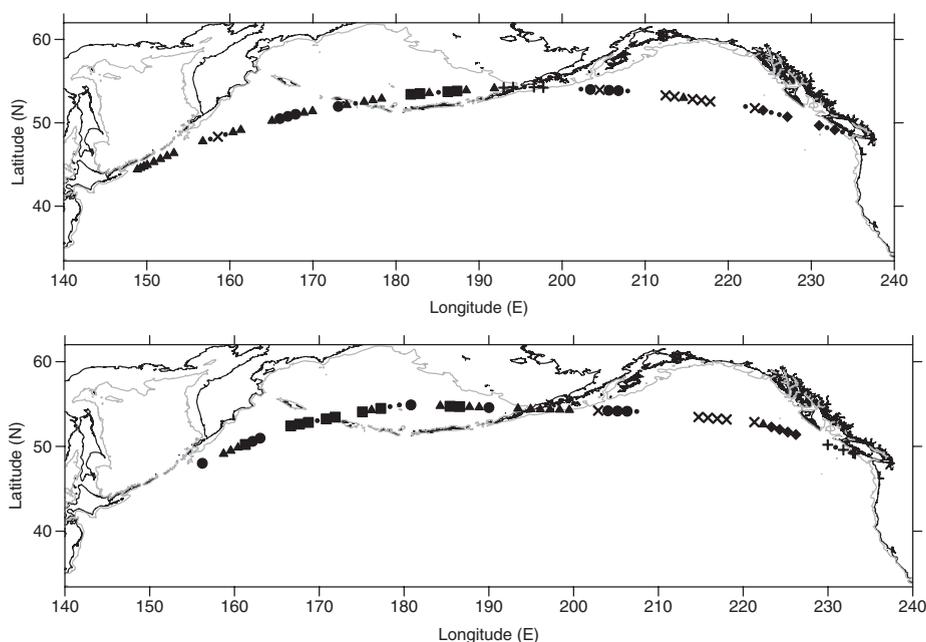


Fig. 6. Plankton community composition analysis for June 2001 (upper panel) and June 2000 (lower panel). Results from hierarchical clustering, separate clusters identified by symbols plotted according to sample location (gaps indicate where night-time samples occurred that were excluded from the analyses). The 1000-m isobath is also shown.

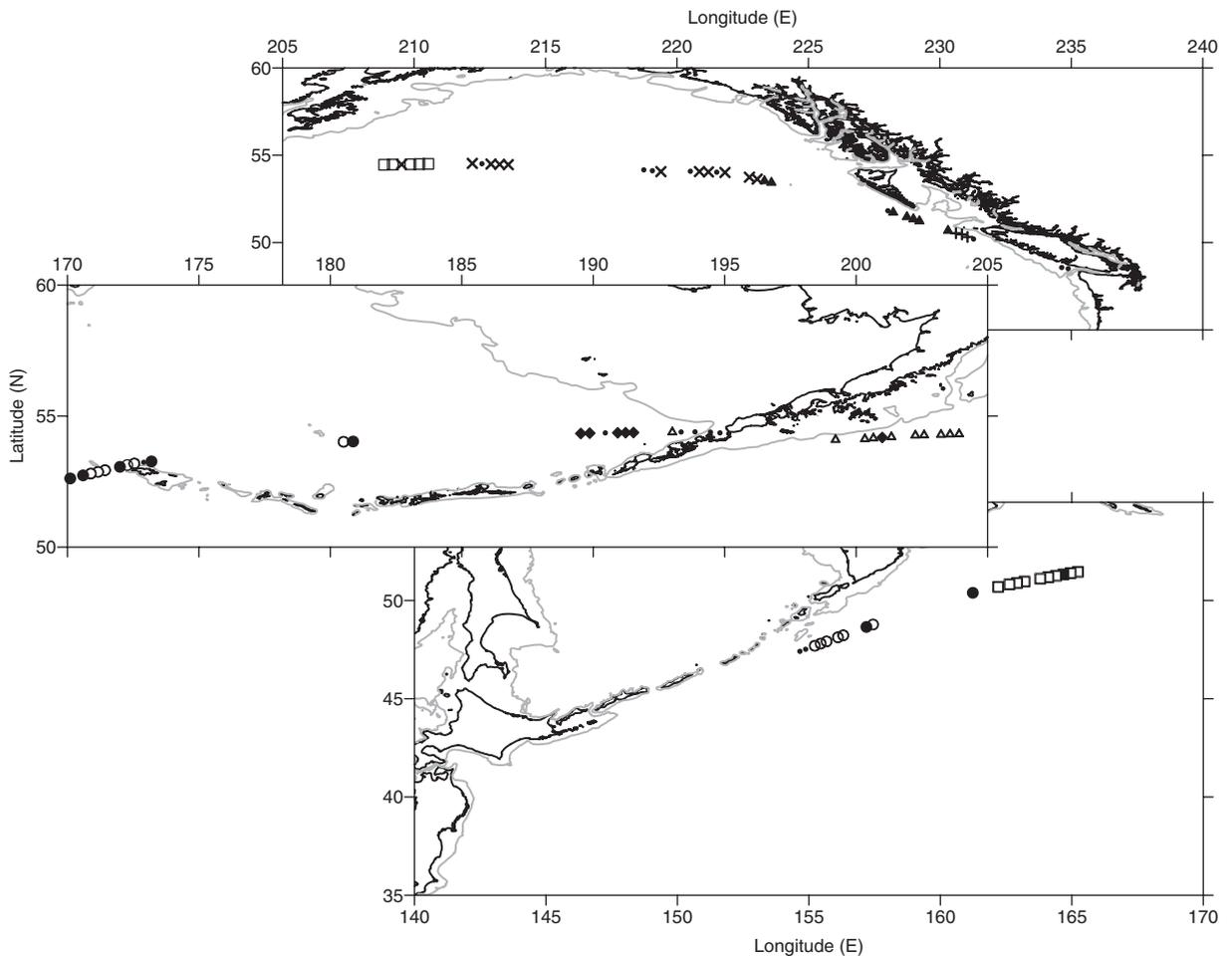


Fig. 7. Seabird community composition analysis for June 2003. Results from hierarchical clustering, separate clusters identified by symbols plotted according to sample location (gaps indicate where night-time samples occurred that were excluded from the analyses). The 1000-m isobath is also shown.

approximately sunrise, and as a result there are no eastern Aleutian shelf observations available to determine whether or not there was an abrupt community change similar to that observed in 2002.

3.8. Taxonomic diversity

We examined the number of taxa (“richness”) recorded in each MME in each year, by trophic group (phytoplankton, zooplankton, seabirds), as the simplest expression of diversity (Fig. 8, note that the identification of plankton to varying taxonomic levels may disguise the true species diversity). Variability was high; however, analyses of variance (single factor ANOVA) showed that there were statistically significant differences in the number of taxa recorded on the samples/sections of each MME

for all three trophic groups in each year, with the one exception being zooplankton in 2001 (in all other cases $p < 0.002$). Clearly, not all MME were significantly different from all over MME, but this result shows that in addition to the changes in biomass between MME described in Section 3.6, taxa diversity also changes between MME. In addition to significant changes in diversity across the North Pacific, consistent patterns were evident from year to year and between trophic groups. The panels in Fig. 8 show a ‘W’ pattern with diversity being highest at the shelf regions and lowest in the open ocean regions. The Aleutian Islands (between 190 and 200° E) showed the highest number of taxa in all three trophic groups so not only is this region richest in terms of biomass, but also in the number of species. Lowest numbers were generally found in

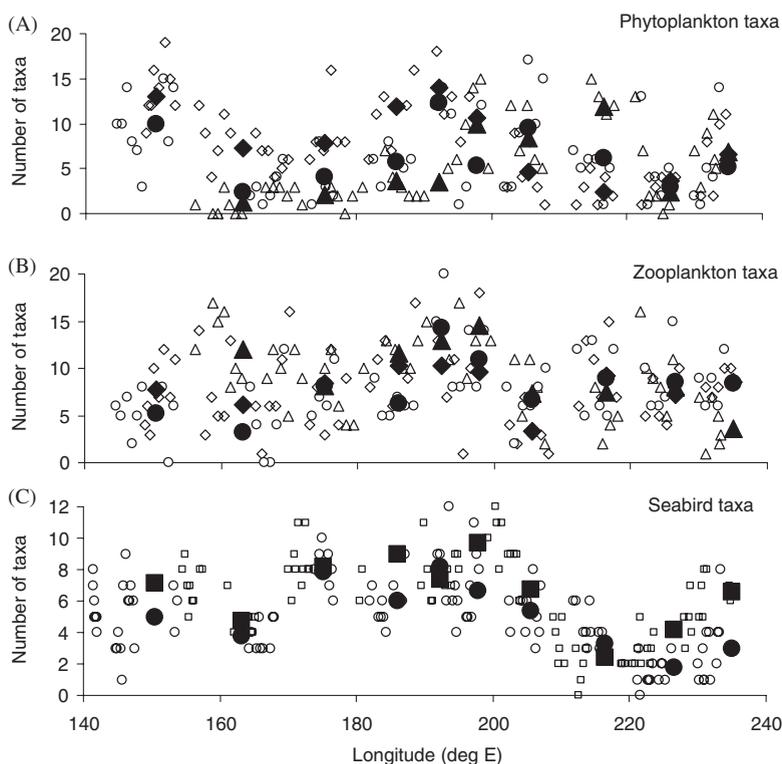


Fig. 8. Number of taxa per sample (plankton, panels A and B) or section (seabirds, panel C) for each year. Circles = 2002, diamonds = 2001, triangles = 2000, squares = 2003 (birds only). The large filled symbols indicate the mean for each MME, plotted at the mid-point.

the eastern GoA and western Pacific MME. The central GoA showed higher numbers of plankton taxa (except phytoplankton in 2001) but the seabirds showed generally low diversity here too, increasing instead in the western GoA.

4. Discussion

We have described an inter-disciplinary approach to defining and characterizing meso-marine ecosystems (or MME) in the North Pacific Ocean. Using biological organisms, supported by information on bathymetry, current systems, and hydrography (Appendix A), we identified 10 MME along a survey track from southern British Columbia, Canada, to Japan along a 'great circle' route through the Gulf of Alaska, southern Bering Sea, and western North Pacific. The 10 MME are: (1) British Columbia shelf/slope, (2) eastern GoA, (3) central GoA, (4) western GoA, (5) eastern and (6) western Aleutian shelf (separated by Unimak Pass), (7) south-central Bering Sea (also known as the Aleutian Basin), (8) southwestern Bering Sea, (9)

western open Pacific, and (10) coastal northern Japan (and the Kurile Islands shelf). We also demonstrated some temporal persistence in MME delineations. However, the persistence of these spatial patterns should be addressed more thoroughly (i.e., with longer time series) before this approach can be widely applied to management and conservation of marine fisheries and wildlife.

4.1. MME and "hot spots" of the North Pacific

The MME we defined differed in the abundance and composition of secondary (zooplankton) and tertiary (seabird) consumers. This is important as it probably reflects variation in ocean productivity at a scale finer than that of existing LMEs (PICES, 2004). While direct correlations between chlorophyll *a* concentrations, mesozooplankton biomass and seabird density within MME were not especially compelling, certain MME had the greatest abundance of each (e.g., eastern and western Aleutian shelf), and the correlation between mesozooplankton biomass and seabird densities was positive and

approaching significance. Data on the larger invertebrates and forage fish (e.g., squid and myctophids, the prey of seabirds in the open ocean MME) would be helpful in establishing relationships between these ecosystem constituents. The food preferences and foraging guilds of the different seabird species could also be used to indicate the relative variability of mid-trophic-level prey in each MME (Hunt et al., 2000).

While the MME described here are in agreement with the previously described physical oceanographic domains (Favorite et al., 1976) and biogeographic provinces (Longhurst, 1998), they provide a novel and finer-scale perspective on within-LME spatial variability and ecosystem dynamics. For example, the Eastern Pacific Subarctic Gyre described by Longhurst encompasses the three MME of the GoA. We hypothesize that circulation of the GoA, comprising the subarctic current and splitting of this structure into the Alaska and California Currents, gives rise to these distinct biological communities. The ‘Dilute’ and ‘Ridge’ domains in the western and eastern GoA (Fig. 41 in Favorite et al., 1976) also resemble our MME in the western and eastern GoA. These distinct domains are likely influenced by the prevailing current systems and the input of freshwater run off from the west coast of North America.

An understanding of the patterns of meso-scale variability in oceanographic processes and productivity encapsulated in these MME is critical to the management of fishery and wildlife resources. In particular, a management approach based on the delineation of MME nested within a larger LME framework may be especially suitable for spatially explicit management and conservation efforts, such as the implementation of time-area fishery closures or the establishment of marine protected areas targeting representative marine ecosystems and/or “hotspots” of biological activity (Pederson et al., 2005).

4.2. Climate change and MME

In recent decades, the North Pacific has experienced at least two ‘regime’ shifts (1976–1977 and 1989–1990) that have affected the productivity and structure of marine ecosystems and the distribution, abundance, and productivity of upper-trophic-level marine predators (Sydeman et al., 2001; Hyrenbach and Veit, 2003; Venrick et al., 2003) and mesozooplankton (Batten and Welch, 2004; Wooster and

Zhang, 2004). Another shift may have occurred in 1998–1999 (Peterson and Schwing, 2003). During these shifts, changes in atmospheric pressure have lead to variation in patterns of wind stress and surface circulation (Francis et al., 1998; Schwing et al., 2000; Mantua and Hare, 2002). Interannual variability and longer-term variation in the spatial distribution of atmospheric pressure cells in the North Pacific may affect the boundaries and dynamics of the MME described herein by shifting the extent and location of water masses that influence the distribution and abundance of plankton and seabirds. We also documented a pattern of declining SST and increasing plankton standing stocks from east to west in the GoA (Table 3), and such spatial gradients in physics and biology may also be affected by climate. This idea (of shifting onshore-offshore and latitudinal–longitudinal gradients in community structure) is not new. Indeed, previous studies of large-scale spatial gradients in ocean productivity, prey biomass, and seabird abundance have documented these kinds of gradients (Gould and Piatt, 1993; Vinogradov et al., 1997; Shimoto et al., 1998). Moreover, seabird and zooplankton communities in the North Pacific may be structured by frontal systems (Fager and McGowan, 1963; Nishikawa et al., 1995; O’Hara et al., this volume). Temperature anomalies generated by changes in wind forcing may also alter the depth and degree of vertical mixing, nutrient input and primary production (McGowan et al., 2003). Such changes in primary production and its cascading effects through MME are likely to influence other top marine predators (including tunas [*Thunnus* spp], salmon [*Onchorhynchus* spp], cetaceans [*Balaenoptera* spp.] and pinnipeds) that migrate to specific regions of the North Pacific to forage during the boreal summer (Polovina, 1996; Polovina et al., 2000). Therefore, continuing efforts to couple predator densities with primary and secondary productivity in North Pacific MME, including assessments of the magnitude and lags in numerical responses should be fruitful in understanding the significance of short- and long-term climate variability and changes to these marine ecosystems.

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Appendix A. Details of North Pacific MME

The mean values of environmental and biological variables (depth, SST, chlorophyll *a*, mesozooplankton biomass and seabird density) within each MME (refer to Table 3 for actual values throughout this section) and the XBT temperature-depth profiles (Fig. A.1) helped interpret the observed biological patterns.

British Columbia shelf/slope: Biological sampling began on the outer edge of the continental shelf and extended across the shelf-break and slope. All plankton samples and bird observations in this region were within 95 km of the 20 m isobath. Chlorophyll *a* concentrations were relatively high and the SST was the warmest along the entire survey transect. The water column was strongly stratified off BC (profile 1 in Fig. A.1). Zooplankton biomass was relatively high, seabird densities were very low and adjacent samples/sections showed a highly variable community composition (Figs. 2 and 3). Because plankton distributions and abundance respond to hydrographic variability, associated with coastal upwelling and frontal systems (e.g., Mackas and Sefton, 1982; Allen et al., 2001), we hypothesize that unresolved small-scale physical processes associated with bathymetric (e.g., shelf-break) and hydrographic (e.g., eddies) features contributed to the observed variability. Similarly, we observed a high degree of interannual variability in the composition of the British Columbia shelf-slope avifauna, also likely related to the dynamics of local oceanographic conditions and prey availabil-

ity. Nevertheless, the spring-time (June) avifauna in this MME appears to differ from that found in waters beyond the continental slope. In particular, the locally breeding species (alcids and gulls) are numerically dominant close to shore, while non-breeding petrels are most numerous in offshore waters.

Eastern GoA: This region covers the base of the slope. Chlorophyll *a* concentrations were higher and more variable than the central GoA. This region is prone to mesoscale eddies, which form along the eastern continental margin of the northeast Pacific in winter, detach from the continental shelf in spring, and propagate westwards. These features are evident in satellite altimetry images as positive sea surface height anomalies, and as regions of higher chlorophyll *a* because of the entrained and advected shelf water (Okkonen et al., 2003). Our transect passed through such an eddy in June 2002 at the western extremity of this region. An XBT was deployed on the south west edge of the eddy, which possibly accounts for the shape of the vertical temperature data (profile 2 in Fig. A.1) with a deeper layer of warm water between 130 and 210 m. Warm water anomalies below 100 m depth are characteristic of anti-cyclonic eddies (Crawford, 2002; Whitney and Robert, 2002). Conversely, the near surface temperature was not very variable in this region. According to the CPR data, this region supported a relatively rich phytoplankton community, which probably accounted for the high mesozooplankton biomass (higher mean than for the adjacent shelf/slope region). However, relatively few seabirds occurred in this region, suggesting that intermediate trophic level prey species such as squid/forage fish were not numerous or available within the diving depths of these predators.

Central GoA: Oceanic depths were sampled in this region of little water depth variability. No XBT profiles were taken in this region in June 2002, and SST was consistent across the region. XBTs deployed in June of previous years (2000 and 2001) show that there is variability in the vertical structure within this region, with warm, presumably more saline layers sometimes occurring at 100–200 m depth. Occasionally colder layers are evident between 50 and 100 m. Chlorophyll *a* was low, the lowest mean concentration of any of the MMEs sampled. Previous studies have shown that the central GoA is dominated by small (<5 μm) phytoplankton cells which, unlike the larger diatoms, appear not to be severely iron limited

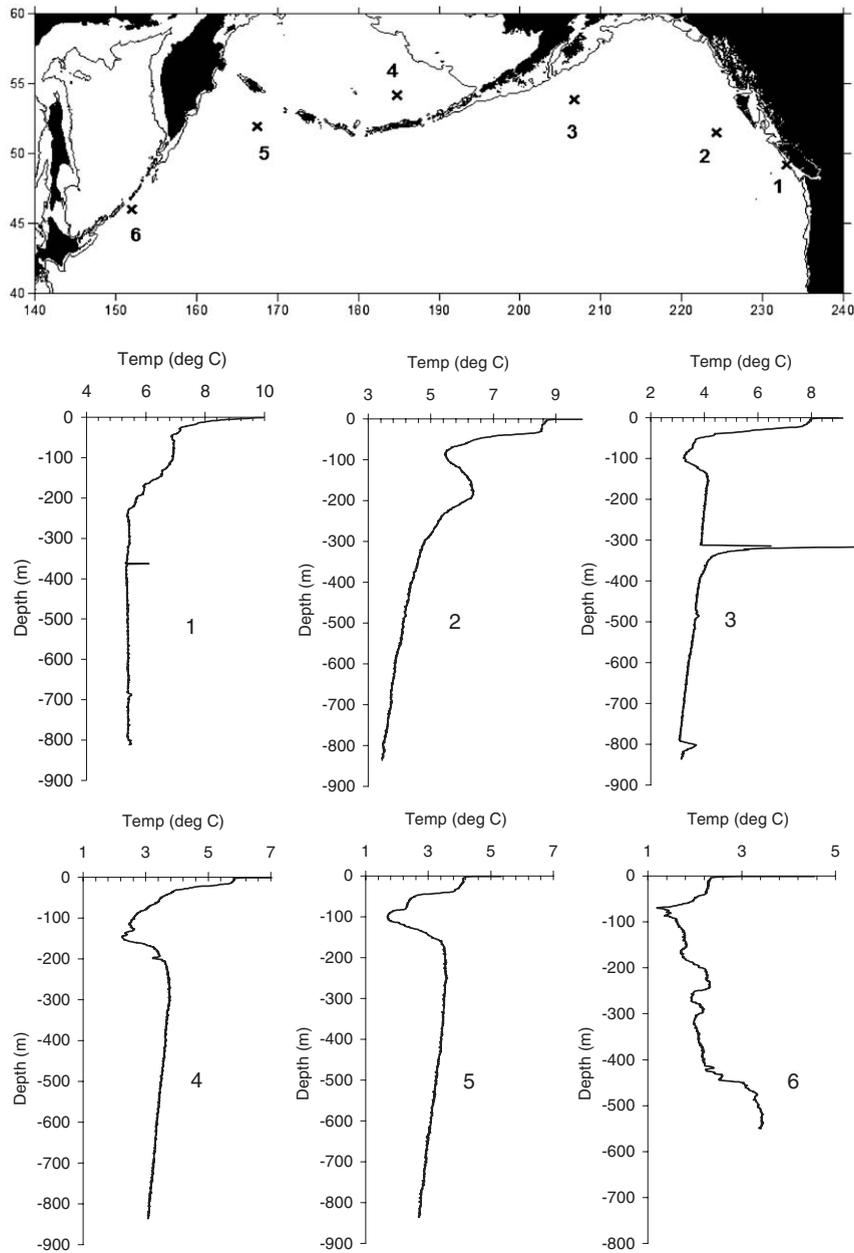


Fig. A.1. Temperature depth profiles from XBTs deployed along the transect in June 2002. Each profile is labeled with a number that also shows its position on the accompanying map.

(Harrison et al., 1999). The productivity of this region is consumed by the microzooplankton ($<200\ \mu\text{m}$), which exert a top-down control and keep the chlorophyll *a* concentrations low (Taniuchi, 1999). The abundant microzooplankton was a distinguishing feature of the CPR samples from this region. Phytoplankton cells $<5\ \mu\text{m}$ are mostly too small to be directly consumed by mesozoo-

plankton ($\sim 1\text{--}4\ \text{mm}$), which instead feed on the ciliates and flagellates that comprise the microzooplankton (Gentleman et al., 2003). The copepod *C. pacificus*, was a zooplankton species characteristic of this region. There are thought to be different subspecies of *C. pacificus*, one associated with the central North Pacific and the West wind drift (probably the form found on this transect),

genetically distinct from the type found in the California Current (Bucklin and LaJeunesse, 1994). Surface circulation patterns (Fig. 5) show that this region encompasses the northward flowing subarctic current, which contribute to the Alaskan Current and presumably advect this species into the region. Seabird densities were the highest east of the Aleutian Islands with the shearwaters (Sooty and Short-tailed) and petrels (Leach's Storm-Petrel and Mottled Petrel) being the numerically dominant species. These seabirds are forage over deep waters on fish and squid, although large plankton (such as euphausiids and jellies) may also be consumed (reviewed in Hunt et al., 2000).

Western GoA: This region encompasses abyssal depths but is adjacent to the continental slope along the Aleutian Island chain (Fig. 4); the survey crossed within 61 km of the 1000 m isobath. Waters comprise the centre and western half of the Alaska Gyre (Fig. 5) with a sharp thermocline at about 38 m (profile 3 in Fig. A.1) and consistent surface temperatures across the region. While the mean chlorophyll *a* is higher in this region than in the eastern and central GoA, we documented substantial spatial variability along the survey transect. Chlorophyll *a* values ranged from a low of 0.2 mg m^{-3} at the centre of the Gyre, rising to a high of 1.8 mg m^{-3} at the outer edge of the gyre, and declining to 0.4 mg m^{-3} at the western end of the region. Anti-cyclonic eddies at the rim of the GoA can entrain coastal water and sweep it seaward (Okkonen et al., 2003) which may explain the elevated chlorophyll *a* values. Phytoplankton taxa were common in the CPR samples, with the presence of large-sized diatoms (*Chaetoceros* spp., *Thalassiothrix longissima* and *Neodenticula* spp.) setting the samples from this region apart from other areas. However, zooplankton grazers were scarce, with only some copepods (*Oithona* spp.) present in large numbers. Seabirds were also in low numbers in this region, with no seabirds recorded during one of the survey sections. These observations suggest that although large-sized phytoplankton were numerous in this region, their standing stocks had not translated into higher secondary productivity of the grazer populations. If the increase in phytoplankton had occurred just prior to our sampling, it may be too early to see a secondary production response lagging behind due to the longer generation times of the grazers.

Eastern Aleutian shelf: The region comprises the continental slope and the shelf to the east of Unimak

Pass and shallow waters near the pass itself. Most of the environmental variables show a high degree of variability within this region (Table 3). Sea surface temperature declined sharply with decreasing water depth, and chlorophyll *a* concentrations increased from the low values at the boundary with the western GoA (1.3 mg m^{-3}) to a peak at the shelf-break (2.5 mg m^{-3}), and subsequently declined over the shelf (0.4 mg m^{-3}) just before the transect reached Unimak Pass. These results are in agreement with previous ocean productivity measurements, which suggest that the Aleutian chain is characterized by a band of elevated productivity ($150\text{--}200 \text{ g C m}^{-2} \text{ y}^{-1}$), higher than values found in deeper waters to the north (Bering Sea) and south (Pacific Ocean) (Springer et al., 1996).

Although the environmental conditions were very variable, the biological data showed similar community structure across this shelf region. The plankton assemblage was characterized by a lack of phytoplankton taxa (in contrast to the region west of Unimak Pass) and was distinguished by the presence of copepods, including ubiquitous taxa and the shelf species *Calanus marshallae*. Mesozooplankton biomass was high in this region, similar to the slope waters off British Columbia, but lower than the region west of Unimak Pass. In contrast, this region contained the highest bird densities observed during this survey, with densities three times higher than to the west of Unimak Pass. There was considerable variability in density across the region, with minimum densities of 9 birds km^{-2} at the shelf-break rapidly rising to a maximum of $1471 \text{ birds km}^{-2}$ in the mid shelf region and subsequently declining towards Unimak Pass. The bird community was distinctly different from other regions, in terms of which species were present (Ancient Murrelets, Common Murres, Thick-billed Murres and Parakeet Auklets) and absent (Leach's Storm-Petrel).

Western Aleutian shelf: North of Unimak Pass, the shelf widens considerably to cover an area almost half the size of the Bering Sea. The survey transect, however, ventured south of this widening and soon crossed the shelf-break (200 m depth) into deeper waters of the Aleutian Basin. The community analyses revealed distinct plankton and seabird assemblages, different from both the adjacent deep-water areas of the Bering Sea and the shelf region to the east of Unimak Pass. Even though the two MMEs east and west of Unimak Pass were very similar in terms of physical variables (e.g., seafloor

depth and SST, Table 3) in June 2002, their biology differed greatly. Chlorophyll *a* concentrations were, on average, twice as high in the west than in the east. The lowest values (0.6 mg m^{-3}) were observed at Unimak Pass, where tidal mixing suppresses primary production in the Pass, and the highest values (6.8 mg m^{-3}) occurred over the slope farther to the west, in water depths of 1400 m. The CPR data showed phytoplankton to be abundant here, which suggests that the chlorophyll *a* signal originated, at least partly, from the presence of the larger-sized diatoms retained by the CPR.

Nutrients mixed into the surface by the strong tidal flows in Unimak Pass and other similar narrow passes between Unimak and Seguam Islands in the Aleutian chain, are carried into the Bering Sea and transported northwards, stimulating primary production in more stratified regions downstream from the turbulent passes. The elevated mesozooplankton biomass in the CPR samples (the highest documented in any region) was likely supported by this elevated primary production. Seabird densities in 2002 were high, though lower than to the east, with the Glaucous-winged Gull (*L. glaucescens*) the numerically dominant species in this region. Dietary analyses of foraging Short-tailed Shearwaters, Northern Fulmars and Least Auklets (*A. pusilla*) showed that zooplankton (mostly euphausiids but also *Neocalanus* copepods) comprised the majority of the diet in the eastern Aleutian Islands (Jahncke et al., in 2005). Our CPR transect documented high densities of mesozooplankton on both sides of the Aleutians, underscoring the importance of this area for foraging seabirds. Many millions of seabirds were breeding on the Aleutian Islands during the period of our survey, in addition to the estimated 18 million Short-tailed Shearwaters that visit the Bering Sea during the boreal summer (Hunt et al., 2000; Stephensen and Irons, 2003).

The Aleutian Basin: The deep waters of the southern Bering Sea contained biological communities distinct from the adjacent Aleutian Island shelf, and dominated by deep-water oceanic species. The plankton assemblages were similar to those found in the eastern GoA, and the avifauna resembled the community documented in the western Pacific. The physical properties within this region were relatively homogeneous; mean SST and chlorophyll *a* concentrations showed low variance (Table 3). The depth profile of temperature from this region (profile 4 in Fig. A.1) showed cooler water from about 30 to 200 m. The phytoplankton

in this region was very diverse and the chlorophyll *a* levels were similar to those from the eastern GoA. Mesozooplankton biomass was high for a deep-water region, with the community including two common and broadly distributed copepod species, the stage V copepodites of *N. flemingeri* and *N. plumchrus*. These data are suggestive of a productive oceanic environment. Similarly, seabird densities were also high; lower than on the Aleutian shelf but higher than in the GoA. The seabird species (Northern Fulmar, Short-tailed Shearwater and Fork-tailed Storm-Petrel) common on all the survey sections from this region in June 2002 feed on a variety of prey, but all are known to consume large crustacean zooplankton (Hunt et al., 2000).

South Western Bering Sea: This deep water region is separated from the Aleutian Basin by Bower's Ridge and from the western open Pacific by the Aleutian Chain and the Commander Islands. In fact, the survey transect passed between these two archipelagos (Fig. 1). The biological properties (chlorophyll *a*, mesozooplankton abundance, and seabird densities) were similar to those in the Aleutian Basin. However, a peculiar community composition which we attributed to the proximity of the islands, set this region apart from the other areas of the Bering Sea. This near-shore influence is underscored by evidence that the plankton samples and the seabird sections were partly clustered with samples from the eastern Aleutian shelf region.

Western Open Pacific: The survey transect bisected the western subarctic Gyre, crossing the Oyashio Current en route to Japan (Fig. 1). This region was characterized by fairly deep and consistent bathymetry. The vertical temperature structure in this region (profile 5 in Fig. A.1) was taken in the gyre and, like other profiles taken across this region in June 2000, reveals a deep, cold layer stretching between about 40 and 180 m. SSTs were the coldest and water depths were the greatest along the entire survey transect. Chlorophyll *a* concentration was low, only slightly higher than in the GoA, and the mean mesozooplankton biomass was much lower than in any other region, particularly compared with the mean for the Alaskan Gyre. The seabird abundance was also very low, similar to the densities observed in the GoA. All of these data are suggestive of low productivity conditions within this oceanic MME.

North-east Japan/Kurile Islands: This section of the transect is a complex area, where the cold waters of the Oyashio current mix with the warm

subtropical Kuroshio current, with variable bathymetry. This heterogeneity is underscored by the large fluctuations in SST along the survey transect and by the complicated thermal structure evident in the XBT profile (profile 6 in Fig. A.1). At least two eddies with positive sea surface height (SSH) anomalies were evident at the time of the transect, in a region where both warm and cool core rings are frequent. Taniguchi (1999) referred to this area as a Mixed Water Region and notes that ‘the oceanographic conditions are complicated and continuously changing, both horizontally and vertically’. Moreover, there is evidence that the location of hydrographic fronts in this region influences zooplankton aggregation and community structure (Nishikawa et al., 1995). Chlorophyll *a* was the highest of any of the regions we surveyed, though highly variable, and mesozooplankton biomass was low. These results are in agreement with reports of low microzooplankton stocks for the Oyashio region, which are unable to graze down the available phytoplankton stocks, leading to high chlorophyll *a* concentrations in this region (Taniguchi, 1999). The community composition of the plankton samples from this region was characterized by the absence of pervasive taxa rather than the presence of indicator species, with these samples clustering with those from the western GoA. Overall seabird densities were five times higher than in the GoA. We did not document a unique seabird species assemblages in this region, with all samples clustering with those from the western Pacific.

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