

# Macro-ecology of plankton–seabird associations in the North Pacific Ocean

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In conjunction with the North Pacific Continuous Plankton Recorder program, we conducted surveys of seabirds from June 2002 to June 2007. Here, we tested the hypotheses of (i) east–west variations in coupled plankton and seabird abundance, and (ii) that surface-feeding and diving seabirds vary in their relationships to primary productivity and mesozooplankton species abundance and diversity. To test these hypotheses, we developed statistical models for 20 species of seabirds and 12 zooplankton taxonomic groups. Seabird density was highly variable between seasons, but was consistently higher in the western than eastern North Pacific. Seabird diversity was greater in the east. Zooplankton abundance did not differ between regions. We found associations at the “bulk” level between seabird density and net primary productivity, but only one association between seabirds and total zooplankton abundance or diversity. However, we found many relationships between seabird species and the abundance of different zooplankton summarized at the genus or family level. Some of these taxonomic relationships reflect direct predator–prey interactions, while others may reflect zooplankton that serve as ecological indicators of other prey, such as micronekton, upon which the birds may feed. Surface or near-surface feeding, mostly piscivorous seabirds, did not differ systematically from diving, mainly planktivorous seabirds in their zooplankton associations. Seabirds apparently respond to zooplankton taxonomic groupings more so than bulk zooplankton characteristics, such as abundance or diversity. Macro-ecological studies of remote marine ecosystems using zooplankton and seabirds as ecological indicators provide a framework for understanding and assessing spatial and temporal variations in these difficult-to-study pelagic environments.

**KEYWORDS:** copepods; ecosystem indicators; euphausiids; Gulf of Alaska; macro-ecology; pelagic habitat; seabirds; western North Pacific; zooplankton

## INTRODUCTION

Macro-ecology is the study of faunal and floral diversity, abundance and distribution relative to environmental variation at large spatial scales (Brown and Maurer, 1989). Generally speaking, macro-ecological research

seeks to explain patterns of abundance, distribution, diversity of species and ecosystem complexity. While macro-ecology, as a sub-discipline of ecology, has been reasonably well-developed for terrestrial environments (Gaston and Blackburn, 2000), macro-ecological

research is in its infancy for aquatic marine systems (Beaugrand *et al.*, 2007; Witman and Roy, 2009).

In the North Pacific Ocean, there have been few previous macro-ecological studies. However, it is understood that there are large-scale variations in ecosystem productivity from lower to upper trophic levels in different regions (Hayward, 1997). Of note, a special volume in *Progress in Oceanography* (1999) was devoted to comparisons of ecosystem dynamics from physics to top predators, in the eastern and western sub-arctic gyres of the North Pacific. In that volume, Taniguchi (Taniguchi, 1999; primary productivity), Mackas and Tsuda (Mackas and Tsuda, 1999; zooplankton), Beamish *et al.* (Beamish *et al.*, 1999; mid-water fish) and Springer *et al.* (Springer *et al.*, 1999; seabirds and marine mammals) reported a tendency for longitudinal gradients in productivity, generally defined, with greater values in the western than eastern North Pacific. Seabirds and marine mammals, in particular, were considerably more abundant in the western rather than in eastern sub-arctic gyre, supporting previous work. For example, Wahl *et al.* (Wahl *et al.*, 1989) documented a 2–3-fold increase in seabird abundance in the western gyre over the eastern. Zooplankton abundance also apparently followed this pattern of high abundance in the western North Pacific, although Mackas and Tsuda considered these results “preliminary” and did not make any firm conclusions regarding this pattern. Due to the disparate nature of the data sets examined by these authors, there has been no attempt to integrate the data from lower to higher trophic levels to examine whether the longitudinal gradient (or regional variation) in seabird communities matched (or was possibly supported by) longitudinal variation in plankton communities.

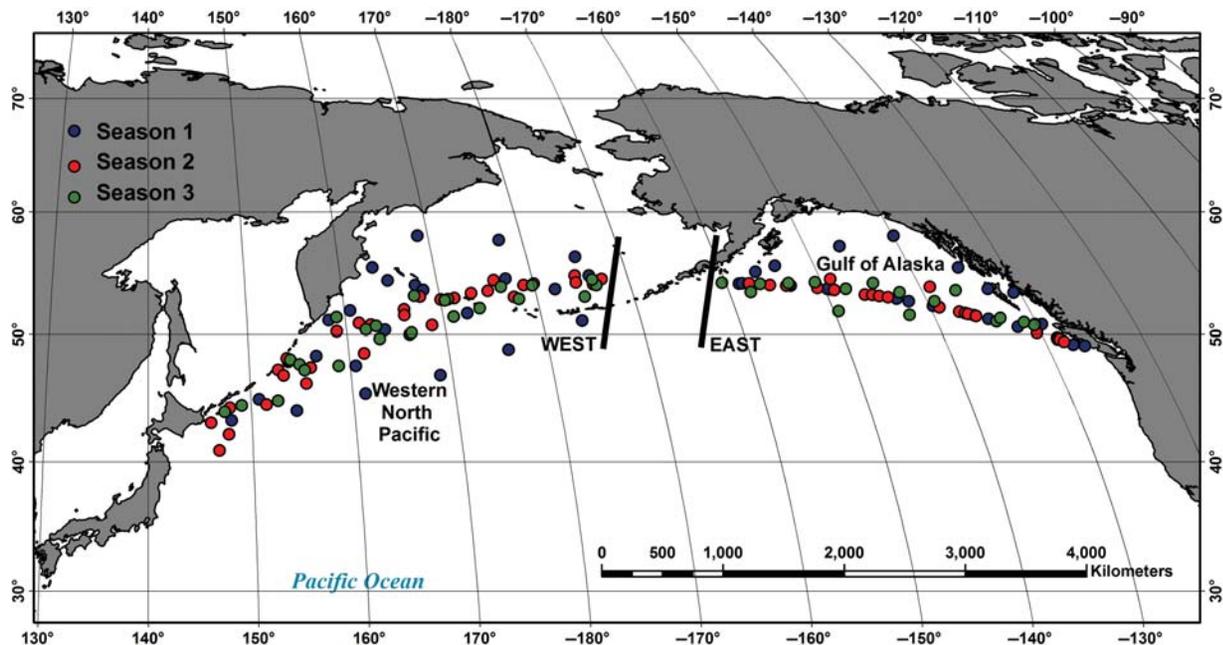
In this study, we address seabird–plankton associations across the North Pacific, following a 6500-km transect from Canada to Japan. Specifically, we investigate mesoscale seabird–plankton associations in pelagic habitats of the Gulf of Alaska (GoA) and western North Pacific. We test the overarching hypotheses of seasonal and regional variations in seabird–plankton diversity and abundance. In particular, we hypothesize that net primary productivity (NPP), mesozooplankton abundance and diversity and seabird abundance and diversity are greater in the western North Pacific than the eastern North Pacific. Moreover, we hypothesize that seabird–plankton associations vary as a function of diet and foraging mode (surface versus diving) of the seabird species examined. Specifically, we surmise that surface (or near surface) foraging procellariid and larid seabirds (e.g. albatrosses, petrels, shearwaters and gulls), which feed substantially on cephalopods and forage fish, would show different associations with zooplankton

taxonomic groups than diving seabirds (alcids), many of whom feed directly on zooplankton. Springer *et al.* (Springer *et al.*, 1999) and Hunt *et al.* (Hunt *et al.*, 2000) provide overviews of seabird diets in the region. Zooplankton associations of primarily piscivorous seabirds would reflect underlying zooplankton–forage fish (or cephalopod) relationships, whereas zooplankton–seabird associations of alcids would most likely reflect direct predator–prey interactions.

We address these operational hypotheses as a means to evaluate the utility of simultaneous plankton and seabird surveys to understand and describe large-scale ecosystem variation and dynamics in the North Pacific Ocean. Both zooplankton (Hooff and Peterson, 2006; Richardson, 2008) and seabirds (Piatt *et al.*, 2007) have been suggested as reliable and cost-effective indicators of ecosystem dynamics, such as the abundance and distribution of micronekton. Because marine birds use prey resources that are not sampled by traditional zooplankton sampling programs in the North Pacific, e.g. forage fish, such as myctophids, and squids that are important to the trophic ecology of fish (e.g. Kaeriyama *et al.*, 2004), we anticipated that observations of these upper trophic level predators would provide complementary information to any zooplankton surveys conducted in the region. Ultimately, we envisioned direct application(s) of plankton–seabird associations to ecosystem-based management (Brander *et al.*, 2003): (i) as indicators of variation in overall ecosystem productivity, (ii) as indicators of ecosystem conditions that drive fish populations, with application to fisheries management and (iii) as indicators of spatial variability in ecosystem dynamics, with applications in the design, monitoring and protection of food webs (e.g. design of marine protected area networks for top predators).

## METHOD

We surveyed plankton and marine birds from British Columbia, Canada (transect began at the mouth of Juan de Fuca Strait, a typical start location was 48.71°N, 125.42°W) to Honshu, Japan (typically the gear was hauled in at 42.78°N, 145.43°E). This survey covers the eastern (northern California Current) and western (Kuroshio Current) boundary currents of the North Pacific, the eastern and western subarctic gyres and portions of the Bering Sea/Aleutian Island eco-region. During the boreal spring (April–May), summer (June–July) and autumn (September–October), we conducted a total of 16 surveys (five spring, six summer and five autumn surveys). Cruise dates and the trackline varied somewhat across seasons and years (Fig. 1, Table 1).



**Fig. 1.** Map of study area and 138 daily sample locations, stratified by season (blue, spring; red, summer; green, autumn). Black bars denote shelf region in the Bering Sea–Aleutian Islands excluded from analyses due to limited sampling, shallow water depth and a unique biological feature (Unimak Pass biological “hotspot”). Deviations from the standard transect area in Season 1 were related to severe weather systems affecting the shipping route.

A total of 199 days of sampling of plankton and predators were made and 27 261 km were surveyed from June 2002 through June 2007.

### Primary productivity

We obtained estimates of NPP ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) for each day of the survey, geo-referenced by the position of the ship at noon each day, from the website: <http://www.science.oregonstate.edu/ocean.productivity/>. NPP is produced by the vertically generalized production model, a chlorophyll-based algorithm based on chlorophyll, available light- and temperature-dependent photosynthetic efficiency (Behrenfeld and Falkowski, 1997). NPP predictably varies with chlorophyll concentrations as measured by SeaWiFS or MODIS sensors (Behrenfeld and Falkowski, 1997). Data were obtained as  $4320 \text{ m} \times 2160 \text{ m}$  global 8-day grids, bounded by coordinates for the beginning and end of each day’s survey observations. Each pixel of data was an 8-day NPP average over  $8 \text{ km}^2$  that ended on the day of observation and began 7 days earlier. We used the geographic information system to overlay NPP and seabird surveys. Hourly cruise path coordinates were linked and a 5-km buffer was incorporated around the daily cruise path. All grid points within the boundaries of this buffer were averaged to yield the NPP for each daily survey.

*Table I: Start and end dates of each Pacific Continuous Plankton Recorder (CPR) Marine Bird and Mammal (MBM) survey, 2002–2007*

| Year | Spring    | Summer    | Autumn     |
|------|-----------|-----------|------------|
| 2002 | –         | 6/1–6/14  | 10/5–10/20 |
| 2003 | 4/1–4/19  | 5/31–6/10 | 9/28–10/14 |
| 2004 | 4/2–4/16  | 6/1–6/15  | 10/2–10/18 |
| 2005 | 4/4–4/17  | 5/28–6/11 | 9/16–9/29  |
| 2006 | 5/3–5/18  | 7/7–7/23  | 9/19–10/4  |
| 2007 | 3/26–4/10 | 5/28–6/11 |            |

### Seabird surveys

During every crossing, a single observer identified and counted birds using strip-transect methodology (using  $10 \times 50$  power binoculars) from the flying bridge of the bulk-cargo carrier M/V *Skabryn*, at an eye height of 25 m above the water. During our two initial surveys, summer and autumn 2002, ~20% of the observations were made from the pilot house and focsle deck (25 m and 10 m above the sea level) to determine the optimal strip width for future studies (summarized by Hyrenbach *et al.*, 2007). The M/V *Skabryn* is 182 m in length and 42.5 m wide. Surveys were conducted during daylight hours while the ship was underway at the speed of 10–15 kt. Due to the large size of the vessel, modifications were made to the standardized marine bird survey

technique (Tasker *et al.*, 1984; Buckland *et al.*, 1993). Species detection and identification curves revealed that the optimal strip-width for this vessel was 400 m (Hyrenbach *et al.*, 2007). During all ensuing surveys, we used a 400-m strip transect to survey birds. The relative abundance of birds is expressed as density. Observations were halted during periods of heavy rain, fog or rough seas, and when impaired visibility of the survey strip made identification or enumeration of marine birds impossible (i.e. sustained Beaufort Sea State 6 or greater). We identified and enumerated all seabirds that entered a 90° arc from bow to the beam on the side of the vessel with the best survey conditions (least sun glare, precipitation). All birds were identified to the lowest taxonomic level possible and behaviors were recorded (mainly “in flight”, or “sitting on water”). For this data analysis, we combined “flying” and “sitting” birds to determine densities ( $\text{km}^{-2} \text{day}^{-1}$ ). Seabird surveys were performed concurrently with zooplankton sampling using the Continuous Plankton Recorder device (see below).

A total of ~18 000 3-km survey “bins” could have been considered in our analyses. However, we selected “day” as the sampling unit, and pooled adjacent bins into daily summaries of bird density to avoid problems of pseudo-replication, spatial autocorrelation and excessive sample size (Zar, 1998), and to align these data with CPR data which were collected at a lower resolution (see below). For this research, we selected days in which at least

100 km of ocean habitat was observed. Excluding the Bering Sea–Aleutian Shelf region, this resulted in 138 sample days (1 day was missing data for NPP, so some analyses are based on  $n = 137$  days—see below); presumably, these were independent samples as each day was separated by night-time periods with no survey effort in which the ship traveled between ~100 and 200 km. We included 20 bird species in the analysis (Table II). We selected these species because they were observed with sufficient regularity to be subjected to statistical analyses. In addition, total bird density by day (all species combined;  $\text{km}^{-2} \text{day}^{-1}$ ) and daily seabird diversity (Shannon-Weiner Index; Colwell and Futuyma, 1971) were parameters selected for analysis in this paper (Table II).

### Zooplankton surveys

Concurrent zooplankton sampling was done using a Continuous Plankton Recorder (CPR) towed behind the vessel at a depth of ~7 m. The CPR contains a filter band (mesh size 270  $\mu\text{m}$ ) that traps plankton as water passes through the device. In the lab, the filter band is cut into 18.4-km blocks and every fourth block is processed microscopically with zooplankton identified to the lowest possible taxonomic resolution. Full details of CPR sampling are given by Richardson *et al.* (Richardson *et al.*, 2006); all standard CPR protocols were followed in the current study. In accordance with the seabird data

Table II: Mean  $\pm 1$  standard deviation of total seabird density, seabird diversity and individual species density (number  $\text{km}^{-2} \text{day}^{-1}$ ) by region and season, 2002–2007

| Region                       | Spring            |                   | Summer            |                   | Autumn            |                   |
|------------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
|                              | East ( $n = 22$ ) | West ( $n = 24$ ) | East ( $n = 22$ ) | West ( $n = 30$ ) | East ( $n = 17$ ) | West ( $n = 23$ ) |
| Total (all spp.) density     | 7.337 (7.770)     | 15.333 (13.681)   | 4.331 (4.074)     | 108.889 (217.697) | 7.498 (13.427)    | 24.248 (36.610)   |
| Diversity                    | 1.601 (0.324)     | 1.270 (0.406)     | 1.291 (0.370)     | 1.010 (0.443)     | 1.450 (0.511)     | 1.466 (0.409)     |
| Ancient Murrelet (A)         | 0.218 (0.471)     | 0.062 (0.222)     | 0.013 (0.036)     | 0.135 (0.314)     | 0.035 (0.084)     | 0.037 (0.142)     |
| Black-footed Albatross (D)   | 0.106 (0.193)     | 0.001 (0.003)     | 0.062 (0.180)     | 0.004 (0.013)     | 0.071 (0.155)     | 0.031 (0.061)     |
| Black-legged Kittiwake (L)   | 1.248 (1.842)     | 1.514 (2.431)     | 0.017 (0.044)     | 0.238 (0.590)     | 0.113 (0.352)     | 2.362 (2.134)     |
| Cassin’s Auklet (A)          | 0.399 (1.111)     | 0.001 (0.006)     | 0.011 (0.025)     | 0 (0)             | 2.639 (10.642)    | 0 (0)             |
| Common Murre (A)             | 0.180 (0.777)     | 0.003 (0.010)     | 0.003 (0.013)     | 0.003 (0.010)     | 0 (0)             | 0.011 (0.020)     |
| Crested Auklet (A)           | 1.177 (4.476)     | 4.729 (10.216)    | 0 (0)             | 32.378 (139.930)  | 0 (0)             | 1.835 (8.213)     |
| Fork-tailed Storm-Petrel (H) | 0.280 (0.368)     | 0.397 (1.109)     | 0.433 (0.528)     | 4.683 (5.342)     | 0.494 (0.663)     | 0.734 (1.278)     |
| Horned Puffin (A)            | 0.003 (0.007)     | 0.002 (0.007)     | 0.090 (0.218)     | 0.061 (0.131)     | 0.052 (0.112)     | 0.034 (0.077)     |
| Laysan Albatross (D)         | 0.019 (0.047)     | 0.077 (0.122)     | 0.005 (0.011)     | 0.697 (1.123)     | 0.102 (0.162)     | 0.884 (1.016)     |
| Leach’s Storm-Petrel (H)     | 0.086 (0.233)     | 0.176 (0.463)     | 1.769 (2.358)     | 1.204 (2.464)     | 1.757 (2.650)     | 0.210 (0.656)     |
| Least Auklet (A)             | 0.007 (0.028)     | 0.856 (1.881)     | 0.001 (0.003)     | 0.064 (0.155)     | 0.001 (0.004)     | 0.039 (0.085)     |
| Mottled Petrel (P)           | 0.081 (0.136)     | 0.559 (2.242)     | 0.084 (0.190)     | 1.138 (3.050)     | 0.148 (0.187)     | 0.142 (0.280)     |
| Northern Fulmar (P)          | 0.739 (1.308)     | 3.755 (4.000)     | 0.332 (0.537)     | 7.692 (10.049)    | 0.627 (1.657)     | 5.081 (5.723)     |
| Parakeet Auklet (A)          | 0.208 (0.610)     | 0.019 (0.055)     | 0.016 (0.052)     | 0.020 (0.036)     | 0.062 (0.167)     | 0.006 (0.012)     |
| Rhinoceros Auklet (A)        | 0.198 (0.661)     | 0.001 (0.005)     | 0.009 (0.021)     | 0.486 (2.406)     | 0.023 (0.077)     | 0.039 (0.182)     |
| Short-tailed Shearwater (P)  | 0.002 (0.007)     | 1.750 (4.622)     | 0.006 (0.013)     | 58.133 (167.453)  | 0.007 (0.019)     | 10.355 (34.464)   |
| Slaty-backed Gull (L)        | 0 (0)             | 0.323 (0.757)     | 0 (0)             | 0.103 (0.305)     | 0 (0)             | 0.079 (0.244)     |
| Sooty Shearwater (P)         | 0.721 (1.628)     | 0.009 (0.034)     | 1.076 (1.829)     | 0.152 (0.614)     | 0.422 (0.910)     | 0.162 (0.378)     |
| Thick-billed Murre (A)       | 0.185 (0.362)     | 0.312 (0.588)     | 0.005 (0.014)     | 0.181 (0.432)     | 0.001 (0.003)     | 0.025 (0.046)     |
| Tufted Puffin (A)            | 0.396 (0.788)     | 0.440 (0.489)     | 0.303 (0.514)     | 1.314 (2.171)     | 0.587 (0.918)     | 0.539 (0.490)     |

(A): Alcidae; (D): Diomedidae; (H): Hydrobatidae; (L): Laridae; (P): Procellariidae.

summarized by day for days with at least 100 km of observation, we filtered the CPR data to include days in which there was a minimum of 54 km (at least three 18-km blocks) of plankton data. We centered the samples on 1200 local time each day to avoid the problem of diel vertical migration of plankton that could influence abundance and biomass estimates. To simplify the plankton data set for the analysis, we summarized estimates of abundance to genus, creating indices for the following genera and higher level taxonomic resolution: *Acartia* spp., *Calanus* spp., Chaetognatha, copepod nauplii, *Eucalanus* spp., Euphausiacea, Harpacticoida, Hyperiidae, Appendicularia, *Limacina helicina*, *Metridia* spp., *Neocalanus* spp., *Oithona* spp., *Paracalanus/Pseudocalanus* spp. sub-adults (i.e. copepodite stages I–V) and *Pseudocalanus* spp. adults (life stage) (Table III). While coarser groupings are possible (e.g. “large” and “small” zooplankton), we wanted to maintain a resolution to the data that might reflect variable zooplankton-based food webs, to which presumably the birds respond. However, for final regression modeling, we dropped the life stages “copepod nauplii” and *Paracalanus/Pseudocalanus* spp. sub-adults (to avoid duplication), and the relatively rare Harpacticoida from the analyses (see below). Abundances ( $3 \text{ m}^{-3} \text{ day}^{-1}$ ) of zooplankton are provided in Table III.

### Data summation and analysis

We examined the relationships between NPP, zooplankton abundance and diversity, and the distribution and abundance of seabirds using ANCOVA and regression

(GLM) techniques. We used the *STATA v8.2* statistical software (Stata Corporation, College Station, TX, USA) for analyses. Due to relatively limited sampling and unique attributes, the Unimak Pass biological “hotspot” (centered at  $54^{\circ}20'N$ ,  $164^{\circ}55'W$ ), within the eastern and western Bering Sea–Aleutian Shelf region, was excluded from this analysis. This region, illustrated in Fig. 1, is one where foraging seabirds, particularly Short-tailed Shearwater (*Puffinus tenuirostris*) and Sooty Shearwater (*P. griseus*) may concentrate in extremely high numbers (Batten *et al.*, 2006). We deleted this location from our analyses due to the unusually high abundance and variance in seabird density seen at there and because it is shallow water habitat. The eastern region, referred to as the “Gulf of Alaska” in Fig. 1, stretches from Vancouver Island in the east to the Alaskan Peninsula in the west. The western region, identified as the “western North Pacific”, extends from the edge of the eastern Bering Sea to coastal Hokkaido in the west. Sampling in the “Aleutian Basin” and “western Bering Sea” occurred essentially in deep, open ocean habitats, and plankton and seabird communities in this region were not distinct from communities further west (Batten *et al.*, 2006; Sydeaman *et al.*, 2006a). Consequently, we combined these samples and refer to this region as “western North Pacific”.

Given that both plankton and seabird communities vary seasonally (Batten *et al.*, 2006), the eastern and western regions were stratified by season, and correlations were calculated for bird densities and diversity against NPP and zooplankton abundances. We used a

Table III: Means  $\pm$  1 standard deviation for total zooplankton abundance and diversity, and genera/family abundances by region and season

| Region                                | Spring          |               | Summer          |                 | Autumn          |                |
|---------------------------------------|-----------------|---------------|-----------------|-----------------|-----------------|----------------|
|                                       | East (n = 22)   | West (n = 24) | East (n = 22)   | West (n = 30)   | East (n = 17)   | West (n = 23)  |
| Total (all groups) abundance          | 1109.9 (1283.3) | 98.3 (958.2)  | 1077.4 (1025.5) | 1259.7 (1108.4) | 1608.6 (2133.6) | 1095.7 (718.3) |
| Diversity                             | 1.4 (0.4)       | 1.3 (0.5)     | 1.4 (0.5)       | 1.4 (0.5)       | 1.4 (0.4)       | 1.4 (0.4)      |
| <i>Acartia</i> spp.                   | 59.9 (90.3)     | 18.4 (57.5)   | 60.1 (94.4)     | 49.0 (105.3)    | 458.3 (1519.7)  | 27.7 (41.3)    |
| <i>Calanus</i> spp.                   | 59.4 (86.2)     | 39.2 (92.9)   | 91.3 (193.9)    | 175.4 (394.9)   | 257.0 (358.3)   | 75.0 (90.1)    |
| Chaetognatha                          | 8.9 (14.4)      | 12.3 (23.0)   | 8.7 (33.2)      | 19.6 (34.4)     | 34.9 (50.5)     | 41.4 (54.1)    |
| Copepod nauplii                       | 127.0 (225.6)   | 75.5 (184.5)  | 86.9 (143.4)    | 145.3 (209.7)   | 60.5 (101.8)    | 183.2 (246.9)  |
| <i>Eucalanus</i> spp.                 | 4.6 (6.5)       | 4.7 (15.5)    | 1.1 (3.8)       | 15.3 (33.1)     | 0.2 (0.5)       | 0.3 (0.6)      |
| Euphausiacea                          | 2.8 (3.9)       | 5.3 (20.1)    | 12.3 (33.5)     | 12.7 (37.5)     | 29.2 (58.4)     | 4.6 (8.7)      |
| Harpacticoida                         | 0 (0)           | 0 (0)         | 6.7 (22.9)      | 0 (0)           | 34.6 (97.6)     | 2.1 (10.2)     |
| Hyperiidae                            | 1.8 (2.6)       | 2.2 (2.8)     | 5.0 (7.9)       | 8.7 (12.5)      | 5.9 (8.7)       | 15.8 (19.9)    |
| Appendicularia                        | 31.2 (84.9)     | 6.1 (22.0)    | 89.1 (263.1)    | 18.0 (56.8)     | 37.5 (78.5)     | 27.7 (76.5)    |
| <i>Limacina helicina</i>              | 13.4 (27.0)     | 16.3 (40.0)   | 20.0 (32.6)     | 32.7 (64.8)     | 54.8 (88.1)     | 25.6 (67.5)    |
| <i>Metridia</i> spp.                  | 11.1 (24.9)     | 10.1 (16.2)   | 2.8 (8.1)       | 3.9 (17.8)      | 5.4 (11.9)      | 10.6 (22.7)    |
| <i>Neocalanus</i> spp.                | 164.1 (268.5)   | 127.3 (117.4) | 198.8 (284.6)   | 127.5 (184.3)   | 0.5 (1.3)       | 4.0 (10.4)     |
| <i>Oithona</i> spp.                   | 258.4 (609.4)   | 75.5 (117.4)  | 220.5 (597.2)   | 223.8 (272.3)   | 221.9 (277.8)   | 347.3 (354.6)  |
| <i>Paracalanus/Pseudocalanus</i> spp. | 162.6 (240.2)   | 102.1 (154.9) | 115.8 (188.6)   | 207.4 (201.7)   | 181.6 (166.9)   | 172.6 (213.0)  |
| <i>Pseudocalanus</i> spp. adults      | 95.8 (199.2)    | 51.0 (137.4)  | 86.9 (156.4)    | 116.0 (196.2)   | 89.4 (143.1)    | 83.1 (117.7)   |

Abundance is number per sample, with sample =  $\sim 3 \text{ m}^3$ .

general linear model, ANCOVA and forward stepwise regression to test for plankton–seabird associations in space and time (Zar, 1998). We included the following independent variables in the ANCOVA and regression models: “year”, “season” [defined as spring (March–May), summer (June–July) and autumn (September–October)], and “region” (Gulf of Alaska and western North Pacific). We used ANCOVA to test whether NPP, seabird and zooplankton abundance and diversity varied by season and how these variables related to one another. NPP and zooplankton (taxon-specific) abundance ( $3\text{ m}^{-3}$ ) were treated as continuous variables, whereas year, season and region were treated as categorical variables. Seabird densities and zooplankton abundance estimates were log-transformed ( $\ln$ ) before the analysis. We used forward stepwise regression to examine the relationship between seabird density and zooplankton species within regions and among seasons. This was done to satisfy our goal for identifying which zooplankton species/groupings were most related to each seabird species, and how other zooplankton related to the seabirds sequentially ordered by interaction strength. Average bottom depth for each day was not included in the stepwise regression model because 91% of survey days (117/129 in 2002–2006) had an average depth  $>1000$  m. Even though the ship traversed 100–200 km per day, the vast majority of the route covered deep seas.

## RESULTS

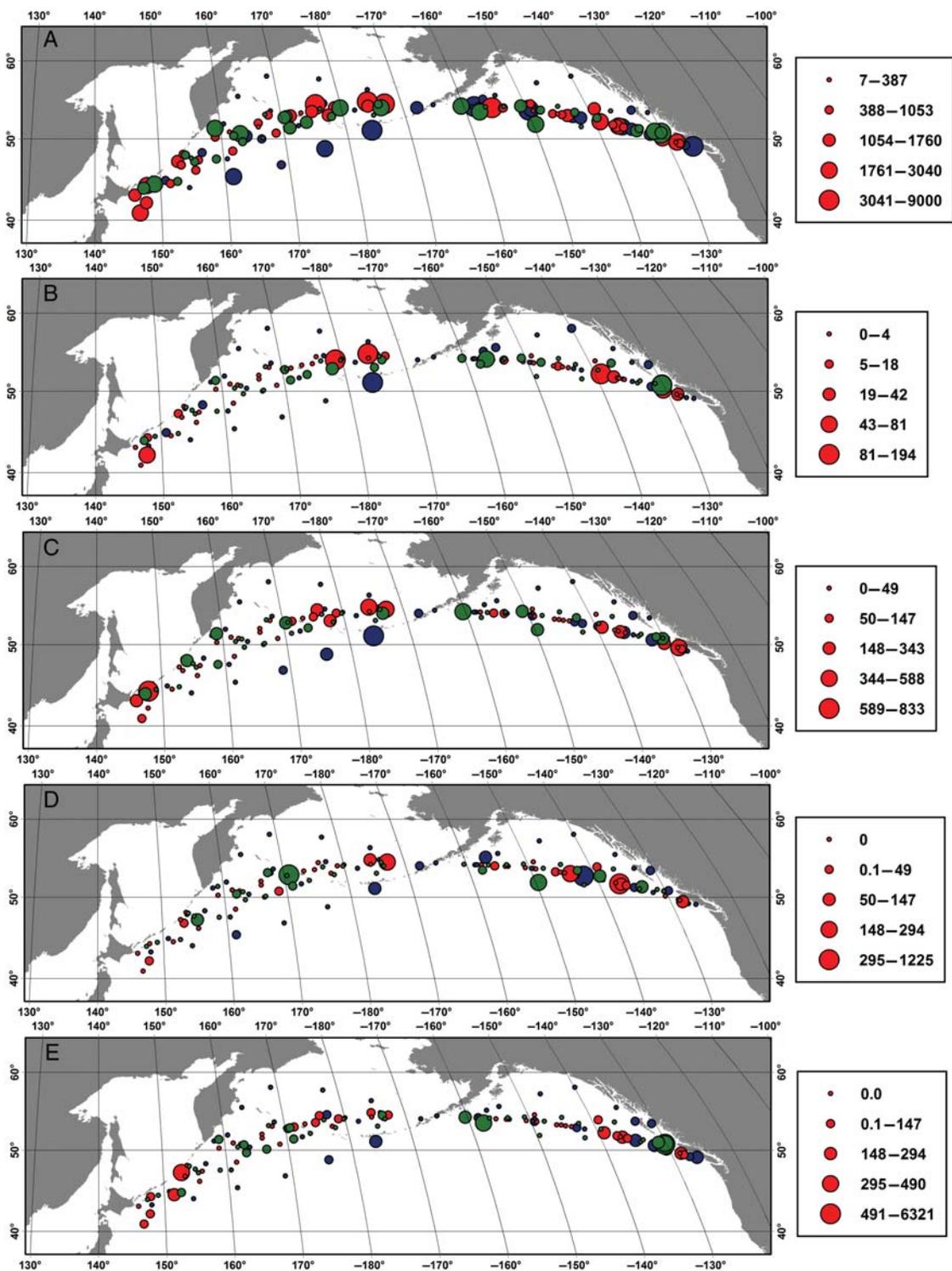
### Distribution of plankton and birds

The distribution of total (all genera and groupings) zooplankton, euphausiids, *Pseudocalanus* spp., Appendicularia and *Acartia* spp. abundance across the North Pacific is shown in Fig. 2. While there clearly were locations of greater abundance of zooplankton (i.e. more zooplankton in coastal B.C., the central Bering Sea and coastal Japan), there were no obvious longitudinal gradients in zooplankton abundance (see also Table III). We found significant regional variation in only four zooplankton groups: *Calanus* spp. (three-way GLM with year, season and region and no two- or three-way interaction terms:  $P_{\text{region}} = 0.034$ , higher in east); Chaetognatha ( $P = 0.034$ , higher in west); Hyperiididae ( $P = 0.008$ , higher in west) and Appendicularia ( $P = 0.020$ , higher in east). Not surprisingly given these patterns of no variation or some groups being more abundant in the east with others more abundant in the west, neither total zooplankton abundance ( $P = 0.731$ ) nor zooplankton diversity ( $P = 0.662$ ) varied regionally. In contrast, there

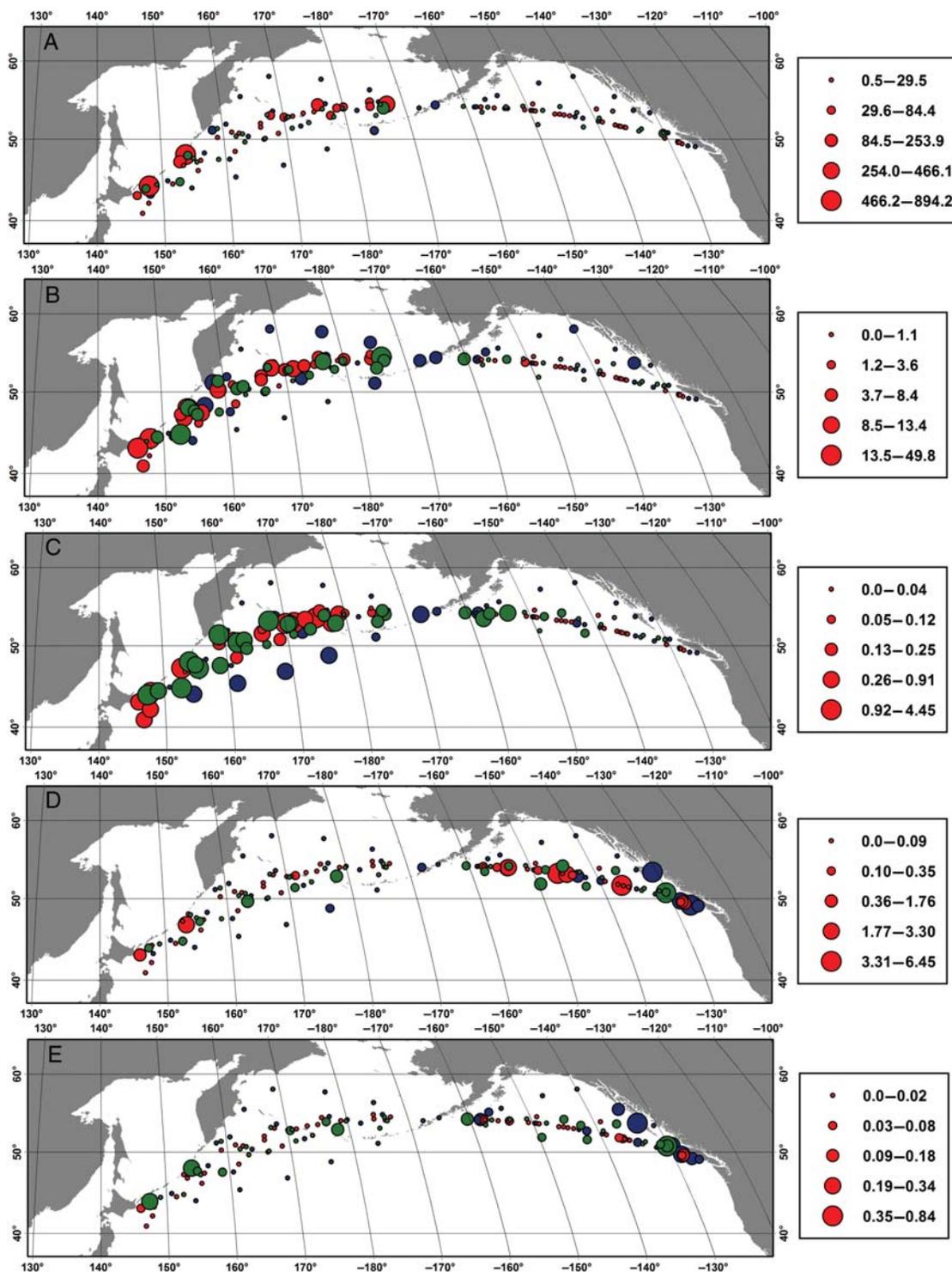
were striking differences in bird distributions (Fig. 3). The density of all species combined, Northern Fulmar (*Fulmarus glacialis*) and Laysan Albatross (*Phoebastria immutabilis*), was clearly greater in the western North Pacific than Gulf of Alaska. Conversely, Sooty Shearwater and Black-footed Albatross (*P. nigripes*) were more abundant in the Gulf of Alaska than western North Pacific (see Table II for statistics and  $P$ -values).

### Plankton–seabird associations

Total zooplankton abundance and diversity were positively related to NPP (Table IV), which varied by season, region and year (Table V). There were annual and regional variations (i.e. more birds occurred in the western North Pacific) in total bird density, but no correlation with total zooplankton abundance (Table VI). Total bird density was positively related to NPP. There were both seasonal and regional variations in bird diversity (i.e. more diversity in the east), but diversity was not related to NPP, zooplankton abundance or zooplankton diversity. We found annual variation in density for three seabird species: Black-legged Kittiwake (*Rissa tridactyla*), Cassin’s Auklet (*Ptychoramphus aleuticus*) and Short-tailed Shearwater, but none of these variations was profound ( $P = 0.02$  to  $0.05$ ), and 17/20 species showed no interannual variation (Table VI). We found seasonal variation in density for 8/20 (40%) species: Black-legged Kittiwake, Cassin’s Auklet, Fork-tailed Storm-Petrel (*Oceanodroma furcata*), Horned Puffin (*Fratercula corniculata*), Laysan Albatross, Least Auklet (*Aethia pusilla*), Leach’s Storm-Petrel (*Oceanodroma leucorhoa*) and Short-tailed Shearwater (Table VI). Regional variation was found in 75% (15/20) of the species including five species which were more abundant in the east [Black-footed Albatross, Cassin’s Auklet, Leach’s Storm-Petrel, Parakeet Auklet (*A. psittacula*) and Sooty Shearwater], and 10 species which were more abundant in the western North Pacific [Black-legged Kittiwake, Crested Auklet (*A. cristatella*), Fork-tailed Storm-Petrel, Laysan Albatross, Least Auklet, Northern Fulmar, Slaty-backed Gull (*Larus schistisagus*), Short-tailed Shearwater, Thick-billed Murre (*Uria lomvia*) and Tufted Puffin (*F. cirrhata*)] (Table VI). Zooplankton abundance was positively associated with Cassin’s Auklet (Fig. 4). Black-footed Albatross, Cassin’s Auklet, Leach’s Storm-Petrel, Northern Fulmar, Rhinoceros Auklet (*Cerorhinca monocerata*) and Sooty Shearwater were positively associated with increasing NPP (Fig. 5). In contrast, Mottled Petrel (*Pterodroma inexpectata*) was negatively associated with increasing NPP (Fig. 5).



**Fig. 2.** Examples of seasonal spatial distribution of zooplankton abundance ( $3 \text{ m}^{-3}$ ) as measured using the CPR during 2002–2007: (A) total zooplankton, (B) euphausiids, (C) *Pseudocalanus* spp., (D) Appendicularia and (E) *Acartia* spp. Zooplankton abundance was partitioned into classes based on natural data breaks using the Jenks method to minimize the average deviation from the class mean, while maximizing the deviation from the means of the other groups. This method reduces the variance within classes and maximizes the variance between classes. Blue is Season 1 (spring), red is Season 2 (summer) and Green is season 3 (autumn).



**Fig. 3.** Examples of seasonal spatial distribution of density (km<sup>-2</sup>) of birds measured at sea during 2002–2007: **(A)** all species, **(B)** Northern Fulmar (*Fulmarus glacialis*), **(C)** Laysan Albatross (*Phoebastria immutabilis*), **(D)** Sooty Shearwater (*Puffinus griseus*) and **(E)** Black-footed Albatross (*Phoebastria nigripes*). Bird densities were partitioned into classes based on natural data breaks using the Jenks method to minimize the average deviation from the class mean, while maximizing the deviation from the means of the other groups. This method reduces the variance within classes and maximizes the variance between classes. Blue is Season 1 (spring), red is Season 2 (summer) and green is Season 3 (autumn).

Table IV: Results from ANCOVA for plankton parameters with independent variables season, region, year, and net primary productivity

| Species               | Model              |               |        | Net primary productivity |                  |
|-----------------------|--------------------|---------------|--------|--------------------------|------------------|
|                       | Model, residual df | $F(P > F)$    | $r^2$  | $F(P > F)$               | Coefficient sign |
| Zooplankton abundance | 9, 127             | 3.20 (0.0016) | 0.1849 | 7.02 (0.0091)            | +                |
| Zooplankton diversity | 9, 127             | 1.92 (0.0541) | 0.1200 | 9.26 (0.0029)            | +                |

Net primary productivity was treated as a continuous variable.

Table V: Results of ANCOVA for net primary productivity with independent variables season, region and year

| Model              |                |        | Season          | Year          | Region        |
|--------------------|----------------|--------|-----------------|---------------|---------------|
| Model, residual df | $F(P > F)$     | $r^2$  | $F(P > F)$      | $F(P > F)$    | $F(P > F)$    |
| 8, 128             | 9.20 (<0.0001) | 0.3651 | 20.39 (<0.0001) | 3.31 (0.0077) | 5.96 (0.0160) |

### Species-specific seabird and zooplankton taxonomic group associations

In each season, 80% of the models were successful in establishing statistical relationships, and ~55–60% showed relationships with zooplankton (Table VII). For 23% of the models, we found regional variation, but no relationships with zooplankton. The only species for which we failed to find any regional variation or zooplankton relationships was Horned Puffin. Most of the models which failed involved alcids; however, not surprisingly, of the models which failed to include any measurements of zooplankton abundance, 71% were based upon procellarids or gulls. Most (66%) of the associations with zooplankton were positive, but some were negative indicating days with lower seabird densities, yet higher zooplankton abundance. For the zooplankton genera/families examined, 10 models included *Pseudocalanus* spp. (7 positive (+)), eight included *Acartia* spp. (5+), seven included *Neocalanus* spp. (3+), six included *Eucalanus* spp. (4+) and *Metridia* spp. (4+), five included Euphausiacea (5+), four included *Calanus* spp. (1+), two included *Oithona* spp. (1+), Chaetognatha (2+) and Appendicularia (2+), and one included *Limacina helicina* (+) and Hyperiididae (+). Five (all) of the euphausiid associations were positive, three with seabird species known or thought to consume euphausiids: Least Auklet (in two seasons), Fork-tailed Storm-Petrel and Sooty Shearwater.

## DISCUSSION

We investigated the macro-ecology (at the basin-wide scale) of Pacific sub-arctic ecosystems using a

combination of continuous plankton and seabird records from a 6500-km *trans*-Pacific survey conducted 16 times over 6 years. To our knowledge, this is one of the first integrative studies of zooplankton–seabird associations conducted at this scale of observation (100–1000 s of km). Therefore, fundamental information pertaining to patterns of ecosystem structure and complexity of the subarctic North Pacific Ocean may be derived from this study.

### Regional variation in plankton–seabird associations

We tested a hypothesis that (i) seabirds and zooplankton would vary in density/abundance regionally and seasonally, and (ii) surface/near surface-feeding seabirds (represented by Procellariiformes and Laridae) and diving seabirds (Alcidae) would vary in their relationships to NPP and mesozooplankton abundance and diversity. Regional variability of seabirds and some zooplankton in this study was high, thereby verifying the first part of our hypothesis. As first described by Wahl *et al.* (Wahl *et al.*, 1989), later by Springer *et al.* (Springer *et al.*, 1999) and corroborated by Sydeman *et al.* (Sydeman *et al.*, 2006a) for this data set, we found that seabird densities in the western North Pacific were considerably greater than in the GoA/eastern North Pacific. Fifteen of 20 seabird species (75%) showed regional variation in abundance, with 10 species showing greater abundance in the west, 5 in the east and 5 with no apparent regional segregation. Despite the compelling nature of this regional variation (i.e. a longitudinal gradient in seabird densities from east to west), we found few relationships with zooplankton

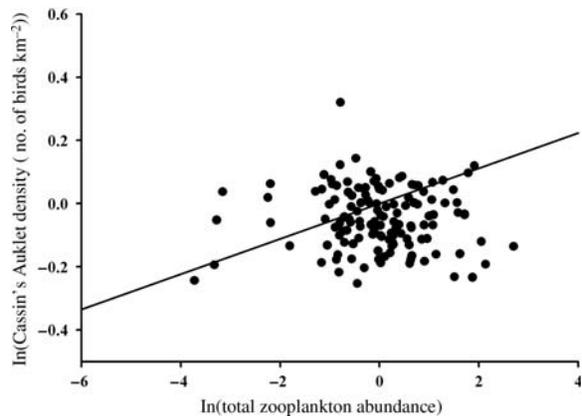
*Table VI: Results of ANCOVA on seabird densities with independent variables season, region, year, net primary productivity, zooplankton diversity and zooplankton abundance. Net primary productivity, zooplankton diversity and zooplankton abundance were treated as continuous variables. (A): Alcidae; (D): Diomedidae; (H): Hydrobatidae; (L): Laridae; (P): Procellariidae*

| Species                      | Model<br><i>F</i> ( <i>P</i> > <i>F</i> ) | df = 12, 124<br><i>r</i> <sup>2</sup> | Year<br><i>F</i> ( <i>P</i> > <i>F</i> ) | Season<br><i>F</i> ( <i>P</i> > <i>F</i> ) | Region                           |                 |
|------------------------------|---|---------------------------------------|--|--|----------------------------------|-----------------|
|                              |   |                                       |  |  | <i>F</i> ( <i>P</i> > <i>F</i> ) | Dominant region |
| Total (all spp.) density     | <b>9.82 (&lt;0.0001)</b>                  | 0.4637                                | <b>3.70 (0.0037)</b>                     | 1.53 (0.2216)                              | <b>71.40 (&lt;0.0001)</b>        | West            |
| Diversity                    | <b>2.73 (0.0034)</b>                      | 0.1937                                | 0.45 (0.8109)                            | <b>7.30 (0.0010)</b>                       | <b>8.29 (0.0047)</b>             | East            |
| Ancient Murrelet (A)         | 1.30 (0.2327)                             | 0.1026                                | 0.79 (0.5621)                            | 2.60 (0.0785)                              | 0.07 (0.7898)                    |                 |
| Black-footed Albatross (D)   | <b>2.92 (0.0019)</b>                      | 0.2042                                | 1.16 (0.3304)                            | 2.94 (0.0565)                              | <b>8.64 (0.0039)</b>             | East            |
| Black-legged Kittiwake (L)   | <b>6.28 (&lt;0.0001)</b>                  | 0.3559                                | <b>2.29 (0.0493)</b>                     | <b>20.33 (&lt;0.0001)</b>                  | <b>15.68 (0.0001)</b>            | West            |
| Cassin's Auklet (A)          | <b>2.80 (0.0027)</b>                      | 0.1975                                | <b>2.80 (0.0197)</b>                     | <b>3.83 (0.0243)</b>                       | <b>4.33 (0.0395)</b>             | East            |
| Common Murre (A)             | 1.15 (0.3281)                             | 0.0920                                | 1.14 (0.3453)                            | 1.92 (0.1504)                              | 0.88 (0.3495)                    |                 |
| Crested Auklet (A)           | 1.15 (0.3320)                             | 0.0916                                | 0.48 (0.7916)                            | 1.03 (0.3618)                              | <b>6.13 (0.0146)</b>             | West            |
| Fork-tailed Storm-Petrel (H) | <b>4.88 (&lt;0.0001)</b>                  | 0.3006                                | 1.72 (0.1351)                            | <b>11.71 (&lt;0.0001)</b>                  | <b>13.26 (0.0004)</b>            | West            |
| Horned Puffin (A)            | <b>2.12 (0.0233)</b>                      | 0.1572                                | 0.91 (0.4770)                            | <b>8.72 (0.0003)</b>                       | 1.50 (0.2231)                    |                 |
| Laysan Albatross (D)         | <b>5.75 (&lt;0.0001)</b>                  | 0.3359                                | 1.55 (0.1804)                            | <b>3.93 (0.0222)</b>                       | <b>33.11 (&lt;0.0001)</b>        | West            |
| Least Auklet (A)             | <b>3.13 (0.0009)</b>                      | 0.2158                                | 0.45 (0.8104)                            | <b>8.21 (0.0004)</b>                       | <b>14.97 (0.0002)</b>            | West            |
| Leach's Storm-Petrel (H)     | <b>4.42 (&lt;0.0001)</b>                  | 0.2802                                | 0.65 (0.6627)                            | <b>5.84 (0.0038)</b>                       | <b>5.00 (0.0271)</b>             | East            |
| Mottled Petrel (P)           | 1.47 (0.1504)                             | 0.1146                                | 0.96 (0.4475)                            | 2.96 (0.0552)                              | 2.25 (0.1363)                    |                 |
| Northern Fulmar (P)          | <b>10.97 (&lt;0.0001)</b>                 | 0.4913                                | 1.57 (0.1732)                            | 0.24 (0.7887)                              | <b>108.54 (&lt;0.0001)</b>       | West            |
| Parakeet Auklet (A)          | 1.17 (0.3123)                             | 0.0936                                | 0.36 (0.8727)                            | 1.64 (0.1975)                              | <b>3.90 (0.0506)</b>             | West            |
| Rhinoceros Auklet (A)        | 1.51 (0.1354)                             | 0.1174                                | 0.28 (0.9257)                            | 2.05 (0.1325)                              | 0.55 (0.4597)                    |                 |
| Short-tailed Shearwater (P)  | <b>6.80 (&lt;0.0001)</b>                  | 0.3744                                | <b>2.55 (0.0308)</b>                     | <b>7.98 (0.0005)</b>                       | <b>29.63 (&lt;0.0001)</b>        | West            |
| Slaty-backed Gull (L)        | <b>2.51 (0.0068)</b>                      | 0.1811                                | 1.23 (0.2987)                            | 0.39 (0.6767)                              | <b>11.25 (0.0011)</b>            | West            |
| Sooty Shearwater (P)         | <b>3.47 (0.0003)</b>                      | 0.2341                                | 1.68 (0.1436)                            | 1.36 (0.2595)                              | <b>15.13 (0.0002)</b>            | East            |
| Thick-billed Murre (A)       | <b>3.16 (0.0009)</b>                      | 0.2173                                | 2.18 (0.0608)                            | 2.28 (0.1061)                              | <b>4.02 (0.0470)</b>             | West            |
| Tufted Puffin (A)            | <b>2.50 (0.0071)</b>                      | 0.1804                                | 2.22 (0.0563)                            | 3.02 (0.0526)                              | <b>7.76 (0.0062)</b>             | West            |

| Species                      | Net primary productivity         |                  | Zooplankton diversity            |                  | Zooplankton abundance            |                  |
|------------------------------|----------------------------------|------------------|----------------------------------|------------------|----------------------------------|------------------|
|                              | <i>F</i> ( <i>P</i> > <i>F</i> ) | Coefficient sign | <i>F</i> ( <i>P</i> > <i>F</i> ) | Coefficient sign | <i>F</i> ( <i>P</i> > <i>F</i> ) | Coefficient sign |
| All species density          | <b>4.84 (0.0296)</b>             | +                | 0.01 (0.9207)                    |                  | 0.93 (0.3379)                    |                  |
| Diversity                    | 0.04 (0.8420)                    |                  | 0.63 (0.4279)                    |                  | 0.21 (0.6504)                    |                  |
| Ancient Murrelet (A)         | 2.62 (0.1080)                    |                  | 1.18 (0.2793)                    |                  | 2.58 (0.1104)                    |                  |
| Black-footed Albatross (D)   | <b>9.09 (0.0031)</b>             | +                | 0.20 (0.6545)                    |                  | 1.74 (0.1893)                    |                  |
| Black-legged Kittiwake (L)   | 1.80 (0.1816)                    |                  | 0.01 (0.9116)                    |                  | 2.06 (0.1539)                    |                  |
| Cassin's Auklet (A)          | <b>4.79 (0.0305)</b>             | +                | 3.47 (0.0648)                    |                  | <b>6.86 (0.0099)</b>             | +                |
| Common Murre (A)             | 2.55 (0.1125)                    |                  | 0.32 (0.5715)                    |                  | 0.78 (0.3782)                    |                  |
| Crested Auklet (A)           | 0.25 (0.6214)                    |                  | 0.23 (0.6296)                    |                  | 0.65 (0.4204)                    |                  |
| Fork-tailed Storm-Petrel (H) | 0.69 (0.4083)                    |                  | 0.65 (0.4213)                    |                  | 0.75 (0.3884)                    |                  |
| Horned Puffin (A)            | 3.02 (0.0849)                    |                  | 0.19 (0.6619)                    |                  | 1.81 (0.1808)                    |                  |
| Laysan Albatross (D)         | 1.37 (0.2444)                    |                  | 0.15 (0.6982)                    |                  | 0.00 (0.9438)                    |                  |
| Least Auklet (A)             | 2.50 (0.1162)                    |                  | 1.00 (0.3191)                    |                  | 0.00 (0.9718)                    |                  |
| Leach's Storm-Petrel (H)     | <b>8.02 (0.0054)</b>             | +                | 0.01 (0.9089)                    |                  | 0.03 (0.8725)                    |                  |
| Mottled Petrel (P)           | <b>4.29 (0.0403)</b>             | -                | 0.52 (0.4734)                    |                  | 0.73 (0.3956)                    |                  |
| Northern Fulmar (P)          | <b>4.25 (0.0414)</b>             | +                | 0.22 (0.6410)                    |                  | 0.26 (0.6109)                    |                  |
| Parakeet Auklet (A)          | 0.00 (0.9864)                    |                  | 1.33 (0.2512)                    |                  | 2.66 (0.1051)                    |                  |
| Rhinoceros Auklet (A)        | <b>9.49 (0.0025)</b>             | +                | 0.06 (0.8014)                    |                  | 0.00 (0.9887)                    |                  |
| Short-tailed Shearwater (P)  | <b>0.77 (0.3819)</b>             |                  | 1.18 (0.2795)                    |                  | 3.27 (0.0732)                    |                  |
| Slaty-backed Gull (L)        | 0.01 (0.9373)                    |                  | 2.54 (0.1136)                    |                  | 3.61 (0.0597)                    |                  |
| Sooty Shearwater (P)         | <b>4.18 (0.0430)</b>             | +                | 0.06 (0.8115)                    |                  | 0.09 (0.7607)                    |                  |
| Thick-billed Murre (A)       | <b>0.29 (0.5939)</b>             |                  | 2.76 (0.0994)                    |                  | 0.25 (0.6145)                    |                  |
| Tufted Puffin (A)            | <b>0.16 (0.6908)</b>             |                  | 0.98 (0.3247)                    |                  | 0.77 (0.3811)                    |                  |

Bold values indicate *P* < 0.05.



**Fig. 4.** Added variable plot showing Cassin's Auklet density as a function of total zooplankton abundance. The plot shows the relationship of density to zooplankton based on a regression model that also included season, region, year, net primary productivity and zooplankton diversity as independent variables. The added variable plot, therefore, illustrates the function between zooplankton abundance and auklet density adjusted by all other variables in the regression model. Three outliers ( $x, y$ ) are not shown:  $(-0.1597, 1.5794)$ ,  $(0.9013, 1.0227)$  and  $(2.6434, 3.5424)$ .

abundance or diversity that would explain this broad bio-geographic pattern. Indeed, the seabird regional associations that might be explained by regional co-variance with zooplankton distributions were limited to Crested Auklet and Hyperiididae, and Short-tailed Shearwater and *Calanus* spp. and Chaetognatha in the west; and Leach's Storm-Petrel and Appendicularia, and Sooty Shearwater and Appendicularia in the east. Tufted Puffin and *Calanus* spp. showed inverse patterns, with puffins being more abundant in the west, and *Calanus* spp. more abundant in the east, and were thus negatively related in one model (refer to Table VII). However, of the seven seabird species showing relationships to NPP, four were distributed more so in the Eastern North Pacific. The only western species to show a relationship with NPP was Northern Fulmar. Two species with no apparent regional affiliation, Mottled Petrel and Rhinoceros Auklet, also showed relationships with NPP. We also investigated patterns of biodiversity and showed greater seabird diversity in the eastern North Pacific, but we were unable to relate this to any zooplankton characteristics.

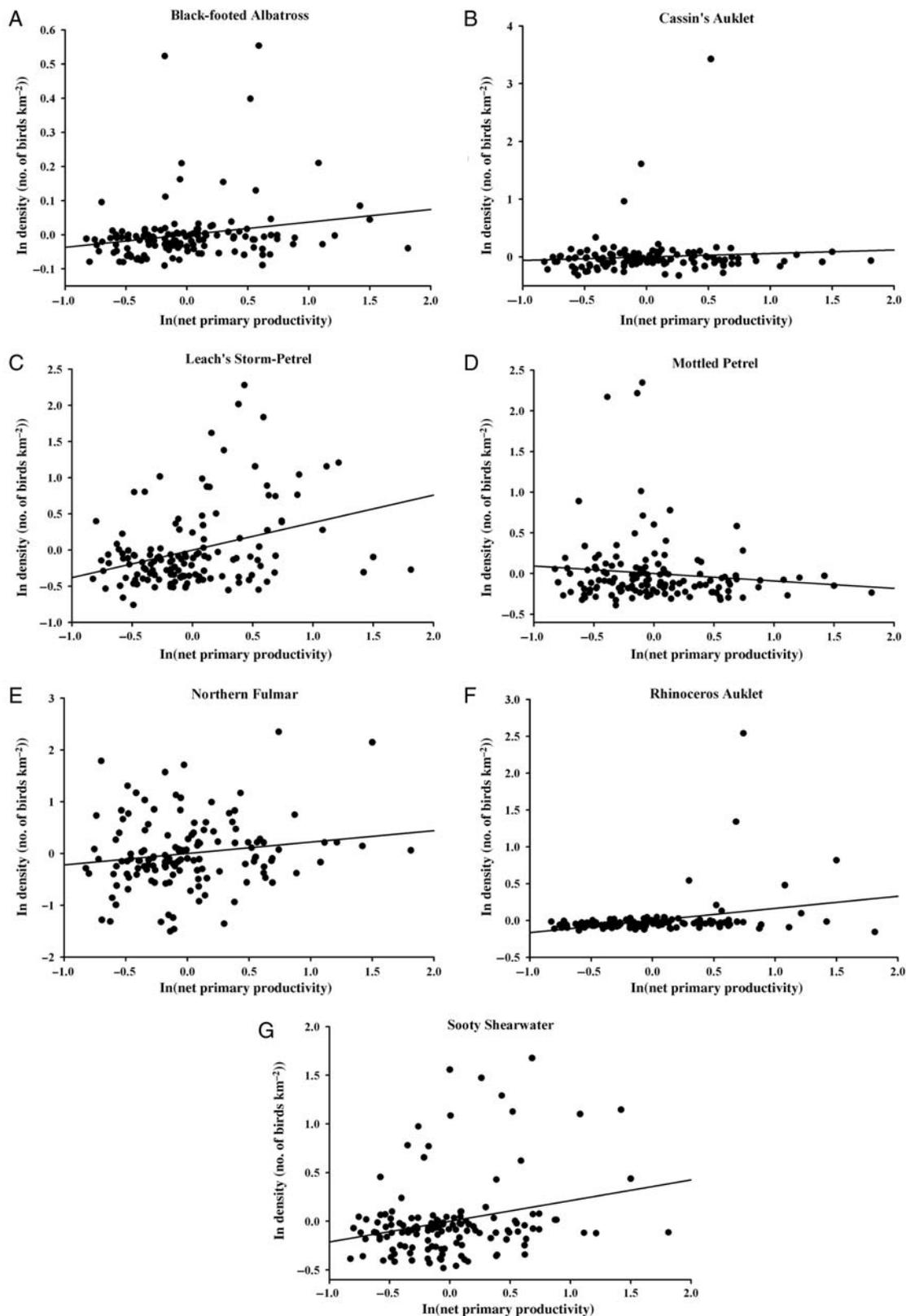
In addition to zooplankton communities, other habitat characteristics may explain higher seabird density in the west. Seabird density in the western North Pacific was  $\sim 2$  (spring) to  $\sim 27$  (summer) times greater than in the Gulf of Alaska. For summertime, Taniguchi (Taniguchi, 1999) found greater nutrient and chlorophyll-*a* concentrations and mesozooplankton biomass in the western Subarctic Gyre than in the Gulf of Alaska in summer, although none of his values

(qualitatively speaking) were as substantial as that for the seabirds. In his study, nitrate, chlorophyll concentrations ( $\text{mg C m}^{-3}$ ) and mesozooplankton ( $\text{mg C m}^{-3}$ ) were 1.5, 1.1 and 1.1 times greater in the western subarctic gyre than the Gulf of Alaska, respectively. Sugimoto and Tadokoro (Sugimoto and Tadokoro, 1997) and Mackas and Tsuda (Mackas and Tsuda, 1999) also provide similar qualitative results. Therefore, it seems reasonable to conclude that the greater seabird density in the west is not related to regional variation in nutrients, primary productivity or greater zooplankton abundance, although additional data, particularly on micronekton (forage fishes and squids) associations, are needed to adequately test this hypothesis directly.

The regional variation in seabird distributions could be related to other biological interactions as well. One of our clear findings was the inverse distributions of Laysan (west) and Black-footed (east) Albatross, Short-tailed (west) and Sooty (east) Shearwater, Fork-tailed (west) and Leach's Storm-Petrel (east), and Least/Crested/Parakeet (west) and Cassin's (east) Auklet. In each case, the abundance of the species in the west was substantially greater than its congener in the east. The habitat segregation shown by these species pair may reflect underlying competitive relationships, but this hypothesis cannot be accepted without further tests, including, for example, an accounting on the distance from land, distance from breeding colonies and other habitat associations that may be species-specific.

### Species- and taxon-specific seabird–zooplankton associations

Seabird species were more closely related to zooplankton taxonomic groups than “bulk” measurements of zooplankton abundance or diversity. This is an important finding and suggests that taxonomically based functional relationships are more useful to understanding macro-ecological patterns than possible functional relationships based on broad zooplankton categories such as “abundance” or “biomass”. However, variability and specificity among the relationships between seabirds and zooplankton did not fall into any general characterizations, including the diving-surface foraging dimension that we thought might be important. Also, of the seabird–NPP relationships that we found (Fig. 5), those for the pelagic procellariid species (albatrosses, storm-petrels, petrels and shearwaters) were more convincing (stronger and linear interactions) than those for the alcids (auklets), which appeared to be related to few data points. The relationships for the auklets, in particular, were driven by apparent statistical outliers, although there was no *a priori* reason to reject these points on



**Fig. 5.** Added variable plots of seabird species densities as a function of net primary productivity based on regression models including season, region, year, zooplankton abundance and zooplankton diversity as independent variables.

Table VII: Results of forward stepwise regression ( $P_{enter} < 0.051$ ) of bird species densities, by season

| Species/factor                   | Season | Model                     |         |                | Factor |        |                  |
|----------------------------------|--------|---------------------------|---------|----------------|--------|--------|------------------|
|                                  |        | F (df model, df residual) | P > F   | r <sup>2</sup> | t      | P <  t | Coefficient sign |
| <b>Ancient Murrelet</b>          | 1      | 10.38 (1, 44)             | 0.0024  | 0.1909         |        |        |                  |
| <i>Acartia</i> spp.              |        |                           |         |                | 3.22   | 0.002  | +                |
|                                  | 2      | 0.00 (0, 51)              | .       | .              |        |        |                  |
| <i>Eucalanus</i> spp.            | 3      | 6.59 (1, 38)              | 0.0143  | 0.1479         | 2.57   | 0.014  | +                |
| <b>Black-footed Albatross</b>    | 1      | 8.89 (1, 44)              | 0.0047  | 0.1681         |        |        |                  |
| Region                           |        |                           |         |                | -2.98  | 0.005  | -                |
|                                  | 2      | 5.70 (3, 48)              | 0.0020  | 0.2627         |        |        |                  |
| <i>Neocalanus</i> spp.           |        |                           |         |                | -3.07  | 0.003  | -                |
| Region                           |        |                           |         |                | -2.78  | 0.008  | -                |
| <i>Pseudocalanus</i> spp. adults |        |                           |         |                | 2.40   | 0.020  | +                |
|                                  | 3      | 8.59 (3, 36)              | 0.0002  | 0.4172         |        |        |                  |
| Euphausiacea                     |        |                           |         |                | 3.72   | 0.001  | +                |
| <i>Pseudocalanus</i> spp. adults |        |                           |         |                | 2.85   | 0.007  | +                |
| <i>Metridia</i> spp.             |        |                           |         |                | -2.50  | 0.017  | -                |
| <b>Black-legged Kittiwake</b>    | 1      | 6.24 (2, 43)              | 0.0042  | 0.2249         |        |        |                  |
| <i>Pseudocalanus</i> spp. adults |        |                           |         |                | -2.69  | 0.010  | -                |
| <i>Eucalanus</i> spp.            |        |                           |         |                | -2.21  | 0.032  | -                |
|                                  | 2      | 8.12 (3, 48)              | 0.0002  | 0.3366         |        |        |                  |
| <i>Limacina helicina</i>         |        |                           |         |                | 2.99   | 0.004  | +                |
| <i>Acartia</i> spp.              |        |                           |         |                | 2.45   | 0.018  | +                |
| <i>Eucalanus</i> spp.            |        |                           |         |                | 2.40   | 0.020  | +                |
| Region                           | 3      | 45.14 (1, 38)             | <0.0001 | 0.5429         | 6.72   | <0.001 | +                |
| <b>Cassin's Auklet</b>           | 1      | 4.74 (1, 44)              | 0.0348  | 0.0972         |        |        |                  |
| Region                           |        |                           |         |                | -2.18  | 0.035  | -                |
|                                  | 2      | 5.82 (4, 47)              | 0.0007  | 0.3312         |        |        |                  |
| Region                           |        |                           |         |                | -2.97  | 0.005  | -                |
| <i>Neocalanus</i> spp.           |        |                           |         |                | -3.26  | 0.002  | -                |
| <i>Pseudocalanus</i> spp. adults |        |                           |         |                | 2.94   | 0.005  | +                |
| <i>Oithona</i> spp.              |        |                           |         |                | -2.54  | 0.014  | -                |
| <i>Acartia</i> spp.              | 3      | 9.84 (1, 38)              | 0.0033  | 0.2058         | 3.14   | 0.003  | +                |
| <b>Common Murre</b>              | 1      | 4.13 (1, 44)              | 0.0482  | 0.0858         |        |        |                  |
| Chaetognatha                     |        |                           |         |                | 2.03   | 0.048  | +                |
|                                  | 2      | 4.97 (2, 49)              | 0.0109  | 0.1685         |        |        |                  |
| <i>Calanus</i> spp.              |        |                           |         |                | -2.87  | 0.006  | -                |
| <i>Pseudocalanus</i> spp. adults |        |                           |         |                | 2.28   | 0.027  | +                |
| <i>Calanus</i> spp.              | 3      | 4.90 (1, 38)              | 0.0329  | 0.1143         | -2.21  | 0.033  | -                |
| <b>Crested Auklet</b>            | 1      | 4.58 (2, 43)              | 0.0157  | 0.1757         |        |        |                  |
| Hyperiididae                     |        |                           |         |                | 2.91   | 0.006  | +                |
| <i>Neocalanus</i> spp.           |        |                           |         |                | -2.18  | 0.035  | -                |
| <i>Eucalanus</i> spp.            | 2      | 14.27 (1, 50)             | 0.0004  | 0.2220         | 3.78   | <0.001 | +                |
| <i>Neocalanus</i> spp.           | 3      | 8.13 (1, 38)              | 0.0070  | 0.1763         | 2.85   | 0.007  | +                |
| <b>Fork-tailed Storm-Petrel</b>  | 1      | 9.84 (1, 44)              | 0.0030  | 0.1828         |        |        |                  |
| Euphausiacea                     |        |                           |         |                | 3.14   | 0.003  | +                |
| Region                           | 2      | 20.92 (1, 50)             | <0.0001 | 0.2950         | 4.57   | <0.001 | +                |
|                                  | 3      | 0.00 (0, 39)              | .       | .              |        |        |                  |
| <b>Horned Puffin</b>             | 1      | 0.00 (0, 45)              | .       | .              |        |        |                  |
|                                  | 2      | 0.00 (0, 51)              | .       | .              |        |        |                  |
|                                  | 3      | 0.00 (0, 39)              | .       | .              |        |        |                  |
| <b>Laysan Albatross</b>          | 1      | 7.01 (2, 43)              | 0.0023  | 0.2460         |        |        |                  |
| <i>Neocalanus</i> spp.           |        |                           |         |                | 2.96   | 0.005  | +                |
| Region                           |        |                           |         |                | 2.59   | 0.013  | +                |

Continued

Table VII: Continued

| Species/factor                   | Season | Model                     |         |                | Factor |        | Coefficient sign |
|----------------------------------|--------|---------------------------|---------|----------------|--------|--------|------------------|
|                                  |        | F (df model, df residual) | P > F   | r <sup>2</sup> | t      | P <  t |                  |
| Region                           | 2      | 9.59 (2, 49)              | 0.0003  | 0.2813         | 3.93   | <0.001 | +                |
| <i>Acartia</i> spp.              |        |                           |         |                | 2.05   | 0.046  | +                |
| Region                           | 3      | 14.64 (1, 38)             | 0.0005  | 0.2781         | 3.83   | <0.001 | +                |
| <b>Least Auklet</b>              | 1      | 7.89 (2, 43)              | 0.0012  | 0.2683         | 3.49   | 0.001  | +                |
| Region                           |        |                           |         |                | 2.27   | 0.029  | +                |
| Euphausiacea                     | 2      | 9.44 (2, 49)              | 0.0003  | 0.2782         | 3.71   | 0.001  | +                |
| Euphausiacea                     |        |                           |         |                | 2.41   | 0.020  | +                |
| Region                           | 3      | 10.12 (1, 38)             | 0.0029  | 0.2103         | 3.18   | 0.003  | +                |
| <i>Metridia</i> spp.             |        |                           |         |                |        |        |                  |
| <b>Leach's Storm-Petrel</b>      | 1      | 9.86 (1, 44)              | 0.0030  | 0.1831         | 3.14   | 0.003  | +                |
| <i>Neocalanus</i> spp.           | 2      | 6.64 (3, 48)              | 0.0008  | 0.2934         | 3.20   | 0.002  | +                |
| Appendicularia                   |        |                           |         |                | -2.82  | 0.007  | -                |
| <i>Neocalanus</i> spp.           |        |                           |         |                | 2.28   | 0.027  | +                |
| <i>Metridia</i> spp.             | 3      | 10.22 (1, 38)             | 0.0028  | 0.2120         | -3.20  | 0.003  | -                |
| Region                           |        |                           |         |                |        |        |                  |
| <b>Mottled Petrel</b>            | 1      | 0.00 (0, 45)              | .       | .              |        |        |                  |
| Region                           | 2      | 4.67 (1, 50)              | 0.0356  | 0.0854         | 2.16   | 0.036  | +                |
| Region                           | 3      | 8.43 (3, 36)              | 0.0002  | 0.4126         | 3.39   | 0.002  | +                |
| <i>Metridia</i> spp.             |        |                           |         |                | -3.50  | 0.001  | -                |
| <i>Acartia</i> spp.              |        |                           |         |                | -2.86  | 0.007  | -                |
| <i>Eucalanus</i> spp.            |        |                           |         |                |        |        |                  |
| <b>Northern Fulmar</b>           | 1      | 12.23 (2, 43)             | 0.0001  | 0.3627         | 3.81   | <0.001 | +                |
| Region                           |        |                           |         |                | -2.07  | 0.044  | -                |
| <i>Pseudocalanus</i> spp. adults | 2      | 63.19 (1, 50)             | <0.0001 | 0.5583         | 7.95   | <0.001 | +                |
| Region                           | 3      | 30.95 (1, 38)             | <0.0001 | 0.4488         | 5.56   | <0.001 | +                |
| Region                           |        |                           |         |                |        |        |                  |
| <b>Parakeet Auklet</b>           | 1      | 6.31 (1, 44)              | 0.0157  | 0.1255         | 2.51   | 0.016  | +                |
| <i>Oithona</i> spp.              | 2      | 0.00 (0, 51)              | .       | .              |        |        |                  |
| <i>Acartia</i> spp.              | 3      | 6.72 (1, 38)              | 0.0134  | 0.1503         | 2.59   | 0.013  | +                |
| <b>Rhinoceros Auklet</b>         | 1      | 0.00 (0, 45)              | .       | .              |        |        |                  |
| Region                           | 2      | 4.72 (1, 50)              | 0.0346  | 0.0862         | 2.17   | 0.035  | +                |
| <i>Pseudocalanus</i> spp. adults | 3      | 0.00 (0, 39)              | .       | .              |        |        |                  |
| <b>Short-tailed Shearwater</b>   | 1      | 7.94 (2, 43)              | 0.0012  | 0.2697         | 3.37   | 0.002  | +                |
| <i>Pseudocalanus</i> spp. adults |        |                           |         |                | 2.92   | 0.006  | +                |
| Region                           | 2      | 12.06 (4, 47)             | <0.0001 | 0.5065         | 5.21   | <0.001 | +                |
| Region                           |        |                           |         |                | 2.07   | 0.044  | +                |
| <i>Calanus</i> spp.              |        |                           |         |                | -2.61  | 0.012  | -                |
| <i>Metridia</i> spp.             |        |                           |         |                | 2.09   | 0.042  | +                |
| <i>Pseudocalanus</i> spp. adults | 3      | 6.38 (3, 36)              | 0.0014  | 0.3473         | 3.28   | 0.002  | +                |
| Chaetognatha                     |        |                           |         |                | 2.18   | 0.036  | +                |
| Region                           |        |                           |         |                | -2.05  | 0.047  | -                |
| <i>Acartia</i> spp.              |        |                           |         |                |        |        |                  |

Continued

Table VII: Continued

| Species/factor   | Season                                      | Model                            |                     |                       | Factor   |                       | Coefficient sign |
|--|---|----------------------------------|---------------------|-----------------------|----------|-----------------------|------------------|
|  |   | <i>F</i> (df model, df residual) | <i>P</i> > <i>F</i> | <i>r</i> <sup>2</sup> | <i>t</i> | <i>P</i> <   <i>t</i> |                  |
| Slaty-backed Gull<br>Region                            | 1   | 6.13 (1, 44)                     | 0.0172              | 0.1223                |          |                       |                  |
|  | 2   | 14.04 (1, 50)                    | 0.0005              | 0.2192                | 2.48     | 0.017                 | +                |
|  | 3   | 0.00 (0, 39)                     | .                   | .                     | 3.75     | <0.001                | +                |
| Sooty Shearwater<br>Region                             | 1   | 6.14 (1, 44)                     | 0.0172              | 0.1224                |          |                       |                  |
|  | 2   | 6.53 (3, 48)                     | 0.0009              | 0.2899                | −2.48    | 0.017                 | −                |
|  | Region                                      |                                  |                     |                       | −2.54    | 0.014                 | −                |
|  | Larvacea                                    |                                  |                     |                       | 2.52     | 0.015                 | +                |
|  | <i>Acartia</i> spp.                         |                                  |                     |                       | −2.12    | 0.040                 | −                |
|  | Euphausiacea                                | 3                                | 7.06 (1, 38)        | 0.0115                | 0.1566   | 2.66                  | 0.011            |
| Thick-billed Murre<br><i>Pseudocalanus</i> spp. adults | 1   | 9.96 (1, 44)                     | 0.0029              | 0.1845                |          |                       |                  |
|  | 2   | 5.01 (1, 50)                     | 0.0298              | 0.0910                | −3.16    | 0.003                 | −                |
|  | Region                                      |                                  |                     |                       | 2.24     | 0.030                 | +                |
|  | Region                                      | 3                                | 4.63 (1, 38)        | 0.0378                | 0.1087   | 2.15                  | 0.038            |
| Tufted Puffin  | 1   | 0.00 (0, 45)                     | .                   | .                     |          |                       |                  |
|  | 2   | 8.28 (1, 50)                     | 0.0060              | 0.1417                |          |                       |                  |
|  | Region                                      |                                  |                     |                       | 2.87     | 0.006                 | +                |
|  | <i>Metridia</i> spp.<br><i>Calanus</i> spp. | 3                                | 6.68 (2, 37)        | 0.0033                | 0.2652   | 3.06<br>−2.54         | 0.004<br>0.015   |

Independent factors were region and zooplankton taxonomic densities. For Season, 1 = spring (March–May), 2 = summer (June–July) and 3 = autumn (September–October).

methodological or biological grounds. We therefore reject this part of our hypothesis and conclude that there are no consistent zooplankton–seabird associations by foraging mode or dietary considerations, at least as revealed by this analysis.

Seasonal variation in seabird densities was substantial with 60% (12/20) of the species showing significant (or nearly significant,  $P < 0.10$ ) variation. The temporal pattern in species density is clearly related to the migratory or transitory behavior of some of the seabird species. As such, we stratified all species-specific analyses by season. In that regard, we established that some of the regional affiliations and associations between seabirds and mesozooplankton abundance were dependent on season. Laysan Albatross, Northern Fulmar and Short-tailed Shearwater were the only species that showed consistent regional variations in all seasons (Table VII). Interestingly, however, no species, including the three listed above, showed consistent relationships across seasons with zooplankton taxonomic groups. As noted above, when considering our second hypothesis that diving, mainly planktivorous species, varied

systematically from surface foraging, mostly piscivorous species, we found no consistency in these relationships. Perhaps this is not surprising given the range of diets and other bio-physical interactions for most seabird species in the subarctic North Pacific, but we anticipated some similarities within families of birds at least. The level of variability seen in this study highlights the need to consider other ways to summarize the data, perhaps by using lower-resolution zooplankton groupings in relation to size of zooplankton, in further attempts to find consistency in these seabird–zooplankton relationships. Alternatively, perhaps these relationships are scale-dependent (Schneider and Piatt, 1986; Hunt *et al.*, 1998), and using a single scale (day) to test for all relationships may have made consistency difficult to obtain. These are considerations for future analyses.

### Seabirds and zooplankton as ecosystem indicators

Seabirds have been put forth as sentinels and indicators of coupled climate–marine ecosystem change (Bertram

*et al.*, 2001; Piatt *et al.*, 2007) in part because they may integrate or amplify variation in physical oceanographic attributes or biological productivity at lower trophic levels (Taylor *et al.*, 2002). Zooplankton has also been put forth as reliable indicators of ecosystem change (McGowan *et al.*, 1996; Beaugrand *et al.*, 2002; Beaugrand, 2005; Hooff and Peterson, 2006; Lavaniegos and Ohman, 2007; Mackas *et al.*, 2007; Richardson, 2008). The CPR-MBM (marine bird and mammal) survey has revealed spatial and temporal variability in zooplankton and seabird abundance and diversity, hence over all community structure in the subarctic Pacific, but this variation is not well understood. Undoubtedly, this variation is related to changes in underlying physical oceanography, and to some of the bulk and species-specific associations described herein. As indicators, the relative abundance of seabirds at sea is thought to reflect water mass and prey base characteristics (Briggs *et al.*, 1987; Cairns, 1987; Hyrenbach and Veit, 2003; Hedd *et al.*, 2006; Piatt *et al.*, 2007; Sydeman *et al.*, 2001, 2006a,b, 2009). We have dealt with the latter, primarily, in this study. Although some of the seabirds we included here consume the larger zooplankton (*Neocalanus* spp., euphausiids) sampled by the CPR, many species feed on other mid-trophic level micronekton, specifically gonatid squids and lanternfish (myctophids), not sampled by the CPR monitoring program. Obtaining information on these species would be clearly advantageous, but in the absence of these data, integrating zooplankton and seabird data may be one of the best ways to obtain a better understanding of the relative abundance and distribution of other key prey fields and mid-trophic level prey items. Micronekton are important to other top predators, such as salmonids, in these ecosystems (Kaeriyama *et al.*, 2004), and it has been well-established that myctophids in the region directly consume many of the mesozooplankton sampled by the CPR (Beamish *et al.*, 1999). Therefore, continuation of the CPR-MBM program for the foreseeable future may be the best option currently available for studying vast expanses of the North Pacific that are difficult to sample using traditional methods.

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