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Data Article

Data on macrobenthic prey from an essential western gray whale feeding habitat, Sakhalin Island, Russia, 2001–2015

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A B S T R A C T

Data in this article presents data (means and standard deviations) for prey biomass from essential feeding habitats for the endangered western gray whale. Prey include Actinopterygii (primarily the sand lance Ammodytes hexapterus), Amphipoda, Bivalvia, Cumacea, Isopoda, and Polychaeta. Total prey biomass (sum of the six prey groups) is also presented. Statistical analyses document spatial and temporal trends in prey biomass concentrations. Multivariate analyses using canonical correspondence analysis characterize relationships of potential drivers of community changes.

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1. Data

Macrobenthic community biomass was determined from the northeastern Sakhalin Island gray whale feeding area, Sea of Okhotsk, Russia [1]. Bottom samples were collected from 2001 to 2015 to determine prey biomass characteristics and distributions. Biomass data presented here include 6 prey (Actinopterygii (primarily sand lance Ammodytes hexapterus), Amphipoda, Bivalvia, Cumacea, Isopoda, and Polychaeta), and total prey (sum of the six prey categories). Average biomass, sample size, and standard deviations are presented for the nearshore (2001–2015) and offshore (2001–2015) study areas (Fig. 1; Tables 1 and 2). Biomass values are also presented for feeding points (opportunistically sampled locations where whales were observed feeding) to determine if feeding areas had different biomass characteristics than other stations (Table 3). ANCOVA and Tukey multiple comparisons document long-term differences for benthic prey among years for the nearshore and offshore surveys (Tables 4–6). Canonical correspondence analyses were conducted to investigate relationships between environmental predictors and community biomass structure using all macrofaunal groups (Fig. 2; Table 7) (see: Table 8).

2. Experimental design, materials, and methods

2.1. Sampling

Bottom sampling was conducted in the summers of 2001–2015 to measure biomass concentrations and environmental characteristics in the GW feeding area adjacent to northeastern Sakhalin Island (the Sakhalin feeding area; Fig. 1). Sampling was conducted aboard the R/V Okean (2001), R/V Nevelskoy
Fig. 1. Sakhalin Island survey grids. Benthic sampling locations were either randomly selected within the grid or repeated from previous years. One location was selected for sampling in each grid and three replicate van Veen grabs were collected at each sampling location.
Benthic biological and sediment samples were collected using a van Veen grab with a surface area of 0.2 m². Research vessel drafts limited operations of van Veen grabs to water depths ≤ 9 m though some slightly shallower samples (7–8 m) were occasionally collected. Onboard, samples were sieved over a 1.0-mm-mesh screen and the organisms preserved in 4% formalin. In the taxonomic laboratory, biological material was sorted from the sediment residues and animals were identified, counted, and weighed. Animals were grouped into classes or higher taxonomic categories. Sediment grain-size analyses were used to determine standard grain-size categories.

Initial investigation of the nearshore feeding area was conducted in 2001 by divers to explore prey habitat (5–30 m water depth) and provide a basis for designing the nearshore Piltun survey grid. The current nearshore sampling grid consists of 72 cells along the northeastern coast of Sakhalin Island encompassing the nearshore (< 20 m) GW feeding habitat and extending to deeper waters to capture environmental gradients. The total area of the nearshore survey area is approximately 1100 km². Sampling was initiated in the offshore feeding area in 2002 and the offshore survey currently includes 48 cells with a total area of approximately 2000 km². Data records for diver sampling in 2001 consists of single biomass estimates for sampling location. Benthos and sediment sample collections from 2002 to 2015 comprised three replicates collected at randomly selected sampling points or by repeated sampling of locations selected in previous years. Samples from 2002 to 2015 were collected in water

| Year | N  | Average Amphipoda | SD | Average Bivalvia | SD | Average Cumacea | SD | Average Isopoda | SD |
|------|----|-------------------|----|-----------------|----|-----------------|----|-----------------|----|
| 2001 | 60 | 36.6              | 62.3| 106.9           | 141.4| 20.8           | 30.6| 25.7           | 39.7|
| 2002 | 88 | 32.2              | 58.7| 27.6           | 56.1 | 12.5           | 29.8| 13.8           | 20.5|
| 2003 | 55 | 56.3              | 62.5| 45.1           | 92.9 | 2.2            | 6.7 | 21.3           | 30.7|
| 2004 | 45 | 46.8              | 50.5| 21.9           | 28.7 | 0.8            | 2.4 | 10.2           | 13.4|
| 2005 | 48 | 30.5              | 34.3| 24.8           | 29.5 | 1.0            | 1.9 | 5.4            | 6.6 |
| 2006 | 60 | 28.2              | 33.5| 15.2           | 38.1 | 2.7            | 8.2 | 11.1           | 11.1|
| 2007 | 78 | 33.4              | 39.7| 53.3           | 92.4 | 4.2            | 14.1| 12.8           | 22.0|
| 2008 | 67 | 37.2              | 32.4| 35.5           | 47.2 | 1.8            | 4.9 | 3.9            | 3.1 |
| 2009 | 74 | 18.6              | 26.1| 23.3           | 35.1 | 0.4            | 0.8 | 3.8            | 5.9 |
| 2010 | 79 | 29.4              | 37.7| 25.1           | 35.7 | 5.1            | 42.7| 7.0            | 9.1 |
| 2011 | 60 | 20.6              | 45.8| 92.4           | 139.0| 0.1            | 0.7 | 6.8            | 14.0|
| 2012 | 73 | 38.4              | 44.9| 56.2           | 70.9 | 0.3            | 0.7 | 10.2           | 13.9|
| 2013_1 | 42 | 40.2             | 35.2| 111.2         | 128.8| 2.2            | 3.4 | 12.7           | 13.2|
| 2013_2 | 70 | 16.8             | 21.6| 58.2           | 83.3 | 0.5            | 1.1 | 8.0            | 10.2|
| 2014 | 72 | 18.0              | 24.1| 45.1           | 81.7 | 0.3            | 0.5 | 6.7            | 12.4|
| 2015 | 63 | 19.8              | 28.5| 55.3           | 94.3 | 0.4            | 0.6 | 4.4            | 5.5 |

| Year | N  | Average Actinopterygii | SD | Average Polychaeta | SD | T6 | SD |
|------|----|----------------------|----|-------------------|----|----|----|
| 2001 | 60 | 4.3                  | 10.8| 24.2              | 37.6| 218.4| 180.6|
| 2002 | 88 | 6.2                  | 10.1| 8.6               | 8.5 | 100.8| 98.9 |
| 2003 | 55 | 4.5                  | 12.5| 12.6              | 26.8| 142.3| 106.9|
| 2004 | 45 | 49.4                 | 88.2| 6.5               | 7.2 | 135.5| 113.6|
| 2005 | 48 | 56.5                 | 102.1| 9.2              | 15.0| 127.3| 119.5|
| 2006 | 60 | 13.7                 | 32.0| 3.2               | 6.6 | 74.0 | 60.3 |
| 2007 | 78 | 9.1                  | 24.2| 4.6               | 4.9 | 117.5| 104.7|
| 2008 | 67 | 3.6                  | 6.8 | 5.2               | 6.2 | 86.4 | 55.1 |
| 2009 | 74 | 8.1                  | 18.8| 2.4               | 2.7 | 56.6 | 47.6 |
| 2010 | 79 | 12.7                 | 30.2| 4.1               | 5.9 | 83.3 | 65.3 |
| 2011 | 60 | 12.9                 | 26.2| 10.7              | 14.4| 143.5| 148.3|
| 2012 | 73 | 3.6                  | 14.3| 6.6               | 7.2 | 115.1| 87.6 |
| 2013_1| 42 | 4.7                  | 6.6 | 7.3               | 5.1 | 178.2| 114.4|
| 2013_2| 70 | 6.1                  | 10.4| 10.7              | 16.2| 100.1| 84.3 |
| 2014 | 72 | 4.2                  | 10.4| 8.8               | 22.9| 82.4 | 97.2 |
| 2015 | 63 | 23.0                 | 37.0| 7.7               | 15.0| 110.7| 101.2|
### Table 2
Sample size, averages, and standard deviations (SD) for the offshore study area for Amphipoda, Bivalvia, Cumacea, Isopoda, Actinopterygii, Polychaeta, and the total prey (T6: sum of 6 prey) biomass, 2001–2015.

| Year | N | Average Amphipoda | SD | Average Bivalvia | SD | Average Cumacea | SD | Average Isopoda | SD |
|------|---|-------------------|----|------------------|----|------------------|----|-----------------|----|
| 2002 | 36 | 268.5             | 313.4 | 50.0             | 79.9 | 24.7             | 30.9 | 0.0             | 0.0 |
| 2003 | 36 | 233.2             | 261.7 | 110.6            | 116.0 | 110.6            | 93.5 | 0.0             | 0.0 |
| 2004 | 32 | 246.7             | 213.3 | 76.8             | 57.0 | 19.7             | 29.7 | 0.0             | 0.0 |
| 2005 | 48 | 200.3             | 191.9 | 146.7            | 44.3 | 10.8             | 49.8 | 0.0             | 0.0 |
| 2006 | 48 | 184.9             | 235.6 | 112.2            | 141.4 | 12.2             | 24.8 | 0.0             | 0.0 |
| 2007 | 48 | 173.6             | 190.2 | 11.3             | 12.7 | 11.3             | 6.5  | 0.0             | 0.0 |
| 2008 | 48 | 140.0             | 191.8 | 141.3            | 83.1 | 33.1             | 42.5 | 0.0             | 0.0 |
| 2009 | 48 | 169.0             | 194.2 | 72.9             | 236.5 | 49.8             | 60.4 | 0.0             | 0.0 |
| 2010 | 48 | 132.3             | 170.0 | 115.4            | 236.1 | 281.9            | 150.3 | 4.1            |
| 2012 | 48 | 143.2             | 276.8 | 65.6             | 219.4 | 94.8             | 264.7 | 14.0          |
| 2013 | 48 | 119.7             | 143.0 | 129.1            | 179.7 | 129.1            | 237.5 | 11.6          |
| 2014 | 48 | 173.5             | 194.1 | 329.1            | 193.8 | 63.9             | 389.0 | 2.4           |
| 2015 | 48 | 132.3             | 194.1 | 103.2            | 193.8 | 63.9             | 389.0 | 2.4           |

### Table 3
Average biomass (g m\(^{-2}\)) of six prey groups and total prey biomass from feeding points in the nearshore and offshore surveys 2002–2015.

| Region | Year | Amp | Biv | Cu | Iso | Act | Poly | T6 |
|--------|------|-----|-----|----|-----|-----|------|----|
| Nearshore | 2002 | 72.9 | 13.9 | 1.2 | 16.1 | 4.0 | 3.0 | 111.1 |
|         | 2003 | 83.5 | 19.3 | 2.5 | 30.1 | 41.1 | 4.0 | 180.5 |
|         | 2004 | 44.3 | 17.7 | 0.8 | 14.9 | 39.6 | 2.4 | 119.7 |
|         | 2005 | 63.8 | 30.9 | 3.2 | 8.5  | 51.3 | 7.8 | 165.5 |
|         | 2006 | 41.2 | 17.0 | 0.8 | 9.7  | 43.1 | 3.9 | 76.8  |
|         | 2007 | 53.5 | 47.9 | 0.9 | 8.2  | 16.5 | 4.8 | 131.7 |
|         | 2008 | 51.8 | 28.5 | 1.6 | 10.6 | 0.4  | 3.3 | 96.1   |
|         | 2009 | 32.8 | 20.5 | 1.6 | 18.3 | 34.6 | 4.4 | 112.3 |
|         | 2010 | 72.4 | 47.7 | 5.0 | 14.2 | 48.8 | 9.1 | 197.2 |
|         | 2011 | 112.9 | 11.1 | 1.7 | 23.9 | 0.0  | 6.9 | 156.4 |
|         | 2012 | 67.1 | 32.1 | 2.5 | 13.0 | 4.0  | 9.8 | 124.9 |
|         | 2013 | 32.4 | 51.8 | 0.5 | 10   | 8.3  | 3.9 | 106.8 |
|         | 2014 | 264.9 | 35.8 | 16.0 | 0.0 | 0.1  | 8.0 | 324.7 |
|         | 2015 | 379.5 | 48.9 | 9.4 | 0.0 | 3.6  | 441.4 |
| Offshore | 2002 | 192.4 | 57.4 | 35.7 | 0.0 | 23.4 | 309.0 |
|         | 2003 | 65.7 | 25.7 | 15.8 | 7.1 | 1.3  | 5.0 | 120.6 |
|         | 2006 | 201.0 | 37.8 | 96.8 | 0.0 | 25.4 | 361.0 |
|         | 2007 | 449.2 | 61.7 | 15.8 | 0.1 | 37.1 | 563.9 |
|         | 2008 | 174.1 | 32.3 | 18.7 | 0.0 | 0.0  | 15.1 | 240.2 |
|         | 2009 | 274.8 | 26.3 | 3.9  | 0.0 | 8.4  | 313.3 |
|         | 2010 | 296.4 | 28.8 | 22.9 | 0.4 | 18.7 | 367.1 |
|         | 2012 | 472.7 | 44.7 | 1.7  | 0.0 | 15.7 | 534.8 |
|         | 2015 | 695.2 | 162.3 | 0.0 | 0.1 | 72.4 | 930.1 |

Act = average Actinopterygii biomass, Amp = Amphipoda, Biv = Bivalvia, Cu = Cumacea, Iso = Isopoda, Poly = Polychaeta, and T6 = total biomass of 6-prey group. Feeding points were not sampled in every year within each study area.
depths ranging from 7 to 35 m nearshore and from 30 to 63 m offshore. Both survey grids in the Sakhalin Island coastal study area are adjacent to or overlap with areas of heightened anthropogenic activities including commercial fishing and oil and gas platforms (Fig. 1). During the course of the investigation, locations where gray whales were observed feeding were opportunistically sampled and three replicates collected at each point. These feeding points were identified by gray whale observers from shore and on vessels associated with oil and gas exploration and production activities. The feeding points provide further information characterizing specific locations where whales feed. Feeding areas were sampled differently in 2015 using a targeted sampling approach with six replicates collected along two transects at 9 m and 13 m for a total of twelve replicates at each location. Feeding areas from 2015 were not statistically-evaluated for differences here but were considered separately (Blanchard et al., unpublished data).

Environmental variables included water depth, year of sampling, percent sand (sand: particles between 0.1 mm and 1.0 mm; other categories were colinear with sand), and the Aleutian Low Pressure Index (ALPI). The Aleutian Low [2] influences winter wind patterns and sea-level pressure throughout the Bering Sea and variations in its strength and position can directly influence water circulation [3,4]. The ALPI is available at https://open.canada.ca/data/.

2.2. Statistical analyses

Analysis of covariance was performed for surveys using mixed modeling to test for differences among years. ANCOVA’s were performed separately for the nearshore (incorporating data from 2001 to 2015) and offshore surveys (using data from 2002 to 2015). The mixed-modeling package nlme [5] was used with the statistical program R [6] for analysis of as it allows incorporation of models for temporally-correlated errors. Autoregressive and moving average correlation models were used in nlme to correct

| Comparison | Amphipoda | Bivalvia | Cumacea | Isopoda | Actinoptygii | Polychaeta | T6 |
|------------|-----------|----------|---------|---------|--------------|------------|----|
| Model      | D + Y     | Y        | D + Y   | D + Y   | Y            | D + Y      | D + Y |
| TS Corr.   | AR(3)     | AR(3)    | AR(2)   | AR(3)   | ARMA         | ARMA       | ARMA |
| 2001–2002  | 0.9973    | <0.0001  | <0.0001 | 0.6426  | 1.0000       | <0.0001    | 0.0647|
| 2001–2003  | 0.8068    | <0.0001  | <0.0001 | 0.3322  | 1.0000       | <0.0001    | 0.2530|
| 2001–2004  | 0.0006    | <0.0001  | <0.0001 | 0.0186  | 0.0796       | <0.0001    | 0.4522|
| 2001–2005  | 1.0000    | <0.0001  | <0.0001 | <0.0001 | 0.0782       | <0.0001    | 0.0331|
| 2001–2006  | 0.9977    | <0.0001  | <0.0001 | 0.0659  | 1.0000       | <0.0001    | <0.0001|
| 2001–2007  | 0.9977    | 0.0001   | <0.0001 | 0.0079  | 1.0000       | <0.0001    | 0.0031|
| 2001–2008  | 0.3991    | <0.0001  | <0.0001 | <0.0001 | 0.9954       | <0.0001    | 0.0001|
| 2001–2009  | 0.2778    | <0.0001  | <0.0001 | <0.0001 | 1.0000       | <0.0001    | <0.0001|
| 2001–2010  | 0.9999    | <0.0001  | <0.0001 | <0.0001 | 0.9991       | <0.0001    | <0.0001|
| 2001–2011  | 0.5761    | 0.1673   | <0.0001 | <0.0001 | 0.9779       | 0.0002     | 0.0535|
| 2001–2012  | 1.0000    | 0.0049   | <0.0001 | 0.0057  | 0.8716       | <0.0001    | <0.0001|
| 2001–2013  | 0.0556    | 0.1513   | <0.0001 | <0.0001 | 1.0000       | 0.0076     | 0.0005|
| 2001–2014  | 0.0325    | 0.0001   | <0.0001 | <0.0001 | 1.0000       | <0.0001    | <0.0001|
| 2001–2015  | 0.4273    | 0.0096   | <0.0001 | <0.0001 | 0.5685       | <0.0001    | <0.0001|
| 2002–2003  | <0.0001   | 1.0000   | 0.0098  | 1.0000  | 0.9888       | 0.9711     | 1.0000|
| 2002–2004  | <0.0001   | 1.0000   | <0.0001 | 0.7780  | 0.0200       | 0.8720     | 0.9999|
| 2002–2005  | 0.3116    | 1.0000   | <0.0001 | 0.0004  | 0.0247       | 0.7152     | 1.0000|
| 2002–2006  | 0.0422    | 0.0207   | <0.0001 | 0.9830  | 0.9909       | <0.0001    | 0.0007|
| 2002–2007  | 0.0454    | 0.9595   | <0.0001 | 0.6299  | 0.9739       | 0.7169     | 0.9991|
| 2002–2008  | <0.0001   | 0.9994   | 0.0005  | <0.0001 | 0.6249       | 0.5288     | 0.7979|
| 2002–2009  | 0.6574    | 0.9838   | <0.0001 | <0.0001 | 1.0000       | <0.0001    | <0.0001|
| 2002–2010  | 1.0000    | 1.0000   | <0.0001 | 0.0102  | 1.0000       | 0.0023     | 0.0002|
| 2002–2011  | 0.9597    | 0.0311   | <0.0001 | <0.0001 | 0.9935       | 0.9558     | 1.0000|
| 2002–2012  | 0.8507    | 0.3228   | <0.0001 | 0.5538  | 0.1436       | 0.8937     | 0.3501|
| 2002–2013  | 0.1300    | 0.0053   | <0.0001 | 0.0005  | 1.0000       | 0.0677     | 0.9652|
| 2002–2014  | 0.0748    | 0.9616   | <0.0001 | <0.0001 | 0.9962       | 1.0000     | 0.0003|
| Comparison          | Amphipoda | Bivalvia | Cumacea | Isopoda | Actinopterygii | Polychaeta | T6   |
|---------------------|-----------|----------|---------|---------|----------------|------------|------|
| 2002–2007           | 0.9581    | 0.9990   | 0.2593  | 0.9548  | 1.0000         | 1.0000     | 0.9295|
| 2003–2008           | 1.0000    | 0.9988   | 0.3596  | 1.0000  | 0.9884         |            |      |
| 2004–2005           | <0.0001   | 0.9998   | 0.2761  | <0.0001 | 0.9959         |            |      |
| 2005–2006           | 0.0001    | 0.1689   | 0.8772  | 1.0000  | <0.0001        |            |      |
| 2006–2007           | 0.8120    | 0.8806   | 0.0900  | 0.0001  | 1.0000         | 0.9875     | 0.0612|
| 2007–2008           | 0.9221    | 0.0304   | 0.3138  | <0.0001 | 1.0000         | 0.9893     |      |
| 2008–2009           | 0.9999    | 0.9998   | 0.0630  | 0.0175  |               |            |      |
| 2009–2010           | 1.0000    | 0.9978   | 0.9671  | 0.7314  |               |            |      |
| 2010–2011           | <0.0001   | 0.0135   | 0.2820  | 0.0001  | 1.0000         | 0.9895     |      |
| 2011–2012           | 0.1641    | 0.9945   | 1.0000  | <0.0001 | 1.0000         | 0.9688     |      |
| 2012–2013           | <0.0001   | 0.0022   | 0.9999  | 0.1257  | 0.5926         |            |      |
| 2013–2014           | <0.0001   | 0.8189   | 1.0000  | 0.0003  | 0.8028         |            |      |
| 2014–2015           | 0.0023    | 0.6855   | 0.0227  | 0.8597  | 0.8892         | 0.0706     |      |
| 2015–2016           | 0.0292    | 0.9996   | 0.0325  | <0.0001 | 0.0011         | 0.0166     |      |
| 2016–2017           | 0.9123    | 0.9998   | 0.4193  | <0.0001 | 1.0000         | 0.9875     |      |
| 2017–2018           | 0.4911    | 0.9707   | 0.3038  | <0.0001 | 1.0000         | 0.9875     |      |
| 2018–2019           | <0.0001   | 0.9584   | 0.8539  | 0.0132  | 0.0120         |            |      |
| 2019–2020           | 0.6591    | 1.0000   | 0.7306  | 0.2469  | 0.8635         | 0.0040     |      |
| 2020–2021           | 0.057     | 0.0263   | 0.5496  | 0.8139  | 0.0423         | 1.0000     |      |
| 2021–2022           | 0.9999    | 0.2697   | 0.6527  | 0.0001  | 1.0000         | 0.7532     |      |
| 2022–2023           | <0.0001   | 0.9948   | 0.1000  | 0.1203  | <0.0001        | 0.9992     |      |
| 2023–2024           | 0.9237    | 0.9480   | 1.0000  | 0.0002  | 0.5981         | 0.0060     |      |
| 2024–2025           | 0.0053    | 0.9960   | 0.9857  | 0.7011  | 0.8434         |            |      |
| 2025–2026           | <0.0001   | 0.0002   | 0.8433  | 0.0204  | 0.0027         | 0.4071     |      |
| 2026–2027           | 0.6534    | 0.1493   | 0.0015  | 0.9981  | 1.0000         | 0.0512     |      |
| 2027–2028           | 0.1794    | 0.0585   | 0.4998  | 0.7059  | 0.6281         | 1.0000     |      |
| 2028–2029           | 0.0002    | <0.0001  | 0.0505  | 0.4307  | <0.0001        | 0.0201     |      |
| 2029–2030           | 0.9743    | <0.0001  | 0.9623  | 0.9323  | 0.0003         | 0.9163     |      |
| 2030–2031           | <0.0001   | <0.0001  | 0.2199  | 0.9033  | <0.0001        | 0.2573     |      |
| 2031–2032           | <0.0001   | <0.0001  | 0.2913  | 0.0067  | <0.0001        | 1.0000     |      |
| 2032–2033           | <0.0001   | <0.0001  | 0.0002  | 0.0039  | <0.0001        | 0.5281     |      |
| 2033–2034           | 0.6318    | 1.0000   | 0.7784  | 0.9999  | 1.0000         | 0.9991     |      |
| 2034–2035           | <0.0001   | 0.1165   | 0.1209  | 0.9891  | 0.0021         | <0.0001    |      |
| 2035–2036           | 0.1780    | 0.8465   | 0.0755  | 0.5618  | 0.7200         | 0.0134     |      |

(continued on next page)
Table 4 (continued)

| Comparison | Amphipoda | Bivalvia | Cumacea | Isopoda | Actinoptygii | Polychaeta | T6 |
|------------|-----------|----------|---------|---------|--------------|------------|----|
| 2008–2015  | <0.0001   | 0.2083   | 0.9238  | 1.0000  | <0.0001      | 0.4112     | 1.000 |
| 2009–2010  | 0.1235    | 0.9593   | 1.0000  | 0.7615  | 0.9987       | 0.6194     | 0.0448|
| 2009–2011  | 1.0000    | <0.0001  | 1.0000  | 1.0000  | 0.9712       |            |     |
| 2009–2012  | 0.0029    | 0.0031   | 1.0000  | 0.0474  | 0.1958       | <0.0001    | <0.001|
| 2009–2013  | 0.9999    | <0.0001  | 1.0000  | 0.9882  | 1.0000       |            |     |
| 2009–2014  | 0.9993    | 0.1336   | 1.0000  | 1.0000  | 0.9993       |            |     |
| 2009–2015  | 1.0000    | <0.0001  | 1.0000  | 1.0000  | 0.3014       |            |     |
| 2010–2011  | 0.5277    | 0.0014   | 1.0000  | 0.9682  | 1.0000       | <0.0001    | 0.0004|
| 2010–2012  | 0.9827    | 0.1310   | 1.0000  | 0.9716  | <0.0001      | 0.0042     | 0.4302|
| 2010–2013  | 0.0250    | 0.0013   | 1.0000  | 1.0000  | 1.0000       | <0.0001    | 0.0075|
| 2010–2014  | 0.0130    | 0.8512   | 1.0000  | 0.9704  | 0.7615       | 0.0009     | 1.000 |
| 2010–2015  | 0.7893    | 0.0011   | 0.0163  | 0.7084  | 0.9735       | 0.0003     | 0.2270|
| 2011–2012  | 0.0091    | 0.9957   | 1.0000  | 0.1419  | <0.0005      | 0.0250     | 0.5077|
| 2011–2013  | 0.9954    | 1.0000   | 1.0000  | 0.9999  |             | 0.9886     | 0.9977|
| 2011–2014  | 0.9866    | 0.7164   | 0.9999  | 1.0000  | 0.4674       | 0.9796     | 0.0500|
| 2011–2015  | 1.0000    | 1.0000   | 0.0076  | 1.0000  | 1.0000       | 0.7658     | 0.8097|
| 2012–2013  | <0.0001   | 0.9728   | 1.0000  | 0.5050  | <0.0001      | <0.0001    | <0.0001|
| 2012–2014  | <0.0001   | 0.9986   | 1.0000  | 0.1228  | 0.8572       | 0.7638     | 0.6908|
| 2012–2015  | 0.0361    | 0.9997   | 0.0079  | 0.0093  | <0.0001      | 0.8612     | 1.000 |
| 2013–2014  | 1.0000    | 0.2713   | 1.0000  | 0.9999  | 0.8392       | 0.0376     | 0.0279|
| 2013–2015  | 0.9448    | 1.0000   | 0.0441  | 0.9927  | 0.8415       | 0.0035     | 1.000 |
| 2014–2015  | 0.8285    | 0.5484   | 0.0473  | 1.0000  | 0.0029       | 1.0000     | 0.1759|

Significant multiple comparisons (α = 0.05; p ≤ 0.05) are highlighted in bold. Comparison = the years compared and T6 = Total 6-prey group biomass. TS corr. = time series correlation model, AR(2) = autoregressive model with 2 lags, AR(3) = autoregressive model with 3 lags, MA(2) = moving average with 2 lags, and ARMA = autoregressive and moving average model, both with 2 lags.

Table 5

Tukey multiple comparisons among years for faunal groups for the offshore surveys, 2002–2015.

| Comparison | Amphipoda | Bivalvia | Cumacea | Polychaeta | T6 |
|------------|-----------|----------|---------|------------|----|
| TS Corr.   | D + Y     | Y        | D + Y   | D + Y      | D + Y |
| ARMA(3,3)  | 0.0001    | 0.0002   | 0.0002  | 0.2527     | 0.9992|
| ARMA(2,2)  | 0.0001    | 0.0001   | 0.3851  | 0.0243     | 0.9916|
| ARMA(2,2)  | 0.0002    | <0.0001  | 0.1863  | 0.0446     | 0.9977|
| ARMA(2,2)  | 0.0003    | <0.0001  | 0.3389  | 0.1211     | 0.7826|
| ARMA(2,2)  | 1.0000    | 0.8730   | 1.0000  | 0.9737     | 1.000 |
| ARMA(2,2)  | 1.0000    | 1.0000   | 1.0000  | 0.9815     | 1.000 |
| ARMA(2,2)  | 1.0000    | 0.5117   | 0.2357  | 0.9895     | 0.7972|
| ARMA(2,2)  | 0.0003    | 0.0008   | 0.9999  | 0.0314     | 0.0005|
| ARMA(2,2)  | 0.9482    | 0.0001   | <0.0001 | 0.0005     | 0.0003|
| ARMA(2,2)  | 0.1498    | 1.0000   | 1.0000  | 0.0125     | 0.7993|
| ARMA(2,2)  | 0.9968    | 0.1000   | 0.5488  | 0.5052     | 0.9997|
| ARMA(2,2)  | <0.0001   | 0.0001   | 0.2664  | 0.0283     | 0.2803|
| ARMA(2,2)  | <0.0001   | 0.0005   | 1.0000  | 0.9999     | 1.000 |
| ARMA(2,2)  | 0.0005    | 0.0003   | 0.3338  | 0.1000     | 0.9158|
| ARMA(2,2)  | <0.0001   | 0.0001   | <0.0001 | 0.1201     | 0.0015|
Table 5 (continued)

| Year 1   | Year 2   | Amphipoda | Bivalvia | Cumacea | Polychaeta | T6     |
|----------|----------|-----------|----------|----------|------------|--------|
| 2004–2009 | 0.2530   | 0.7377    | 1.0000   | 0.5613   | 0.9196     |        |
| 2004–2010 | 0.9997   | 0.9056    | 0.5002   | 0.9997   | 1.0000     |        |
| 2004–2012 | <0.0001  | 1.0000    | 0.2401   | 0.9874   | 0.3746     |        |
| 2004–2013 | <0.0001  | 0.6861    | 1.0000   | 0.6652   | 1.0000     |        |
| 2004–2014 | 0.0010   | 1.0000    | 0.9998   | 0.7816   | 1.0000     |        |
| 2004–2007 | 0.0002   | <0.0001   | 0.9592   | 0.4042   | 0.0001     |        |
| 2004–2008 | 0.9197   | <0.0001   | <0.0001  | <0.0001  | 0.0204     | 0.0001 |
| 2005–2009 | 0.0748   | 1.0000    | 0.9940   | 0.2594   | 0.8002     |        |
| 2005–2010 | 0.9972   | 1.0000    | 0.8307   | 0.9951   | 0.9999     |        |
| 2005–2012 | <0.0001  | 0.9692    | 0.5280   | 0.9903   | 0.1811     |        |
| 2005–2013 | <0.0001  | 0.0767    | 1.0000   | 0.6329   | 1.0000     |        |
| 2005–2014 | <0.0001  | 0.4933    | 1.0000   | 0.7603   | 1.0000     |        |
| 2005–2015 | 0.0002   | 0.0021    | 1.0000   | 0.4540   | 1.0000     |        |
| 2006–2007 | <0.0001  | 0.3203    | 0.3780   | 0.2298   | 0.0349     |        |
| 2006–2008 | 0.9125   | 0.1501    | 0.0421   | 0.0135   | 0.0828     |        |
| 2006–2009 | 0.0600   | 0.6124    | 0.4948   | 0.2288   | 1.0000     |        |
| 2006–2010 | 0.9984   | 0.3892    | <0.0001  | 0.9938   | 0.9980     |        |
| 2006–2012 | <0.0001  | <0.0001   | <0.0001  | 0.9920   | 0.9982     |        |
| 2006–2013 | <0.0001  | <0.0001   | 0.0659   | 0.6449   | 0.9798     |        |
| 2006–2014 | 0.0001   | <0.0001   | 0.0188   | 0.7782   | 0.9939     |        |
| 2006–2015 | 0.0002   | <0.0001   | 0.0543   | 0.4768   | 0.6488     |        |
| 2007–2008 | 0.0554   | 1.0000    | <0.0001  | 0.9807   | 1.0000     |        |
| 2007–2009 | 0.9985   | 0.0003    | 1.0000   | 1.0000   | 0.1458     |        |
| 2007–2010 | 0.9925   | 0.0001    | 0.0548   | 0.9920   | 0.0052     |        |
| 2007–2012 | 0.0495   | <0.0001   | 0.0138   | 0.0188   | 0.8439     |        |
| 2007–2013 | 0.4141   | <0.0001   | <0.0001  | 0.9948   | 0.0005     | 0.0019 |
| 2007–2014 | 0.9859   | <0.0001   | 0.9426   | 0.0012   | 0.0041     |        |
| 2007–2015 | 0.9914   | <0.0001   | 0.9889   | 0.0002   | 0.0001     |        |
| 2008–2009 | 0.6368   | <0.0001   | <0.0001  | 0.9990   | 0.0280     |        |
| 2008–2010 | 1.0000   | <0.0001   | <0.0001  | 0.3915   | 0.0015     |        |
| 2008–2012 | <0.0001  | <0.0001   | <0.0001  | 0.0001   | 0.7550     |        |
| 2008–2013 | <0.0001  | <0.0001   | <0.0001  | <0.0001  | 0.0010     |        |
| 2008–2014 | 0.0109   | <0.0001   | <0.0001  | <0.0001  | 0.0024     |        |
| 2008–2015 | 0.0198   | <0.0001   | <0.0001  | <0.0001  | <0.0001    | <0.0001|
| 2009–2010 | 0.2747   | 1.0000    | 0.0178   | 0.8717   | 0.9811     |        |
| 2009–2012 | 0.0001   | 0.5881    | 0.0151   | 0.0031   | 0.9984     |        |
| 2009–2013 | 0.0176   | 0.0003    | 0.9992   | 0.0001   | 0.9648     |        |
| 2009–2014 | 0.5311   | 0.1166    | 0.9819   | 0.0003   | 0.9891     |        |
| 2009–2015 | 0.6324   | 0.0001    | 0.9980   | <0.0001  | 0.5882     |        |
| 2010–2012 | <0.0001  | 0.7537    | 1.0000   | 0.2194   | 0.3635     |        |
| 2010–2013 | <0.0001  | <0.0001   | 0.5934   | 0.0329   | 1.0000     |        |
| 2010–2014 | 0.0003   | 0.2393    | 0.8696   | 0.0794   | 1.0000     |        |
| 2010–2015 | 0.0014   | 0.0004    | 0.7858   | 0.0234   | 0.9969     |        |
| 2012–2013 | 0.9987   | 0.2182    | 0.1115   | 0.9981   | 0.1617     |        |
| 2012–2014 | 0.5788   | 0.9991    | 0.5554   | 0.9999   | 0.4733     |        |

Significant multiple comparisons (α = 0.05; p < 0.05) are highlighted in bold. Comparison = the years compared and T6 = Total 6-prey group biomass. Model = the regression model, D = water depth, Y = year, TS corr. = time series correlation model, AR(2) = autoregressive model with 2 lags, ARMA(2,2) = autoregressive and moving average model, both with 2 lags, and ARMA(3,3) = autoregressive and moving average model, both with 3 lags.
Table 6
Analysis of variance of nine prey groups from feeding points in the nearshore and offshore study areas, 2002–2015.

| Taxon     | Est. | P-Value | Comparison | Taxon     | Est. | P-Value | Comparison |
|-----------|------|---------|------------|-----------|------|---------|------------|
| Amphipoda | 0.91 | <0.0001 | FP>GS      | Amphipoda | 0.84 | <0.0001 | FP>GS      |
| Bivalvia  | 0.13 | 0.1891  |            | Bivalvia  | −0.20| 0.6907  |            |
| Cumacea   | 0.14 | 0.9340  |            | Cumacea   | −0.46| <0.0001 | GS>FP      |
| Isopoda   | 0.67 | <0.0001 | FP>GS      | Isopoda   | −0.02| 0.8683  |            |
| Actinopterygi | −0.02 | 0.8683 |            | Actinopterygi | 0.08 | 0.2404 |            |
| Polychaeta| 0.02 | 0.7072  |            | Polychaeta| 0.44 | <0.0001 | FP>GS      |
| Total Prey| 0.56 | <0.0001 | FP>GS      | Total Prey| 0.56 | <0.0001 | FP>GS      |

Est. = the difference between feeding point biomass – grid station biomass for transformed biomass data used in the mixed models, and P-values from mixed models. A positive estimate value indicates that average biomass was higher at feeding points. The “Comparison” columns denote whether biomass was higher in feeding points (FP) or grid stations (GS). Years included in the ANOVA were 2002–2012 for the nearshore and 2002–2015 for the offshore.

Fig. 2. Canonical correspondence analysis (CCA) of the nearshore (a) and offshore (b) study areas, 2002–2015. The survey from 2001 was not included due to missing data. Plots on the left present the ordination by stations and the plots on the right side present species ordinations. The correlations of predictor variables are presented as biplots where the length and direction of an arrow represents the direction and strength of association with the axes. The positioning of an arrow in the direction of the spread of stations and location of a group label indicates joint associations. The faunal groups in the analysis are Am = Amphipoda, Ant = Anthozoa, As = Ascidiacea, B = Bivalvia, C = Cumacea, E = Echinoidea, G = Gastropoda, Ho = Holothuroidea, Hy = Hydrozoa, I = Isopoda, N = Nemertea, Pi = Pisces, and Po = Polychaeta. ALPI = the Aleutian Low Pressure Index.
Correcting for temporal correlations among errors increases the precision of statistical tests by correcting variances. Here, we limited our consideration to models of at most 3 lags, or up to 3 years distant. We also presumed that any spatial correlation structures would be approximated by and incorporated in the correlation models. Models considered for adjusting errors were autoregressive (AR), moving average (MA), and combined models (ARMA).

Model selection included determination of the variables appropriate for inclusion as well as the best correlation model. The available models included depth, year, and Depth and Year. Depth was a continuous variable and Year a fixed factor. Station was included as a random factor in mixed models. Akaike’s Information Criterion (AIC) was used to determine the best model of the three for each faunal group analyzed. The choice for which correlation model to use was guided by likelihood ratio tests that compare the variance reductions among correlation models. Tukey multiple comparisons were performed using the lmerTest package in R [7].

### 2.3. Multivariate analyses

Multivariate analyses were applied to characterize changes in benthic community biomass concentrations related to environmental predictors. Canonical correspondence analysis (CCA) was used to test the hypothesis that environmental and temporal covariates were predictors of biomass concentrations.

#### Table 7
Correlations among environmental variables canonical correspondence analysis axes, cumulative proportion of variance accounted for, and permutational analysis of variance for variables and axes (p-values) for the Piltun and Offshore study areas, 2002–2015. Correlations ≥ |0.30| are in bold.

|         | Piltun |        |        |        |        |        |        |        |
|---------|--------|--------|--------|--------|--------|--------|--------|--------|
|         | CCA1   | CCA2   | CCA3   | CCA4   | P-Values |
| Sand    | −0.18  | −0.08  | −0.01  | −0.09  | 0.001   |
| Year    | −0.07  | −0.47  | −0.01  | 0.01   | 0.001   |
| Depth   | 0.67   | −0.01  | 0.01   | 0.00   | 0.001   |
| ALPI    | −0.01  | 0.09   | 0.14   | 0.00   | 0.079   |
| P-Values| 0.001  | 0.001  | 0.341  | 0.944  |
| Cum Prop. Var. | 9% | 11% | 12% | 12% |        |

|         | Offshore |        |        |        |        |        |        |        |
|---------|----------|--------|--------|--------|--------|--------|--------|--------|
|         | CCA1     | CCA2   | CCA3   | CCA4   | P-Values |
| Sand    | 0.22     | −0.12  | 0.17   | −0.02  | 0.001   |
| Year    | 0.30     | −0.15  | <0.001 | −0.12  | 0.002   |
| Depth   | −0.49    | −0.09  | −0.07  | −0.02  | 0.001   |
| ALPI    | −0.02    | 0.11   | <0.001 | −0.01  | 0.337   |
| P-Values| 0.001    | 0.040  | 0.483  | 0.990  |
| Cum Prop. Var. | 6% | 7% | 8% | 8% |        |

#### Table 8
Analysis of covariance for the nearshore and offshore study areas adjacent to Sakhalin Island, 2001–2015.

|         | Nearshore |        |        |        |        |        |        |        | Offshore |        |        |        |        |        |        |
|---------|-----------|--------|--------|--------|--------|--------|--------|--------|----------|--------|--------|--------|--------|--------|--------|
| Group   | Factor    | F      | P-value | Factor  | F      | P-value |
| Actinopterygii | Depth | 0.1    | 0.7782  | Depth  | 7.8    | 0.0053  |
|          | Year      | 8.7    | <0.001  | Year   | 7.3    | <0.001  |
| Amphipoda | Depth    | 151.2  | <0.001  | Depth  | 15.3   | <0.001  |
|          | Year      | 19.8   | <0.001  | Year   | 10.4   | <0.001  |
| Bivalvia | Depth    | 1.5    | 0.2219  | Depth  | 0.0    | 0.9674  |
|          | Year      | 17.0   | <0.001  | Year   | 15.5   | <0.001  |
| Cumacea | Depth    | 15.3   | <0.001  | Depth  | 63.3   | <0.001  |
|          | Year      | 39.2   | <0.001  | Year   | 11.1   | <0.001  |
| Isopoda | Depth    | 84.3   | <0.001  | Depth  | 12.2   | <0.001  |
|          | Year      | 10.2   | <0.001  | Year   | 3.2    | <0.001  |
| Polychaeta | Depth   | 10.0   | <0.001  | Depth  | 63.2   | <0.001  |
|          | Year      | 18.5   | <0.001  | Year   | 6.0    | <0.001  |
| Total Prey | Depth    | 87.1   | <0.001  | Depth  | 3.8    | 0.0515  |
|          | Year      | 13.4   | <0.001  | Year   | 5.9    | <0.001  |

Mixed models were adjusted for time-series errors. F-statistics (F) and p-values are presented.
community structure. The community data set was benthic biomass of all categories identified with rare animals excluded. Biomass data were ln(X+1)-transformed prior to analyses to reduce influences of extreme values on the ordination. The covariates were water depth, year, the ALPI (a measure of macro-scale climate variability), and percent sand. CCA was conducted using the vegan package [8].

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