



NOAA Technical Memorandum NMFS-AFSC-162

Abundance and Spatial Pattern of Salps Within the North Pacific Subarctic Frontal Zone, August 1991

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S. E. Ignell, B. L. Wing, B. D. Ebberts, and M. M. Masuda

U.S. DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

National Marine Fisheries Service

Alaska Fisheries Science Center

February 2006

NOAA Technical Memorandum NMFS

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This document should be cited as follows:

Ignell, S. E., B. L. Wing, B. D. Ebberts, and M. M. Masuda. 2006. Abundance and spatial pattern of salps within the North Pacific Subarctic Frontal Zone, August 1991. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-162, 26 p.

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February 2006

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ABSTRACT

An intensive oceanographic and zooplankton survey of a small portion of the North Pacific Ocean's Subarctic Frontal Zone (SAFZ) was conducted in August 1991. Over 91% of the total displacement volume of the zooplankton samples consisted of salps, followed by copepods (2.1%), euphausiids (2.0%), chaetognaths (1.7%), and amphipods (1.0%). Salps also accounted for almost half (44.7%) of the total caloric value in the samples. Salp abundance was not correlated with abundances of the crustacean zooplankton groups. Salps exhibited a reverse diel vertical migration pattern; other species exhibited diel patterns.

CONTENTS

ABSTRACT.....	iii
INTRODUCTION.....	1
MATERIALS AND METHODS.....	2
RESULTS.....	4
Oceanographic data.....	4
Zooplankton species composition.....	4
Zooplankton displacement volume and caloric value.....	6
DISCUSSION.....	8
ACKNOWLEDGMENTS.....	11
LITERATURE CITED.....	12
TABLES.....	17
FIGURES.....	21

The mid-Pacific Subarctic Frontal Zone (SAFZ) is an important but poorly understood portion of the Transition Zone separating the Subarctic Domain from the Subtropical Domain. The SAFZ is usually defined in terms of salinity and temperature fronts above the permanent pycnocline: its southern limit is defined by the surfacing of the 33.8 practical salinity units (psu) isohaline and disappearance of the temperature inversion in the subarctic halocline and its northern limit is defined by the outcropping of the 33.0 psu isohaline (Roden 1991). In the central and western North Pacific Ocean, the SAFZ is approximately 300 km wide, generally ranging from 40°N to 43°N latitude.

The SAFZ encompasses the southern limit of salmonid (*Oncorhynchus* spp.) migrations and the northern limit of many subtropical and transitional squid and fish species. The complex variations in thermohaline structure of the frontal zone are matched by large variations in nekton abundances at various space and time scales. For example, catch rates of salmonids differ sharply from north to south near the SAFZ (Ignell et al. 1995; Welch et al. 1995; Murphy 1995) and by several orders of magnitude between the western and eastern portions (longitudes 170°E and 145°W, respectively) of the SAFZ (Ignell, 1991). This same level of variability persists at much smaller scales (Ignell and Murphy 1993), especially in the western portion; near 170°E, salmonid catches range from 0 to 2000 fish per driftnet operation in the space of a few tens of kilometers. Using satellite imagery, Ignell and Murphy (1993) also showed that at least some of this variability was associated with changes in sea surface temperature (SST), and that patchiness in salmonid spatial patterns was associated positively with mean SST and variance in SST.

Spatial differences in nekton abundances, however, may also reflect changes in their forage (Murphy 1995). Fish growth and survival is a function of habitat richness which is modified by competitive interactions and may be constrained by predator avoidance (Sogard 1994). Forage type and

availability are major factors determining habitat richness, particularly for salmon in the oceanic waters, where their increased size reduces predation risk and enables them to select optimal habitat based on growth potential (Pearcy 1992).

To better understand the relative importance of forage and oceanographic conditions in determining nekton spatial patterns, an oceanographic and zooplankton survey of a portion of the SAFZ (Fig.1) was conducted in 1991 from the R/V *Acania*. The survey occurred in conjunction with an international monitoring program of neon flying squid (*Ommastrephes bartrami*) driftnet vessels operating in that region, resulting in fine-scale data on the physical environment, zooplankton abundances, and nekton spatial patterns. This paper reports on the widespread occurrence of salps found in the zooplankton samples. Patterns in salp abundance are compared with temperature and salinity data collected from CTD (conductivity, temperature, and depth) casts, and with abundance patterns of other zooplankton taxa.

MATERIALS AND METHODS

The survey location was originally set at 45°04.5'N, 171°55.6'E, but then moved eastward to 45°00.0'N to 43°40.0'N and 174°00.0'E to 178°00.0'E, because of inclement weather. The final survey consisted of 41 stations arranged in a grid and generally spaced every 20 minutes of latitude and every 30 minutes of longitude (Fig. 1). CTD casts to 300-500 m were made at each station (Murphy and Ebberts 1997). Salinity and temperature data at 10- and 100-m depths (temperature data are hereafter denoted as t10 and t100) were extracted from the CTD data.

Biological sampling at each station consisted of a double oblique bongo net tow to 100 m. The bongo nets were 0.6 m in diameter, with 0.505-mm mesh nets. Depth of tow was measured by a bathykymograph attached to the bongo net. The volume of water filtered through each net was measured with a flow meter attached inside the net opening.

After the net was retrieved, zooplankton were washed from the codend and preserved immediately in buffered 10% formalin. In the laboratory, the samples were rinsed in tap water for 1-3 days and then examined using a microscope. Squid and fish larvae were removed for later identification. Displacement volume (DV) of the total sample was measured using methods described in Smith and Richardson (1977). The percent composition of the sample volume was then estimated visually for the following seven taxonomic categories: gelatinous zooplankton (primarily salps), chaetognaths, copepods, amphipods, euphausiids, fish, and other.

The total volume of zooplankton per cubic meter was computed by dividing DV by the volume of water filtered, and then apportioned into the seven taxonomic categories according to the estimate of sample composition, and averaged across each pair of bongo tows. The total zooplankton volume was also converted into calories per cubic meter by a species-independent ratio of DV to wet weight (WW) computed from data in Nakai and Honjo (1961) and WW to caloric value data in Davis (1993) (Table 1). The concentration of non-gelatinous zooplankton was computed by first subtracting estimated salp DV from measured total DV, and then multiplying the result by the DV/WW ratio. Means of total volume, caloric value, and concentration are presented with \pm one standard deviation.

Caloric and DV values were normalized by log-transformation for use in statistical tests and contour plots. Statistical tests consisted of correlations between taxonomic categories and *t*-tests of night-day differences in zooplankton abundance. Zooplankton abundance data were fitted by a lowess

function to a generalized additive model (GAM) with a single variable (time of day), which allowed for a nonlinearity in the explanatory term (Hastie 1992). Fitted values of the resulting GAM models were plotted as a function of time of day, and the residuals plotted as a function of latitude and longitude. The latter plots allowed us to identify spatial variation in zooplankton abundances independent of time-of-day effects.

RESULTS

Oceanographic Data

Based on latitude-by-depth sectional plots of temperature along each end of the survey area and on contour plots of temperature and salinity, the SAFZ's northern boundary was located inside the survey area, whereas the southern boundary was outside the survey area (Figs. 2 and 3). Along the 174°E longitude transect, the northern boundary was characterized by a front ranging from 44.4°N to 44.8°N; along the 178°E longitude transect, the northern boundary-defining front ranged from south of the survey area to 44.0°N latitude. Surface salinities north of the northern boundary were less than 32.7 psu; south of the northern boundary, surface salinities were 33.0 psu or greater, confirming the placement of the SAFZ's northern boundary based on temperature gradients. The northern boundary was also highly variable, exhibiting sharp turns and meanders across the survey area (see plot of temperature at 100 m, Fig. 2).

Zooplankton species composition

Although more than 80 species of zooplankton were identified during the processing of the samples, we did not attempt a detailed analysis by species or life-history stages. Nearly all of the

gelatinous zooplankton consisted of salps; of these, about 80% were *Salpa fusiformis*, with a few individuals of *Cyclosalpa bakeri*, *Thalia democratica*, *Thetys vagina*, and *Dolioletta gegenbauri*. Other gelatinous zooplankton included hydromedusae, siphonophores, scyphomedusae, ctenophores, pteropods, and heteropods.

Chaetognaths were dominated by *Sagitta elegans*. *Sagitta scrippsae* occurred frequently but in very low numbers, and *Eukhronia hamata* occurred rarely.

Copepods were dominated by *Neocalanus cristatus* (~60%), *N. plumchrus* or *N. flemengeri* (~20%), and *Calanus marshallae* and *C. pacificus* (~20%, both species combined). We did not attempt to distinguish *N. plumchrus* from *N. flemengeri*. Other calanoid copepods (14 species) were present but did not make up a significant portion of the non-gelatinous zooplanktonic volume; often only one or two individuals of a species were found in a sample.

Amphipods were dominated by the free-living *Themisto pacifica*. Other hyperiid amphipods (10 genera) known or believed to be associated with gelatinous zooplankton were observed in small numbers and did not contribute significantly to the non-gelatinous zooplankton volume. The gammarid *Cyphocaris challengerii* was observed in small numbers at only eight stations.

Euphausiids were dominated by *Thysanoessa inspinata* (~60%), *Euphausia pacifica* (~40%), and larval forms. *Nematocelis difficilis*, *Nematobranchion flexipes*, and *Tessarabranchion oculata* occurred rarely in the samples.

Fish and fish eggs were never numerous in our samples. Larval myctophids occurred most frequently but never contributed significantly to the total zooplankton volume in our study, although rare adult or large juvenile specimens made up 5-35% of the total volume in occasional samples.

Squid larvae, although frequent in occurrence (~50% of the samples), were a significant portion of the total zooplankton volume at only one station (45.0°N, 175.5°E). Other zooplankton that were present but never a significant portion of the total zooplankton volume were pelagic polychaetes (*Tomopteris septentrionalis*, *Sagittella kowalewskii*, and *Travisiopsis lobifera*), larval cirripeds (*Lepas* spp. cyprids), ostracods (*Conchoecia alata*, *C. daphnoides*, and *Conchoecia* spp.), mysids (*Caesaromysis hispida*), decapod shrimp (*Serjestes similis*), and megalopa of a grapsoid crab.

Zooplankton displacement volume and caloric value

Total DV of net zooplankton varied between 0.048 and 9.529 ml·m⁻³, a 198-fold difference between stations. Computed caloric value ranged from 23.6 to 1,111.0 cal·m⁻³, a 47-fold difference between stations. Concentrations of non-gelatinous zooplankton ranged from 1.9 to 515.6 g·1,000 m⁻³, a 271-fold difference between stations. Mean DV was 1.7 ± 2.2 ml·m⁻³, mean caloric value was 286.0 ± 251.1 cal·m⁻³, and mean concentration of non-gelatinous zooplankton was 110.8 ± 126.8 ·1,000 m⁻³.

Over 91% of the total DV of the samples in the survey area consisted of salps, followed by copepods (2.1%), euphausiids (2.0%), chaetognaths (1.7%), and amphipods (1.0%). This order among taxonomic categories persisted for the caloric value data; even though salps have a low caloric to DV ratio compared to crustaceans (Davis 1993), they still accounted for almost one-half (44.7%) of the total caloric value in the samples.

Caloric value (Table 1) and DV of night samples exceeded that of day samples (Table 2). In the survey area, night-day differences were greatest for euphausiids (17.8:1) and least for salps (1.3:1). The night-day differences were highly significant ($P < 0.0005$) for euphausiid and copepod DVs and caloric

values, and significant ($P < 0.005$) for amphipod and chaetognath DVs. Salp DV and caloric value, and total DV showed no significant night-day differences.

Lowess plots of log-transformed abundance versus time of day showed that zooplankton abundances changed gradually between night and day (Fig. 4). Except for salps, peak abundances occurred near midnight and low abundances from about 1000 to 1700 hours (Alaska Daylight Time). Fitted lowess values between nighttime peaks and daytime lows varied about 9-fold for euphausiids and about 2.5-fold for chaetognaths, copepods, and amphipods. Salps exhibited a reverse diel vertical migration (RDVM) pattern, with peak abundances near dawn and dusk (Fig. 5, upper left panel).

The time-of-day adjusted abundance and distribution of zooplankton varied extensively throughout the western survey area. Salps were broadly abundant along the northeastern, southwestern, and southeastern regions (Fig. 5) and constituted more than 80% of the total zooplankton in about one-half of the survey area. Non-gelatinous zooplankters were abundant in the northeastern, central southern and northern areas (Fig. 5). Euphausiids, copepods, and amphipods were abundant along two northern areas and one southern area. Chaetognaths were abundant primarily in the northwestern area (Fig. 6). Except for chaetognaths, highest abundances of each zooplankton taxon occurred in areas exhibiting gradual changes in temperature at 100 m (compare Figs. 2 and 6).

Abundances of gelatinous and non-gelatinous taxa (time-of-day adjusted) were not correlated ($r = -0.52$; $P < 0.01$); otherwise, they were not correlated with any other zooplankton group. Pair-wise correlations between chaetognath, copepod, amphipod, and euphausiid abundances were all significant ($P < 0.05$); of these, euphausiids and amphipods were most closely related ($r = 0.71$).

Zooplankton caloric values generally followed the distribution pattern of salps. The greatest caloric values occurred in the northeastern and southwestern regions, where salps made up over 90% of

the total zooplankton volume (Fig 7). High caloric values in a small area along the southern portion of the survey area, however, were due to high abundance of copepods and euphausiids.

Zooplankton abundance and caloric values in areas with a strong horizontal temperature gradient (t_{100}) were generally lower than those in weak-gradient areas. Large differences were observed for chaetognath ($P = 0.089$) and euphausiid abundance ($P = 0.087$) and for total zooplankton caloric value ($P = 0.048$).

DISCUSSION

The extensive coarse-scale heterogeneity of zooplankton abundances in our survey area (e.g., Fig. 4) is characteristic of biological processes within frontal zones and is comparable with spatial variations in zooplankton abundances from data collected in October 1989 along a series of five meridional transects (85 total stations) bisecting the SAFZ and ranging from 155°W to 171°W longitude and from 37°N to 47°N latitude (Murphy et al. 1998). The much lower number of salps observed by Murphy et al. (1998) versus our data may be attributed to differences in study area, season, and year, which are all significant factors affecting the geographic distribution and abundance of salps (e.g., Hubbard and Percy 1971).

Concentrations of non-gelatinous zooplankton in our study area were more than double observed at Ocean Station P, or in the Sargasso Sea, Norwegian Sea, and the Central Equatorial Pacific Ocean, but less than those observed in the Bering Sea, coastal waters of British Columbia, and the northwestern Pacific Ocean (McAllister 1961). Our relatively high concentrations might be expected, because our survey area lies within the SAFZ, a prominent area of convergence across the North Pacific

Ocean (Roden 1991). Zooplankton production is typically high in areas where physical processes promote high primary production. Such areas often occur along coasts, in the centers of cyclonic gyres, between currents, and in convergence areas (Daly and Smith 1993).

Dense patches of salps, such as those observed in our study, have been reported for a wide variety of pelagic and neritic waters. At Ocean Station I in the North Atlantic Ocean, salps make up 10-40% of the total dry weight of zooplankton from April to October (Parsons and Lalli 1988). Salps were the dominant zooplankton in open waters of the Weddell Sea (Siegel et al., 1992), and off Tasmania in windy periods (Harris et al. 1992). Wind stress also affected Mediterranean salp populations, promoting the generation of dense blooms through renewed pelagic production (Menard et al. 1994). Salps have been found in concentrations ranging from 5 to 275 individuals per cubic meter along coastal regions of Ivory Coast and Florida (Paffenhofer and Lee 1987), and swarms of *Thalia democratica* off California have reached densities of 500 salps per cubic meter (Alldredge and Madin 1982).

These high densities arise because of the extraordinary life histories and foraging characteristics of salps, which allow them to react with maximum flexibility to variations in ocean conditions (Alldredge and Madin 1982). In optimal environments, salps grow quickly, forming large swarms through asexual reproduction. They are also non-selective filter feeders, eating everything that they trap in their feeding net, enabling them to filter much larger volumes of water and capture a larger range of food sizes than other pelagic herbivores (Alldredge and Madin 1982). As a result, growth rates are extremely high: body length of young *Thalia democratica* increases by 10% per hour, and growth of a solitary *Salpa fusiformis* can exceed 40% of its length each day (Madin and Purcell 1992). The combined effect of high feeding rates, asexual budding, and high growth rates enables salps to increase

population sizes rapidly under favorable conditions, even to the point of replacing other zooplankton in a region (Madin and Purcell 1992; Paffenhofer and Lee 1987).

Gelatinous zooplankton occupy an important, but often overlooked, role in pelagic and neritic ecosystems. They are often sampled inadequately by nets or are excluded from processing of plankton samples (Parsons and Lalli 1988). For example, McAllister (1961) excluded medusae from measures of zooplankton concentration because they were not “edible” species. Also, many medusae are damaged easily and therefore difficult to enumerate. As a result, analyses of zooplankton populations in the subarctic North Pacific Ocean are often restricted to non-gelatinous species, giving results such as those summarized in Parsons and Lalli (1988), where copepods are reported to make up from 75-95% of the planktonic biomass in subarctic waters.

Nevertheless, gelatinous zooplankton have a substantial impact on the trophic structure of marine communities and in the transport of carbon from the sea surface to the deep sea. Biggs (1977) estimated that excreted ammonia from salps in the North Pacific Gyre may provide about one-half of the nitrogen requirements for phytoplankton in that region, and may limit abundance of diatoms in the late summer (Madin et al. 1997). Gelatinous zooplankton produce large quantities of rapidly sinking fecal pellets, which can contribute significantly to benthic communities (Alldredge and Madin 1982; Anderson and Nival 1988). Phytoplankton remain largely intact in these pellets because digestion is incomplete. As a result, upper-layer carbon that is fixed by phytoplankton is transported quickly to the deep sea in a salp-dominant ecosystem. With high filtration rates, a salp swarm can remove a large portion of phytoplankton from an area, making them major competitors of other herbivorous zooplankton for phytoplankton food resources (Loeb et al. 1997) and of fish for zooplankton resources (Purcell and Sturdevant 2001). Salps are also a major component of the diet of some fish species such as the chum

salmon (*Oncorhynchus keta*), ocean sunfish (*Mola mola*), louvar (*Luvarus imperialis*), and pelagic armorhead (*Pentaceros pectoralis*) that inhabit our survey area and feed on salps (Eschmeyer et al. 1983; Kashkina 1986; Salo, 1991).

ACKNOWLEDGMENTS

We thank Susan McGregor and John Karinen for assistance in processing the samples, Wendy Carlson for assistance in preparing figures, and Molly Sturdevant, Richard Brodeur, and Jack Helle for their reviews of the manuscript.

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Table 1.--Data used to compute calories/ml of net plankton collected aboard the R/V *Acania* cruise to the Subarctic Frontal Zone of the North Pacific Ocean, August 1991. Caloric value (per gram) data are from Davis (1993) and the weight/volume (0.674) ratio is an average of data given in Nakai and Honjo (1961). Percent composition of taxonomic category in group was based on visual estimates by one of the authors (BLW).

Group/Taxonomic category	Composition of			
	taxa in group			
	(%)	g·ml ⁻¹	cal·g ⁻¹	cal·ml ⁻¹
<hr/>				
Salp - Gelatinous				
Salpidae	100	9.674	96	64.7
Chaetognaths				
<i>Sagitta elegans</i>	100	0.674	488	328.9
Copepods				
<i>Neocalanus cristatus</i>	60	0.674	748	504.2
<i>Neocalanus plumchrus/flemengeri</i>	20	0.674	995	670.6
<i>Calanus pacificus</i>	20	0.674	872	587.4
Weighted average				554.1

Table 1. –Continued.

Euphausiids				
<i>Thysanoessa</i> spp.	60	0.674	1197	806.8
<i>Euphausia pacifica</i>	40	0.674	1138	767.0
Weighted average				790.9
Amphipods				
<i>Themisto pacifica</i>	100	0.674	725	488.7
Wet weight/displacement volume data (Nakai and Honjo, 1961)				
<i>Calanus</i> spp.				0.729
				0.662
				0.529
				0.679
				0.716
<i>Euphausia recurva</i>				0.679
<i>Salpa fusiformis</i>				0.724
Average				0.674

Table 2.--Caloric and displacement volume (DV; in milliliters) statistics: ratio of night to day averages, overall average, and percent of total DV by taxonomic category for stations in the survey area.

	Night/day	Fraction of DV	
	Ratio	Mean	(%)
Calories	2.143	292.460	
DV: Total	1.460	2.033	
Salps	1.349	1.859	91.5
Chaetognaths	2.150	0.035	1.7
Copepods	3.535	0.043	2.1
Amphipods	4.342	0.020	1.0
Euphausiids	17.811	0.040	2.0
Stations	18/22	40	

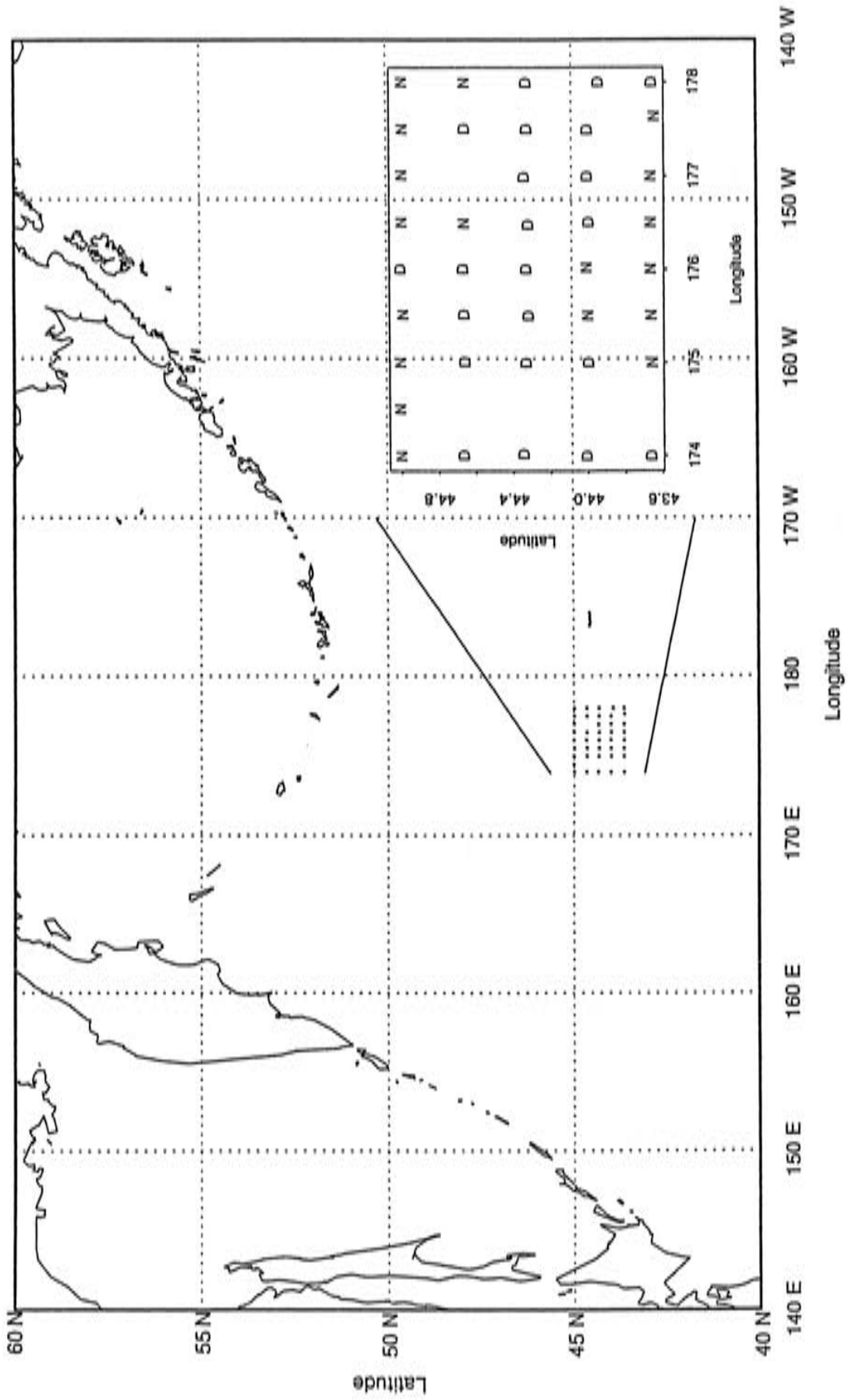


Figure 1.-- Survey area and sampling locations of the R/V Acania North Pacific squid driftnet research cruise in 1991.
 N = night station; D = night station.

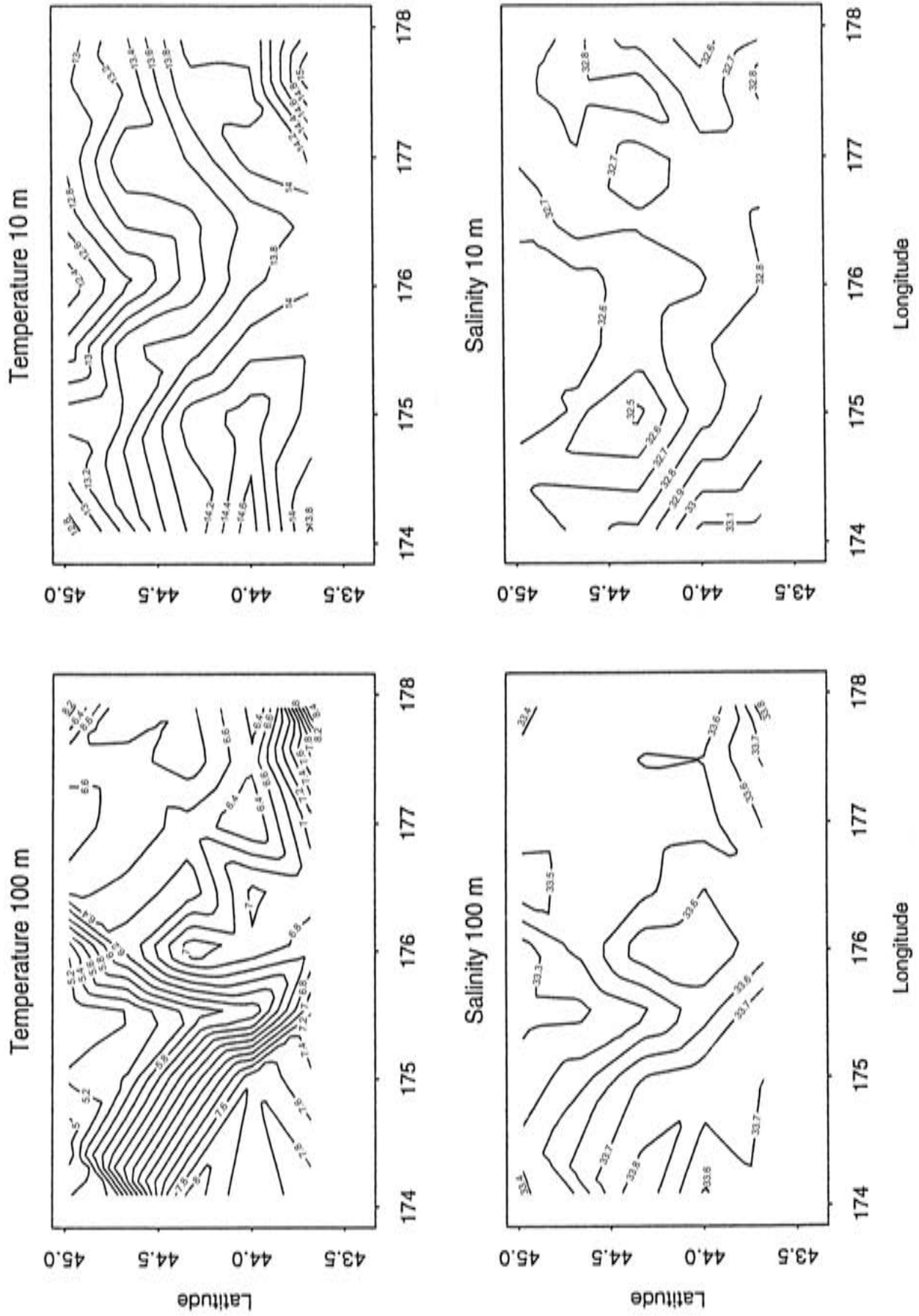


Figure 2.-- Contour plot of temperature at 100 m, salinity at 100 m, temperature at 10 m, and salinity at 10 m, in the survey area.

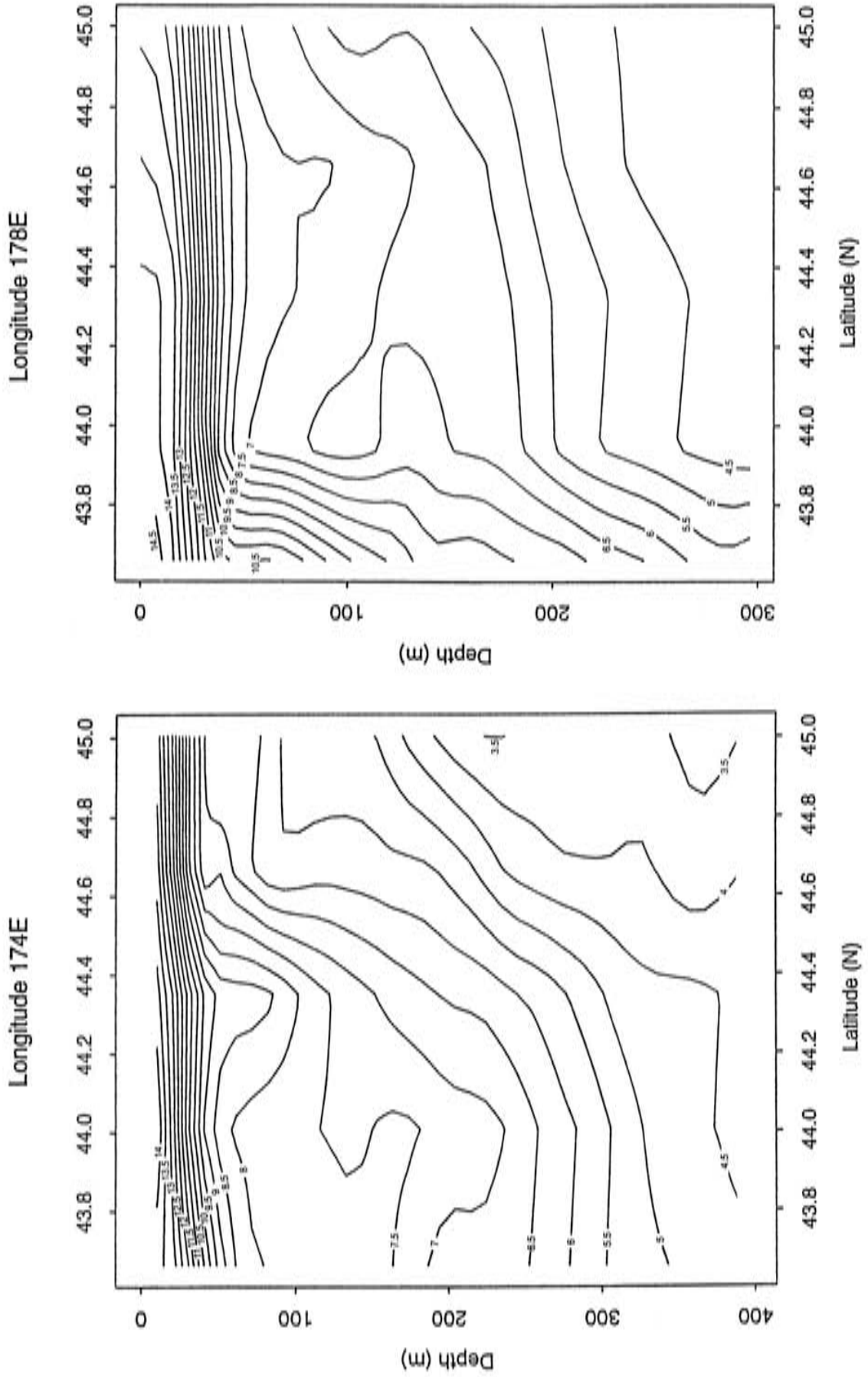


Figure 3.-- Latitude by depth sectional plots of temperature along each end of the survey area.

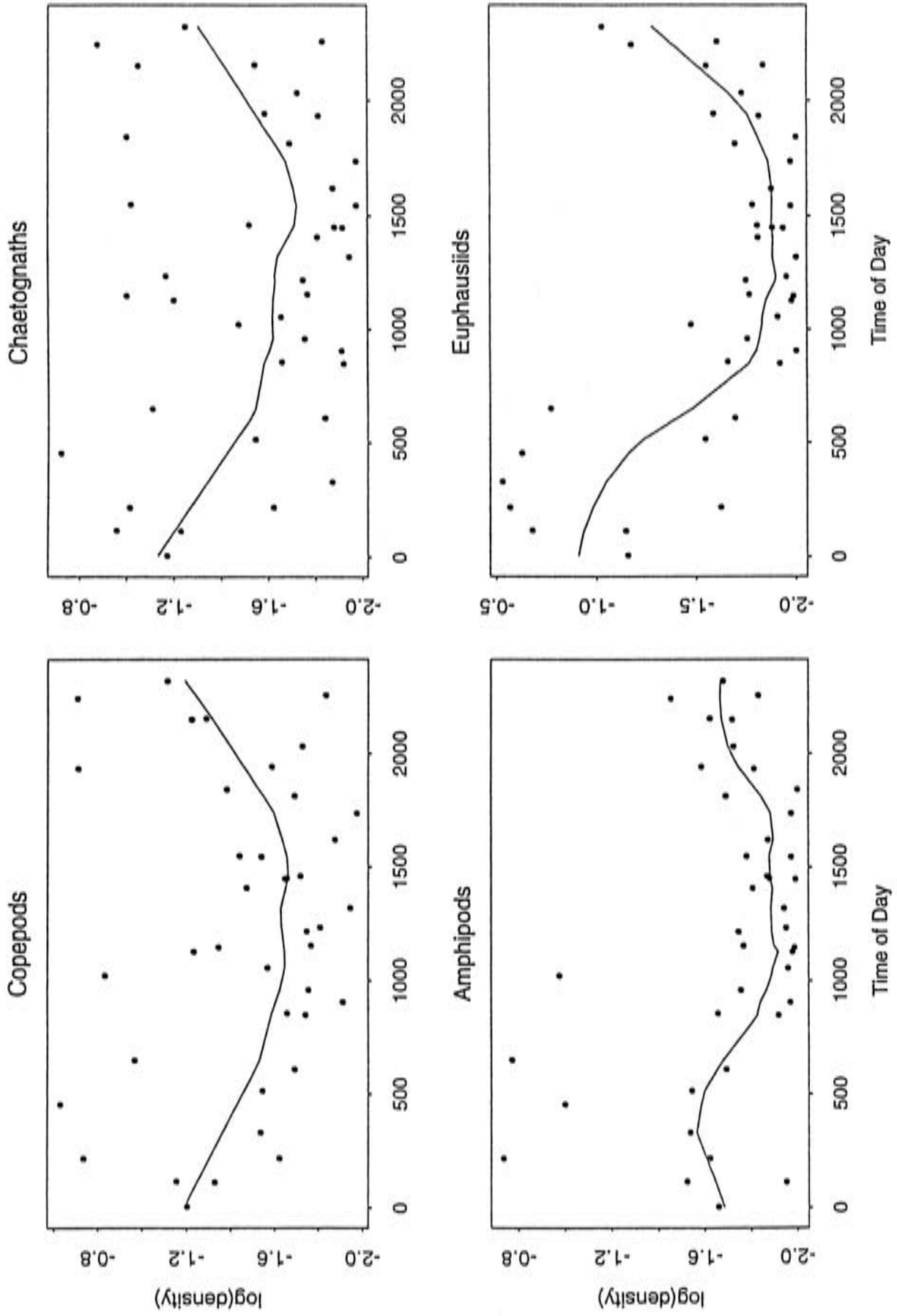


Figure 4.-- Lowess plot of the log-transformed density of copepods, chaetognaths, amphipods, and euphausiids versus time of day.

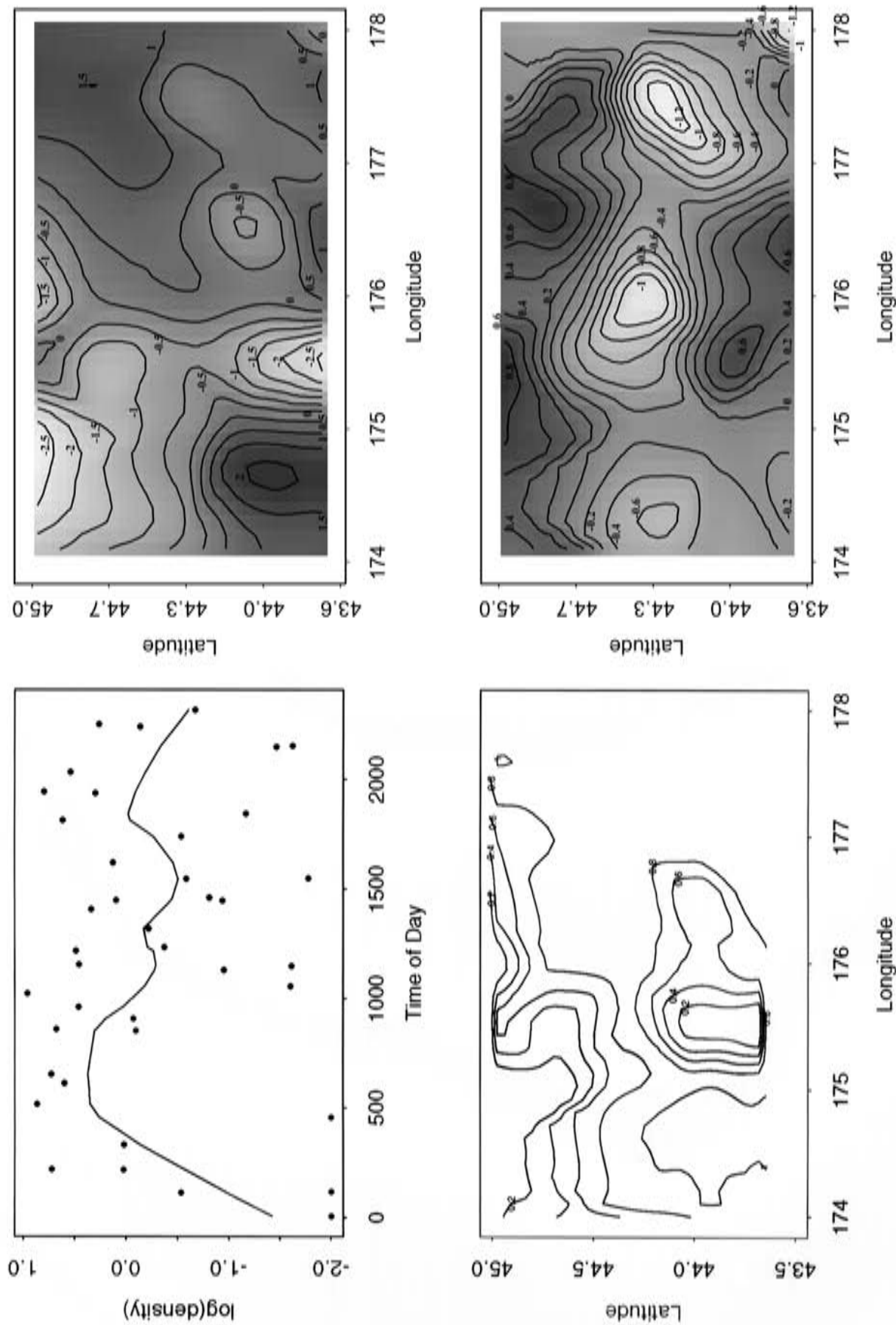


Figure 5.-- Lowess plot of the log-transformed density of salps versus time of day (upper left), image plot of the density (ml/m^3) of salps in the survey area (upper right), contour plot of the ratio of salp displacement volume to total plankton displacement volume (ml/m^3) of non-gelatinous plankton in the survey area (lower left), and image plot of the density (ml/m^3) of non-gelatinous plankton in the survey area (lower right).

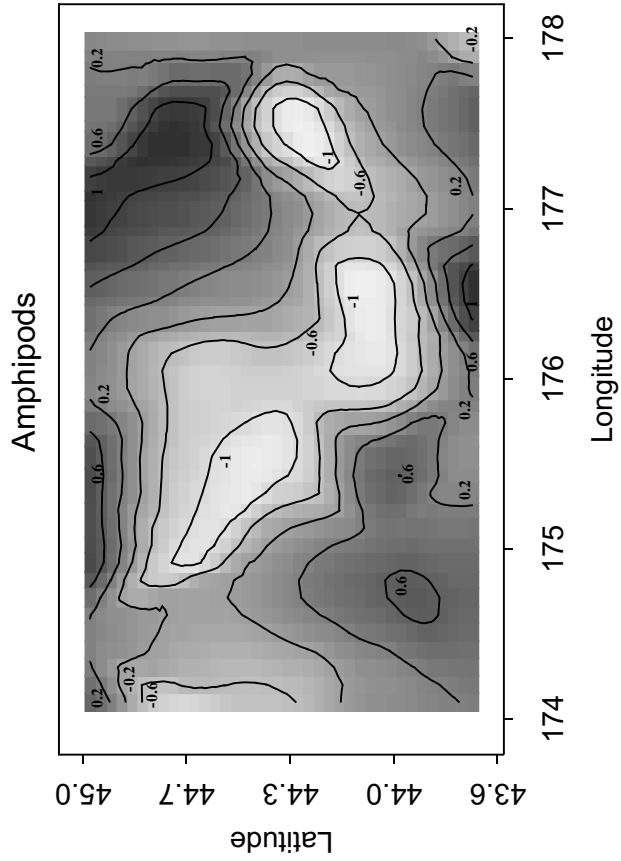
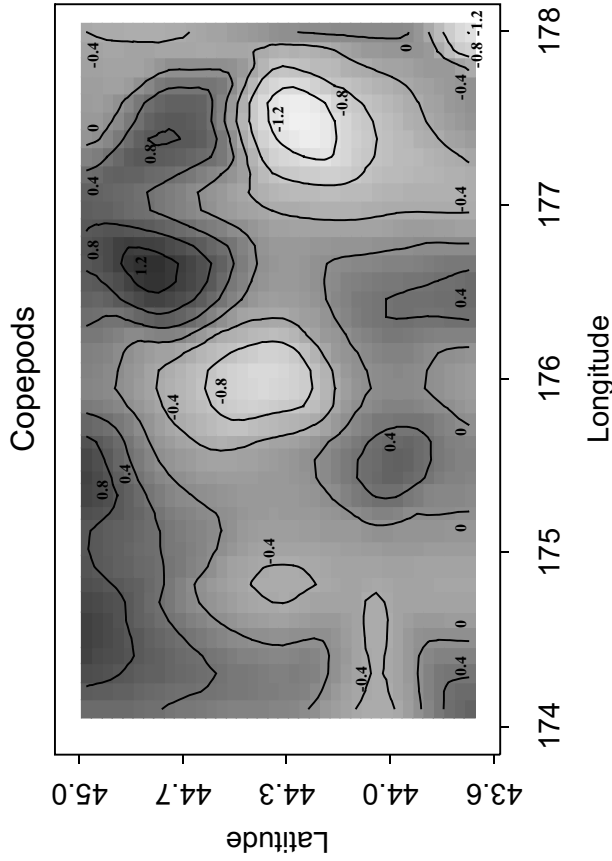
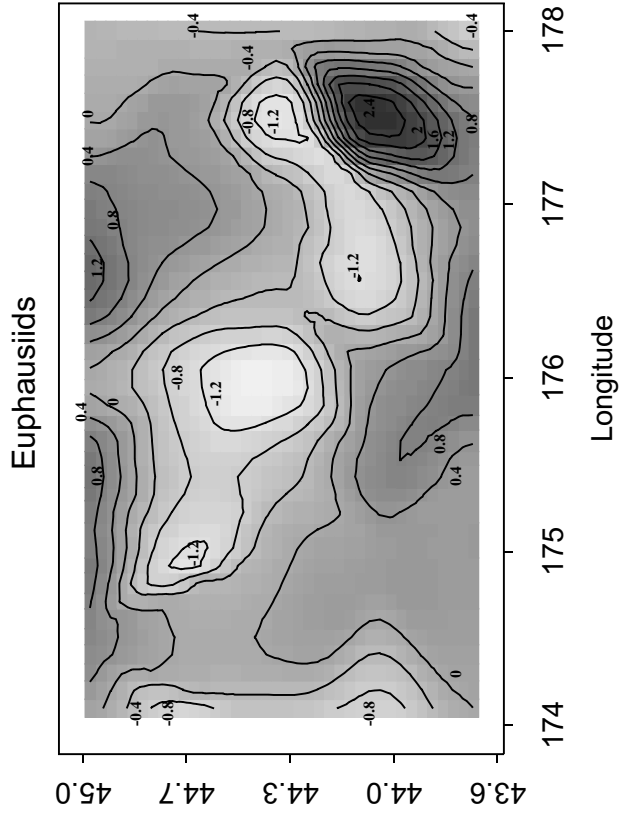
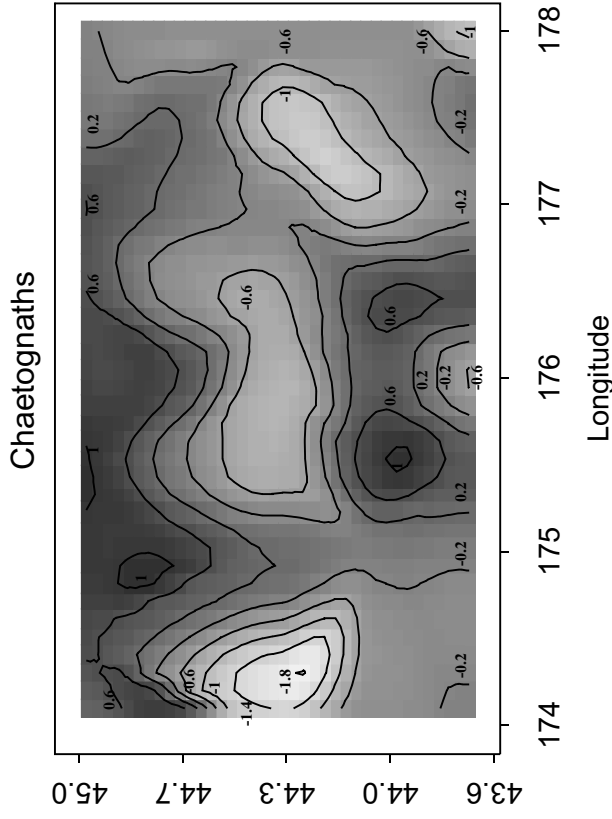


Figure 6.-- Image plots of the densities (ml/m³) of copepods, chaetognaths, amphipods, and euphausiids in the survey area.

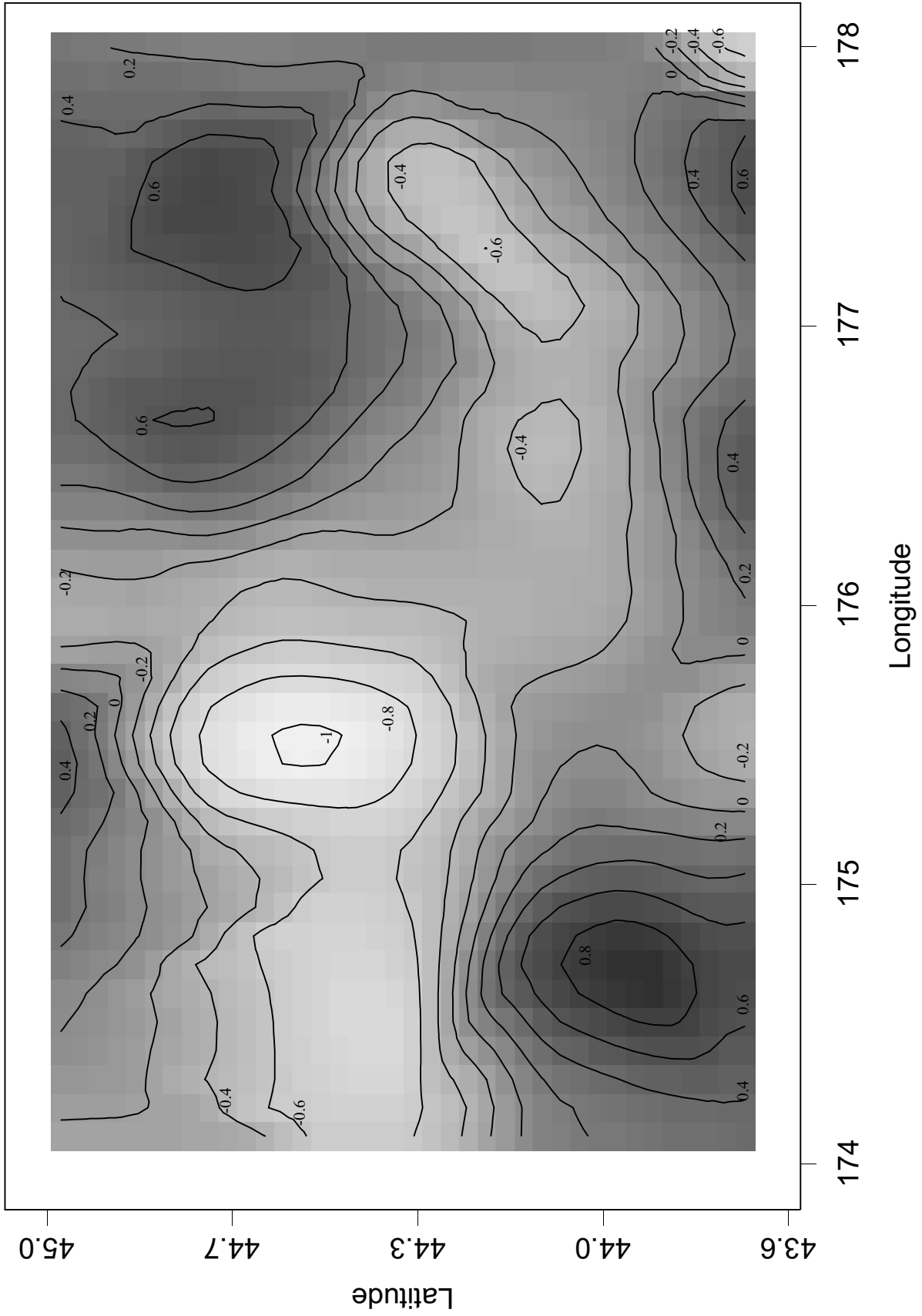


Figure 7.-- Image plot of time-of-day adjusted (residuals from GAM model) caloric value in the survey area.

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