DISTRIBUTION, PRODUCTION, AND ECOLOGY OF GRAY WHALE PREY SPECIES

by

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ABSTRACT

The productivity, ecology and distribution of ten amphipod species that form the principal prey of the gray whale were studied in the Chirikof Basin. Near St. Lawrence Island, a station for estimation of secondary productivity of amphipods was sampled by divers in July and September 1982 and with a grab through the ice in January, March and May 1983.

The benthos in most of the Chirikof Basin and all areas sampled near St. Lawrence Island was dominated by amphipods, especially the ampeliscid Ampelisca macrocephala in deep water, and the corophiid Photis fischmanni in shallow water. Ten amphipod species accounted for 95% of the density of all amphipod species collected. Multiple regression analyses on the densities of the species, using as predictor variables water depth, grain size, sorting coefficient, caloric content of the substrate, carbon content of the substrate, and carbon:nitrogen ratio of the substrate showed distinct niche separation in most species, as did analysis of gut contents. Where species showed similar habitat preferences, they were spatially separated.

Young of Ampelisca macrocephala are released in spring and fall at a length of about 3 mm, grow about 6 mm per year, may mature after 2 years, and live 2.5 years. Annual productivity to biomass ratio estimated by cohort summation was 1.8. Young of Photis fischmanni are released in fall and spring at a length of 1.4 mm; some may mature in 6 months, and they live 1 year. Growth is about 5.5 mm over the year. Annual productivity to biomass ratio was 3.7. Annual productivity to biomass ratio for the amphipods of the central Chirikof Basin as a whole was estimated at 1.9.

INTRODUCTION

The infaunal benthic communities of the Bering and Chukchi seas have been described in detail by Stoker (1978, 1981). Benthic samples collected during our study were taken in conjunction with observations of the behavior and distribution of gray whales and with observations of the bottom disruption caused by feeding gray whales. The objectives of the study as a whole were to characterize gray whale feeding areas, to assess food available to the whales, and to estimate the amount of food consumed by the whales.

In the northern part of the Bering Sea, gray whales feed on the upper strata of the benthos, primarily on amphipods (Nerini in press; Thomson and Mart in, this report). This chapter discusses the ecology of the common amphipod species that appear to form the major part of the diet of gray whales in the Chirikof Basin and near St. Lawrence Island. Data on amphipod feeding habits and ecology, including relationships to the physical characteristics of their environment, can be used to assess food web relationships and energy flow along trophic pathways leading to gray whales.

As a part of this study, year-round sampling was conducted to determine the secondary productivity of the amphipods. These data were used to assess the total amount of gray whale food production in the area (see Thomson and Martin, this report).

MATERIALS AND METHODS

Studies were conducted in the central Chirikof Basin and off the east, west and south coasts of St. Lawrence Island (Fig. 1). The numbers and locations of samples collected are presented in Appendix Tables 1 and 2.

Sampling was conducted from the NOAA vessels MILLER FREEMAN (11-25 July 1982) and DISCOVERER (12-29 September 1982). Winter sampling was conducted from the ice near Southeast Cape, St. Lawrence Island, on 13 January, 5 March and 15 May 1983.

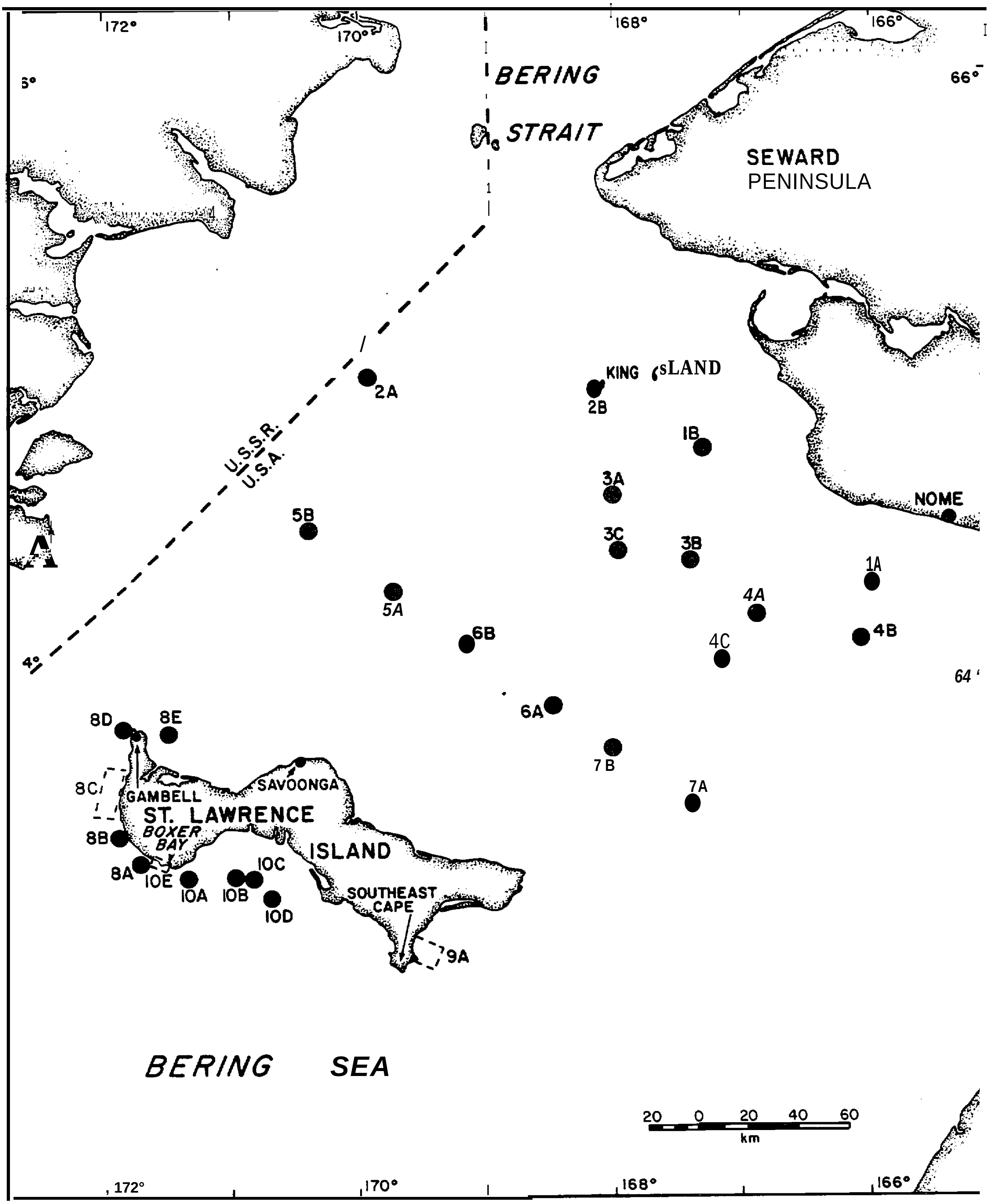

Figure 1. Sampling stations in the Chirikof Basin and near St. Lawrence Island occupied during July and September 1982.

Benthic Sampling

On board ship, benthic samples were taken with a 0.15 m2 Van Veen grab. The volume of sediment in the grab was measured to the nearest 500 mL. A subsample of sediment was taken for grain size analysis and an additional subsample was frozen for later analysis of caloric content, carbon and nitrogen. A sample of surface detritus was retained and preserved in 10% formalin. On board ship the sample was washed through 5.6 and 1 mm nested sieves with seawater. With the exception of rocks, all material retained on the sieves was preserved in 10% formalin for later analysis in the laboratory.

In winter, samples were taken through the ice with a 0.05 m2 Ponar grab and preserved whole for later processing in the laboratory.

Diver Sampling

Observations, photographs and samples were obtained by a team of 2 divers. All diving operations were carried out from small boats launched by the NOAA ships. Diving effort was restricted to shallow (<25 m) water in the vicinity of St. Lawrence Island.

Qualitative Sampling Procedure

Observations of the flora, fauna and the physical environment were recorded in waterproof notebooks during the dives and/or during a debriefing session immediately following the dive. Photographs were taken with a Nikonos or Olympus OM1 camera in an Ikelite housing, using color film and strobes.

Quantitative Sampling Procedure

A transect rope connected to an anchor was used to orient divers. Infauna was sampled by means of a self-contained diver-operated airlift. The airlift consisted of a weighted 2 m length of 8 cm diameter PVC pipe fitted at the top with a 1 mm mesh net which retained the sample and could be removed quickly and capped. Air was supplied from two 3000 psi SCUBA tanks fitted with the first stage of a diving regulator that reduced air pressure to 125 psi over ambient. Areas of substrate to be sampled were demarcated by a 0.1 m2 round aluminum frame that was pushed into the soft substrate as far as possible. The airlift was operated until the upper 10 to 15 cm of substrate within the frame was removed. The net was then removed, capped and replaced. Airlift samples contained little mud and were not sieved further. They were preserved in 10% formalin.

Laboratory Analyses

Invertebrates

The preserved samples were washed on a 0.5 mm sieve. Subsequent analysis depended on the purpose for which the sample was collected and the nature of the sample. All animals were picked from samples that contained little detrital material. When samples contained over 100 g of detrital material, large (>9 mm) conspicuous organisms were picked from the whole sample. A subsample then was taken and all organisms were picked from the subsample.

In a few selected samples (45) all animals were identified to specific level. In remaining samples, all amphipods, bivalves and common conspicuous animals were identified to specific level while remaining animals were identified to familial level. Voucher specimens of each species that was identified were sent to appropriate authorities for verification.

Where required for productivity determinations, amphipods were measured to the nearest millimeter. Measurements were from the end of the telson to the tip of the rostrum on straightened animals.

Preserved animals were weighed wet, in groups, at the lowest taxonomic level to which they were identified; a Mettler electronic balance (accurate to 10 mg) was used.

Dry weights for amphipods used in productivity experiments were determined using a Sartorius substitution balance (0.1 mg) after drying overnight at 80°C. Amphipods for caloric determination were dried to a constant weight at 60°C in a vacuum oven. Triplicate observations were made for samples having enough material. Amphipods were pelletized for combustion and a Phillipson microbomb calorimeter was utilized to obtain calories per dry gram. Ash free dry weights were measured after drying at 450°C.

Feeding Habits of Amphipods

The length of each animal was measured, the gut was dissected out, and the contents mounted on a slide and examined under a compound microscope. In addition, maturity status, sex and presence of eggs or embryos in the brood pouches were noted where evident.

Subsamples of the surface detritus were examined to determine the flora and fauna available as potential food items. Subsamples were drawn with a Pasteur pipette and placed on a slide for examination under a compound microscope.

Sediment Analysis

Grain Size Analysis

The coarse fractions (<4.0 Φ) were separated by dry sieving and the fines by Day's (1965) hydrometer method.

Bomb Calorimetry

All samples were dried to a constant weight at 60°C in a vacuum oven. Triplicate observations were made for samples having enough material.

Sediments were sieved through a 0.5 mm screen using only the liquid present in the sample. Dry sediments were powdered and benzoic acid added to enhance combustion. Powdered samples, naturally difficult to combust (such as sediments), often are partially ejected from the crucible during combustion. This was a common occurrence with these samples and, to minimize the error caused by this methodological problem, only the closest two values, of three, were averaged to obtain the mean value. We did not attempt to obtain ash free dry weights of sediments because of the occurrence of carbonates in the samples. Even after sieving, sediments may have contained meiofauna or faunal parts.

Carbon and Nitrogen

Samples (approx. 50 g) were placed into beakers and weighed. The beakers were oven-dried at 60°C overnight and reweighed to determine water content (%). The dried samples were then acidified with 5 mL of 7% HCl to destroy carbonates. They were again oven-dried at 60°C for 12 h, powdered, and homogenized.

Approximately 30 mg of sample were used for analysis. The apparatus used for the CHN determinations was a Perkin-Elmer model 240C CHN elemental analyzer. The analytical precision, based on 3 replicate analyses, was better than 0.2%.

Chlorophyll a

Preweighed sediment samples were extracted for 1 h in 10 mL of 90% acetone at 4°C in darkness. Samples were centrifuged at 4000 rpm for 10 min. Then, the acetone solution was pipetted into a glass photometer cell with a 10 cm light path. Extinction of the solution was measured against 90% acetone at 6650, 6450 and 6300 nm in a spectrophotometer. After correction for the blank, the following equation was used to estimate mg Ca per g sediment wet weight (Strickland and Parsons 1972):

$$\text{mg Ca} = 11.6\,(E665) - 1.31\,(E645) - 0.14\,(E630) \,/\, \text{sediment weight g (cell path length)}$$

Observations were in triplicate. Small pieces of shell and animal parts were present in the samples and displaced sediment in samples. Organisms were removed from samples under a microscope, but it was impractical to remove all faunal parts and meiofauna.

Data Processing and Analysis

All data were coded and entered into Hewlett Packard HP9845B or AMDAHL 470 computers and later transfered to an IBM 3033 computer for analysis. Data tabulation was accomplished with programs developed by LGL, and additional analyses were performed using SAS (SAS 1982) and BMDP (Dixon 1981) statistical software.

RESULTS

Benthic Habitats

Mat Community

The shallow (10-15 m) shelf off Southeast Cape, St. Lawrence Island, was covered with a cohesive 'mat' that had a gelatinous texture. Presence of this 'mat' allowed bottom features made by feeding gray whales to be conspicuous and well defined.

Photis fischmanni was the dominant amphipod in samples from the shallow shelf off Southeast Cape, St. Lawrence Island. In this area its mean density was close to 100,000 indiv/m^2 and mean biomass was 125 g/m^2. This small (2-7 mm) amphipod inhabits a rather long soft tube, and it was the presence of these tubes that was the most conspicuous feature of the 'mat' layer in this area. Mean biomass of all tubes (not including sediment or animals) in airlift samples was 1470 ± s.d. 812 g/m2 (n = 20) in July and 771 ± 395 g/m^2 (n = 20) in September. Sediments taken in 6 surface samples of this 'mat' were all very fine sand (range 3.47 to 4.03 Φ) and were all poorly sorted (range 1.23 to 2.14 Φ).

Amphipods accounted for 98% of the total. numbers of animals and 65% of biomass in airlift samples that penetrated to a sediment depth of 10 to 15 cm (the thickness of the mat). Cumaceans, isopods and other crustaceans contributed a further 0.5% to total numbers.

Ostracods, foraminifera and nematodes were conspicuous meiofaunal animals in the surficial sediments (Table 1).

Table 1. Total numbers of meiofauna counted in 3 subsamples from each of 5 samples of surficial sediments from the 'mat' layer in shallow water near Southeast Cape, St. Lawrence Island.

Ostracods	13	Foraminifera	18
Harpacticoid copepods	7	Nematodes	20
Crustacean larvae	1		

Large numbers of pennate and centric diatoms were also found in samples taken from the surface of the 'mat'. As a result, the chlorophyll a content of these sediments was high, 11.8 ± s.d. 2.0 mg chl a/g sediment wet weight (n = 5) in July and 7.1 • s.d. 2.3 mg/g (n = 5) in September.

A 'mat' may also be present in deeper waters of the Chirikof Basin. Density of animal tubes is high (Nelson et al. 1981; Johnson et al. 1983) but not as high as in shallow areas off Southeast Cape. Mean biomass of animal tubes, not including animals or sediment, in samples from that part of the Central Chirikof Basin dominated by amphipods was 344 * 160 g/m^2 (n = 25). These tubes were similar in construction to the ampeliscid amphipod tubes found on Southeast Cape. Tubes were uncommon in areas not dominated by amphipods. Surficial sediments from this area also contained pennate and centric diatoms, nematodes and harpacticoid copepods.

Sediment Characteristics

Surface sediments in the Central Chirikof Basin are fine sand (Nelson 1982; Table 2). In the northeastern part of the basin, surface sediments are Yukon-derived sandy silt. Surface sediments south of the Seward Peninsula are coarser than those found in the central basin (Table 2). Fine sand substrates are also found in the study areas off the west, south and east coasts of St. Lawrence Island (Table 2). The total range of mean grain size

Table 2. Physical and chemical characteristics of sediments of the Chirikof Basin and nearshore areas of St. Lawrence Island in the summer of 1982. All values were measured and calculated on dry sediment.

Location	Mean grain size[1] Φ	sorting Coefficient Φ	Caloric content cal/g	organic carbon mg/g	Nitrogen mg/g	C/N ratio
<u>Chirikof Basin</u>						
South of Nome (Stn lA, 4A, 48; Fig. 1)	3*9 * 0.1 (3)[2]	2.2 * 0.4	266 *43 (3)3	4.6 ± 1.2	0.48 * 0.07	9.6 ± 1.1
South of Seward Pen. (Stn lB, 3B, 3A, 2B)	2.5 ± 0.3 (4)	2.1 * 0.2	414 * 349 (4)	2.7 * 0.8	0.38 * 0.13	8.5 ± 2.7
Central Basin (Stn 4C, 3C, 2A, 7A, 7B, 6A, 6B, 5A, 5B)	3.3 ± ().3 (9)	1.8 ± 0.4	395 * 193 (9)	2.8 * 0.5	0.39 ± 0.06	7.3 * 1.2
<u>St. Lawrence Island</u>						
West coast (Stn 8C)	3.2 ●0.0 (2)	1.4 * 0.0	444 ●173 (2)	2.2 (1)	0.32 (1)	6.7 (1)
South coast (Stn 10C, 10D, 1(E)	2.8 ± ().2 (3)	1.4 * 0.3	193 * 91 (3)	3*0 * 0.9	0.42 ± 0.07	6.7 ± 1.0
Southeast Cape - offshore (Stn 9A >20 m)	2.8 ± 0.3 (2)	1.6 * 0.1	187 * 182 (2)	4.1 * 0.0	0.53 * 0.08	7.8 ± 1.2
Southeast Cape - nearshore (Stn 9A <20 m)	3.7 ± 0.2 (6)	1.7 * 0.3	382 * 163 (7)	3.4 * 2.1	0.40 * 0.20	8.5 ± 2.2

[1] $\Phi = \frac{-\log_{10} \text{mm}}{\log_{10} 2}$, 2-3 Φ = fine sand, 3-4 Φ = very fine sand, 4-5 Φ = coarse silt .

[2] Sample size for grain analysis.

3 Sample size for caloric content and carbon and nitrogen determination.

for the sediments of the study area is very small (2.2-4.00) and is categorized as fine or very fine sand (4 Φ is the cutpoint between sand and silt).

The sorting coefficient indicates the amount of dispersion around the mean grain size. Large values (e.g. 1-4) indicate a heterogeneity of substrates in a sample. All areas show poorly (l-2 Φ) to very poorly sorted (2-4 Φ) substrates. Surface sediments from the nearshore waters of St. Lawrence Island showed less heterogeneity than those of the central basin.

Infaunal Benthos

One hundred and fifty benthic samples were taken in the Chirikof Basin and in nearshore waters of St. Lawrence Island. Standing stock biomass of all infauna was highest off Southeast Cape and the west coast of St. Lawrence Island (Table 3). The lowest infaunal biomass was found in the Chirikof Basin (Table 3). Overall, amphipods were the dominant taxa in terms of both density and biomass (Tables 3 and 4), followed by bivalves and polychaetes.

The benthic infaunal communities of the Bering Sea have been described by Stoker (1978, 1981). He found that a community dominated by ampeliscid amphipods occupied the central and western portions of the Chirikof Basin and the west and east coasts of St. Lawrence Island. The presence of this community is indicated by areas with a high biomass of amphipods and high density of the ampeliscid amphipod Ampelisca macrocephala (Figs. 2 and 3a). We found that stations off the south coast of St. Lawrence Island also showed high biomass of amphipods and a high density of Ampelisca macrocephala.

A community dominated by a sand dollar and a bivalve characterized the central-eastern portion of the Chirikof Basin (Stoker 1981). Farther east, the area south of Nome was characterized by a community dominated by the cockle Serripes groenlandicus, two polychaetes and two ophiuroids. The presence of these two communities is indicated by low biomass of amphipods and low density of Ampelisca macrocephala in Figures 2 and 3a. Station 5B (Fig. 1) falls within an area dominated by echinoderms (Stoker 1981) and also shows a low biomass of amphipods.

Table 3. Biomass (g/m^2 wet weight) of major taxa and dominant species in all samples taken in the Chirikof Basin and near St. Lawrence Island in the summer of 1982.

		St. Lawrence Island		Southeast Cape	
Location	Chirikof Basin	South Coast	West Coast	Depth 11-15 m	Depth 22-23 m
Stations[1]	1-7	10	8	9	9
Sample size	75	15	16	34	10
Total	210.8 ± 166.8	284.5 * 99.5	327.1 * 286.6	297.8 ± 144.9	353.1 ± 129.8
Amphipoda	69.3 ± 92.5	119.9 * 48.7	129.6 ± 50.0	194.1 ± 77.8	139.3 ± 52.0
Polychaeta	26.8 ± 31.3	19.5 ± 13.2	51.2 ± 54.0	38.5 ± 56.6	25.4 ± 22.0
Bivalvia	64.4 ± 112.4	93.1 ± 65.1	118.1 ± 265.5	29.4 * 63.5"	142.8 ± 134.6
Isopoda	0	0	0	4.4* 7.5	1.9 * 1.4
Echinodermata	27.1 * 65.7	0*5 * 1.9	0	9.0* 19.1	701 * 8.8
Ascidiacea	2.8 ± 8.4	26.6 * 26.2	24.9 ± 54.9	3.6 ± 11.0	14.6 ± 13.8
Ampelisca eschrichti (A)	7.5 ± 14.7	().5 * 1.3	0	0.8 ± 2.0	24.4 ± 41.0
Ampelisca macrocephala (A)	42.6 ± 61.4	67.5 ± 34.4	79.2 * 43.5	10.9* 11.7	82.3 * 29.6
Byblis gaimardi (A)	10.0 ± 22.4	0.7 ± 0.8	17.2 ± 25.7	5.2 ± 5.6	2.9 ± 5.4
Photis fischmanni (A)	0.2 ± 0.4	1.8 ± 3.4	0	124.5 * 65.5	0.4 ± 006
Liocyma flexuosa (B)	1.8 ± 5.5	23.1 ± 46.2	6.8 * 8.8	3.8 ± 6.8	0.4 * 1.0
Liocyma viridis (B)	1*1 ± 9*7	6.6 ± 25.6	0.8 ± 3.1	0	14.7 * 28.2
Macoma calcarea (B)	33.3 ± 69.8	47.4 * 35.3	37.5 ± 54.6	14.3 * 59.5	73.4 * 102.1
Nephtyidae (P)	9.2 ± 21.8	3.3 ± 8.9	12.3 ± 26.1	15.6 * 24.0	10.2 * 13.1
Sabellidae (P)	0.7 ± 2.1	0	7.6 ± 13.1	0	0.1 ± 0.2
Travesia sp. (P)	0.0 ± 0.2	0.4 * 1.7	15.4 * 40.1	0.2 ± 0.8	0.2 ± 0.6
Dendraster extenuata (E)	16.0 ± 55.0	0	0	0.4 ± 2.2	0
Pelonaia corrugata (T)	2.6 ± 8.3	25.7 ± 26.2	6.9 ± 16.4	3.6 ± 11.0	14.4 ± 13.8

A = amphipod, B = bivalve, P = polychaete, E = echinoderm, T = tunicate
[1] See Figure 1 for locations.

Table 4. Mean density (no. /m^2) of major taxa and dominant amphipod species in all samples taken in the Chirikof Basin and near St. Lawrence Island in the summer of 1982.

		St. Lawrence Island		Southeast Cape	
Location Sample size	Chirikof Basin 75	South Coast 15	West Coast 16	Depth 11-15 m 34	Depth 22-23 m 10
Total	6204 ± 6195	12918 ± 8515	10419 ± 5306	110262 * 56084	9909 * 4444
Amphipoda	5086 ± 5907	11056 ± 7790	9088 ± 4951	107873 ± 57192	8808 ± 4106
Polychaeta	651 ± 638	766 ± 787	740 * 993	1256 * 1943	704 ± 594
Bivalvia	150 ± 249	677 ± 522	251 ± 300	327 ± 490	162 ± 195
Cumacea	117 ± 248	140 ± 206	27 ± 48	406 ± 569	96 ± 75
Echinodermata	67 ± 136	1 * 5	0	10 ± 21	16 * 18
Ascidiacea	18 ± 63	46 * 55	280 ± 740	6 ± 13	13 ± 17
Ampelisca eschrichti	74 *551	4 ± 8	0	31 ± 100	246 ± 286
Ampelisca macrocephala	2061 * 3182	2582 ± 2391	2841 * 2163	1080 * 1278	5030 ± 2478
Byblis gaimardi	402 ± 865	74 ± 120	1573 ± 2652	952 ± 927	55 ± 82
Photis fischmanni	74 * 143	1032 * 2139	17 ± 36	95572 * 54565	139 * 164
Protomedia fasciata	607 * 1795	191 * 448	133 ± 264	50 ± 148	124 * 148
Protomedia grandimana	872 ± 3446	5367 ± 5331	872 ± 1090	2800 ± 2997	1041 ± 1319
Grandiphoxus acanthinus	91 *213	205 * 203	251 * 368	153 * 220	71 * 144
Harpinia gurjanovae	113 ± 187	40 * 79	70 ± 135	1439 * 1130	187 * 152
Pontoporeia femorata	65 *254	233 ± 377	34 ± 79	66 ± 134	500 ± 651
Orchomene lepidula	119* 269	198 * 374	502 * 659	2697 * 1759	117 * 180

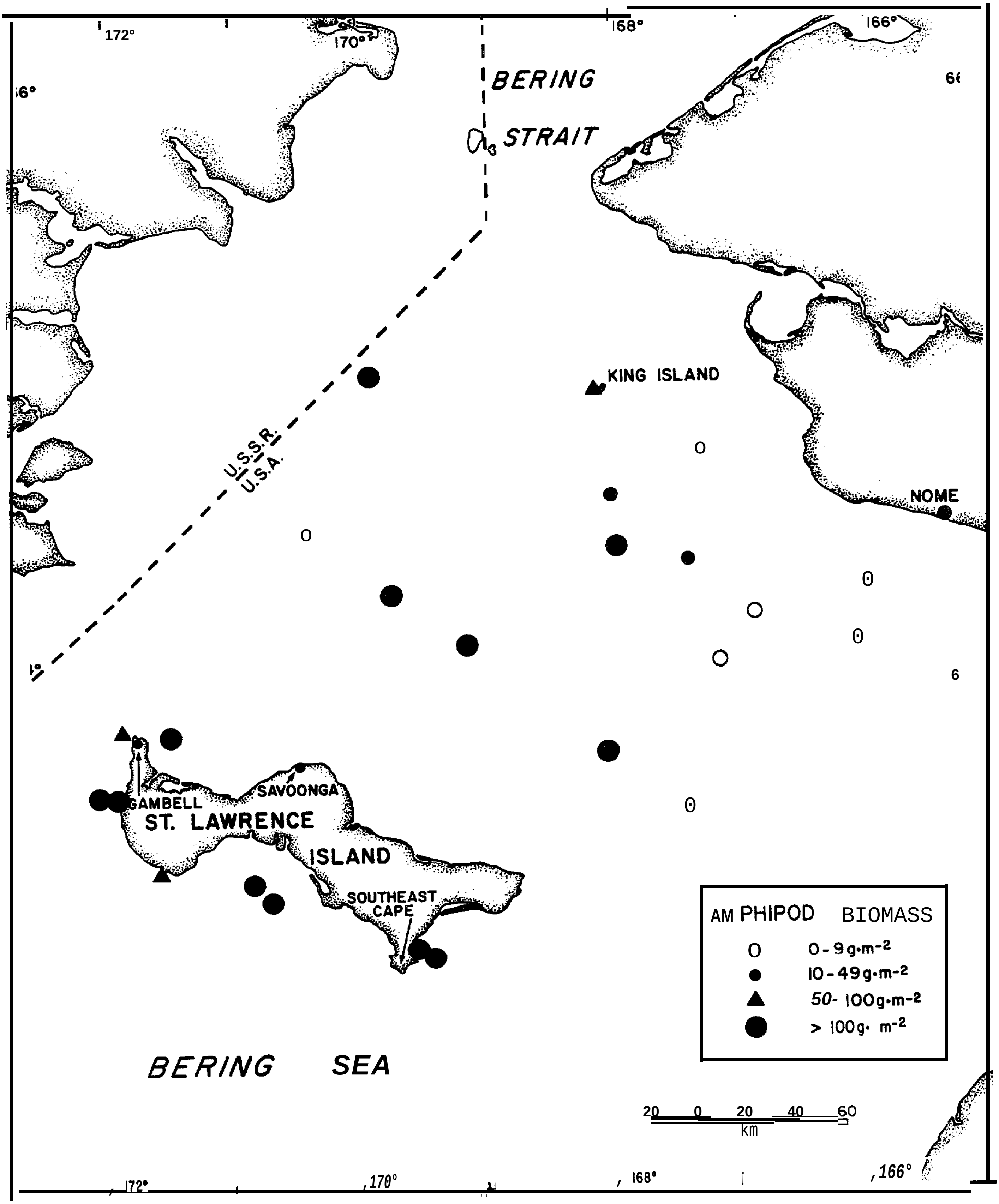

Figure 2. **Amphipod** biomass (wet weight) in the Chirikof Basin and near St. Lawrence Island in July and September 1982.

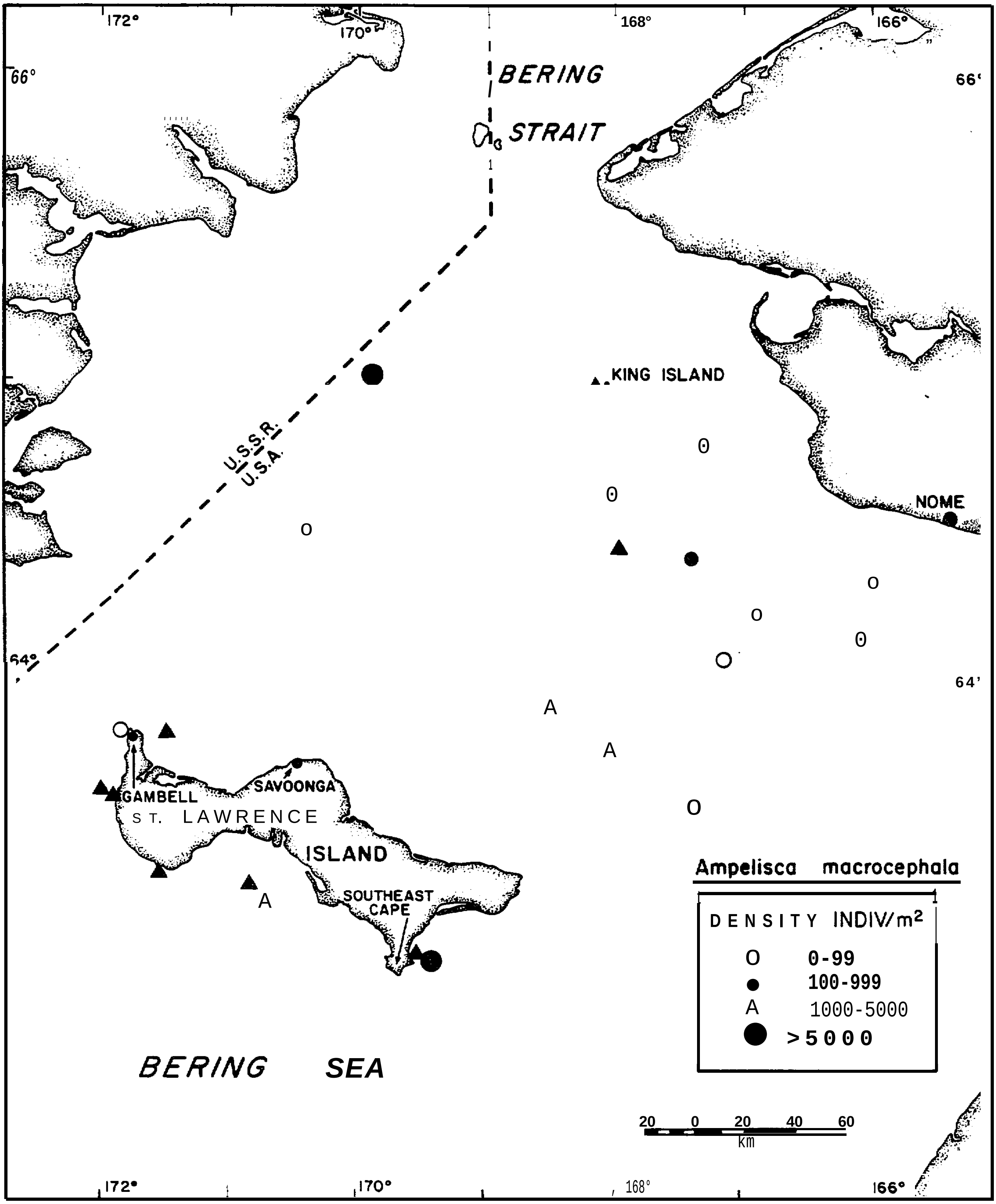

Figure 3a. Density of the common amphipod species collected in the Chiriko Basin and near St. Lawrence Island in July and September 1982.

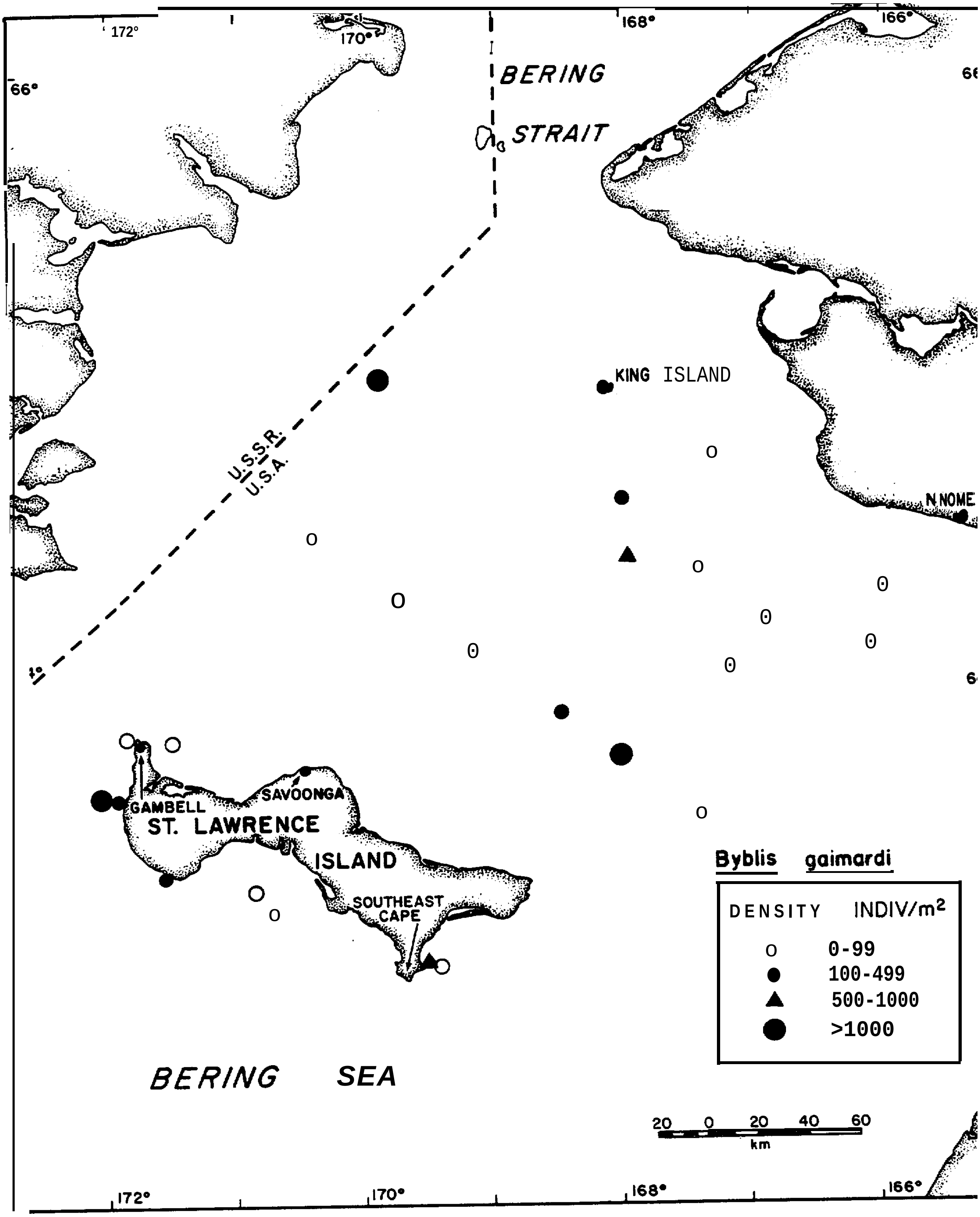
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Figure 3b.

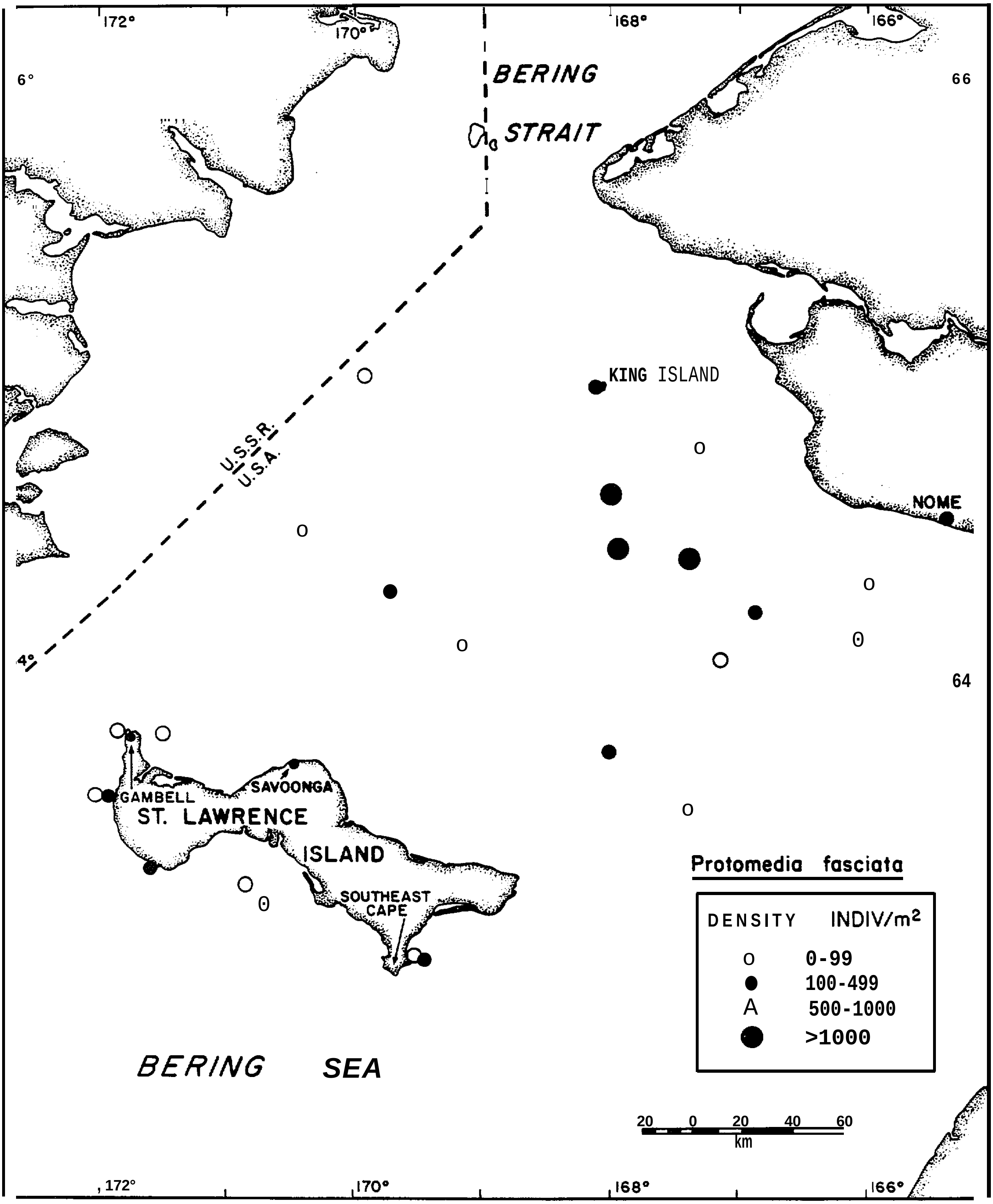
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Figure 3c.

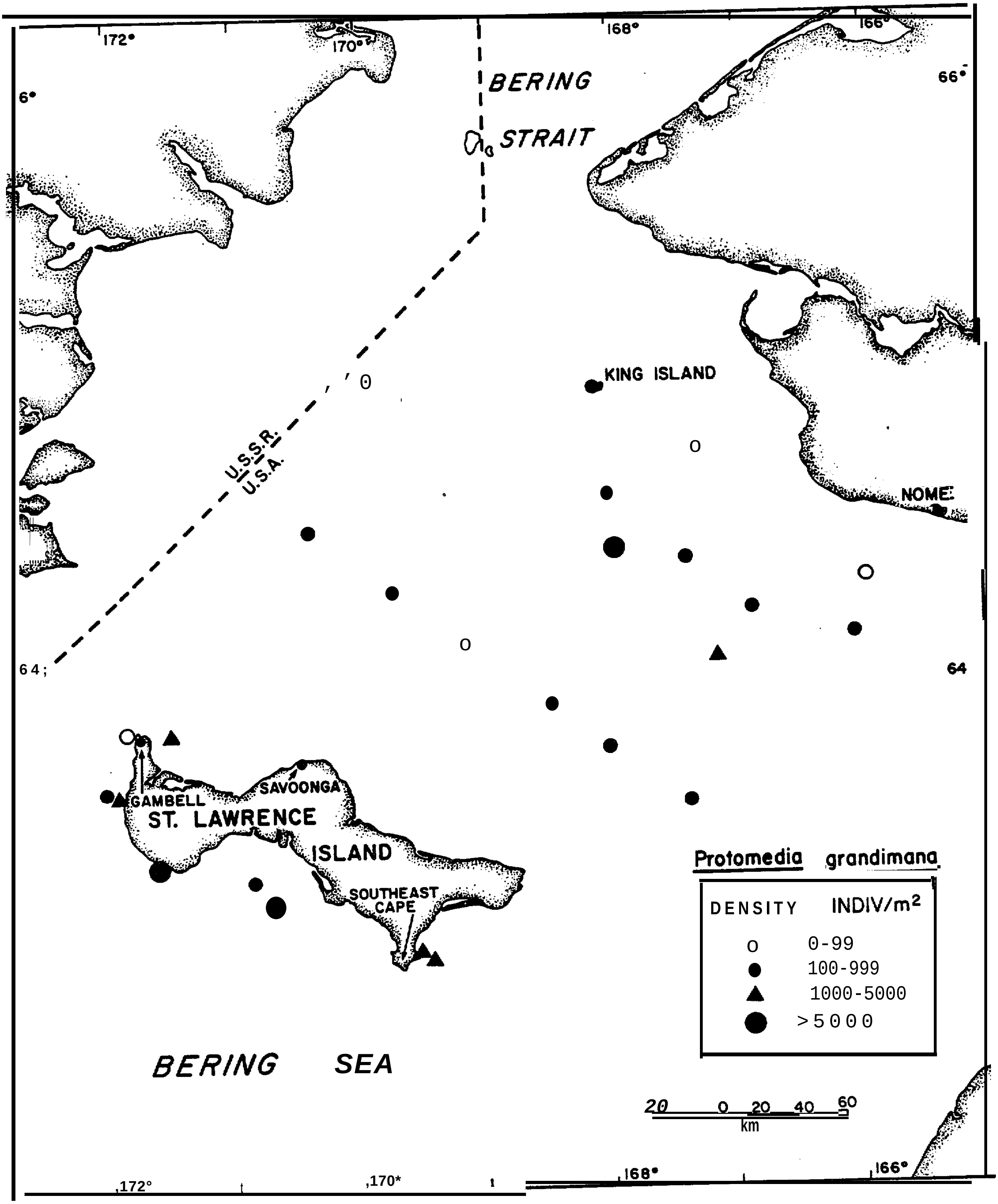
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Figure 3d.

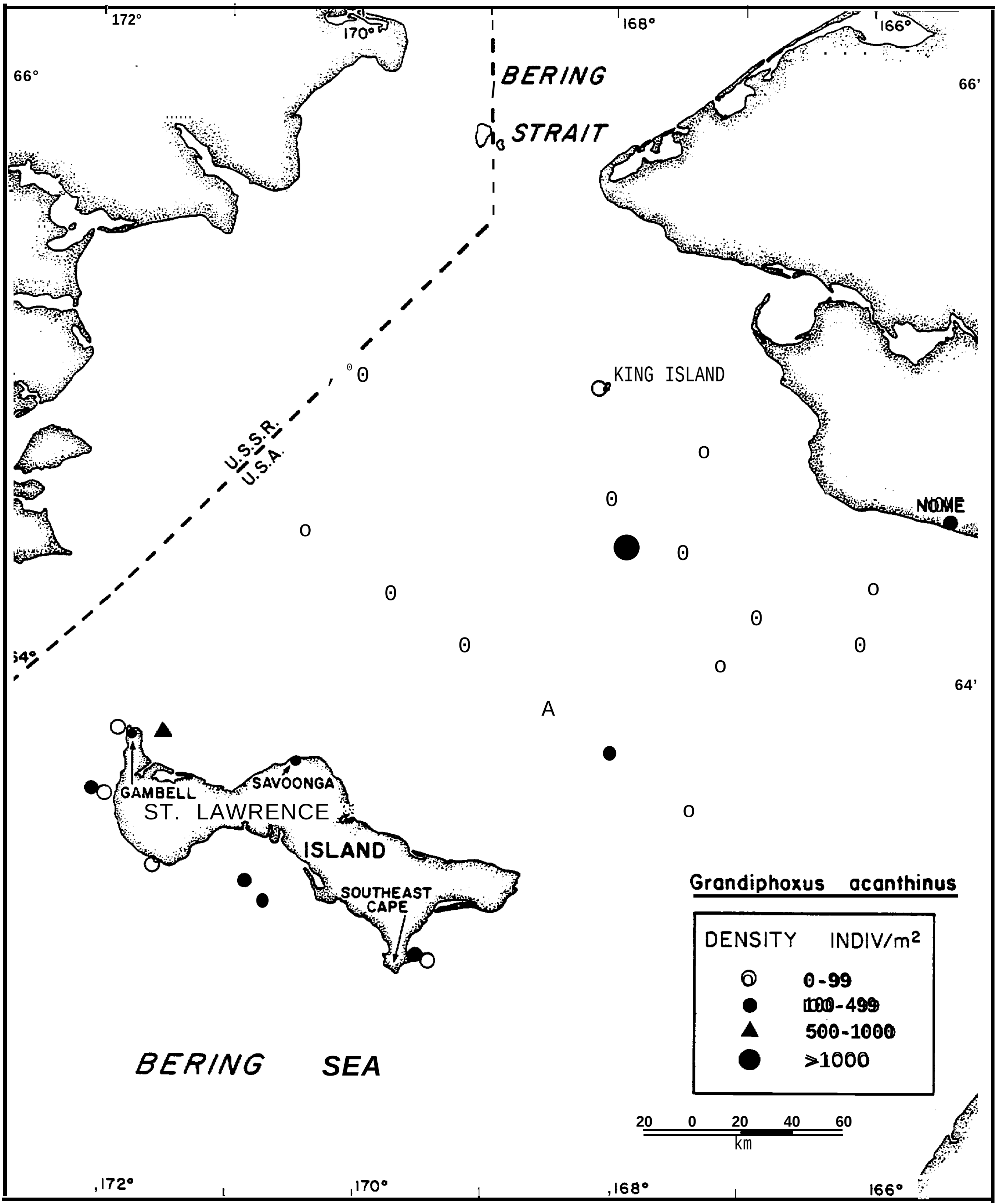
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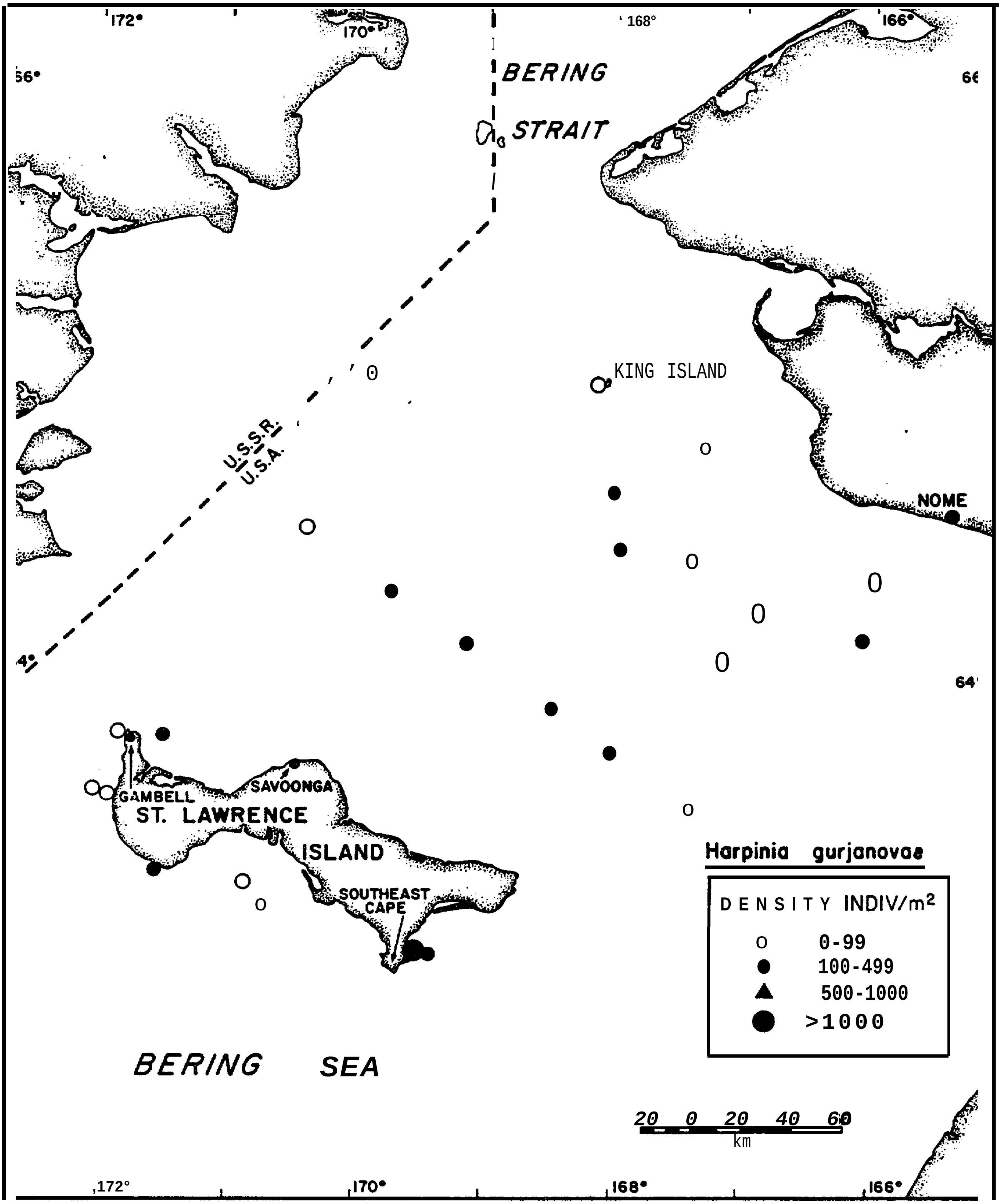
Figure 3e.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Harpinia gurjanovae
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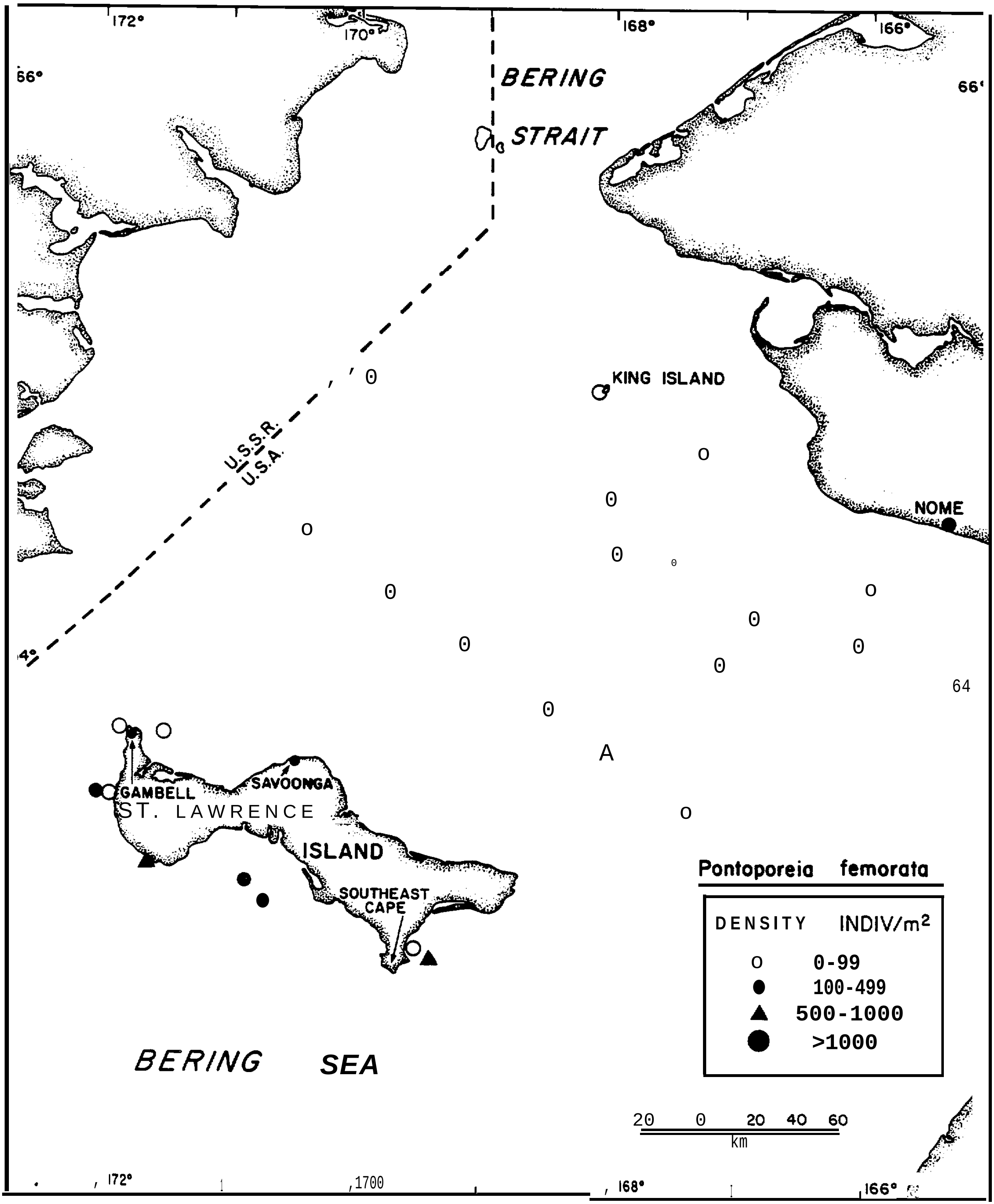
km

Figure 3f.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Pontoporeia femorata
DENSITY INDIV/m2
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66°
64

Figure 3g.

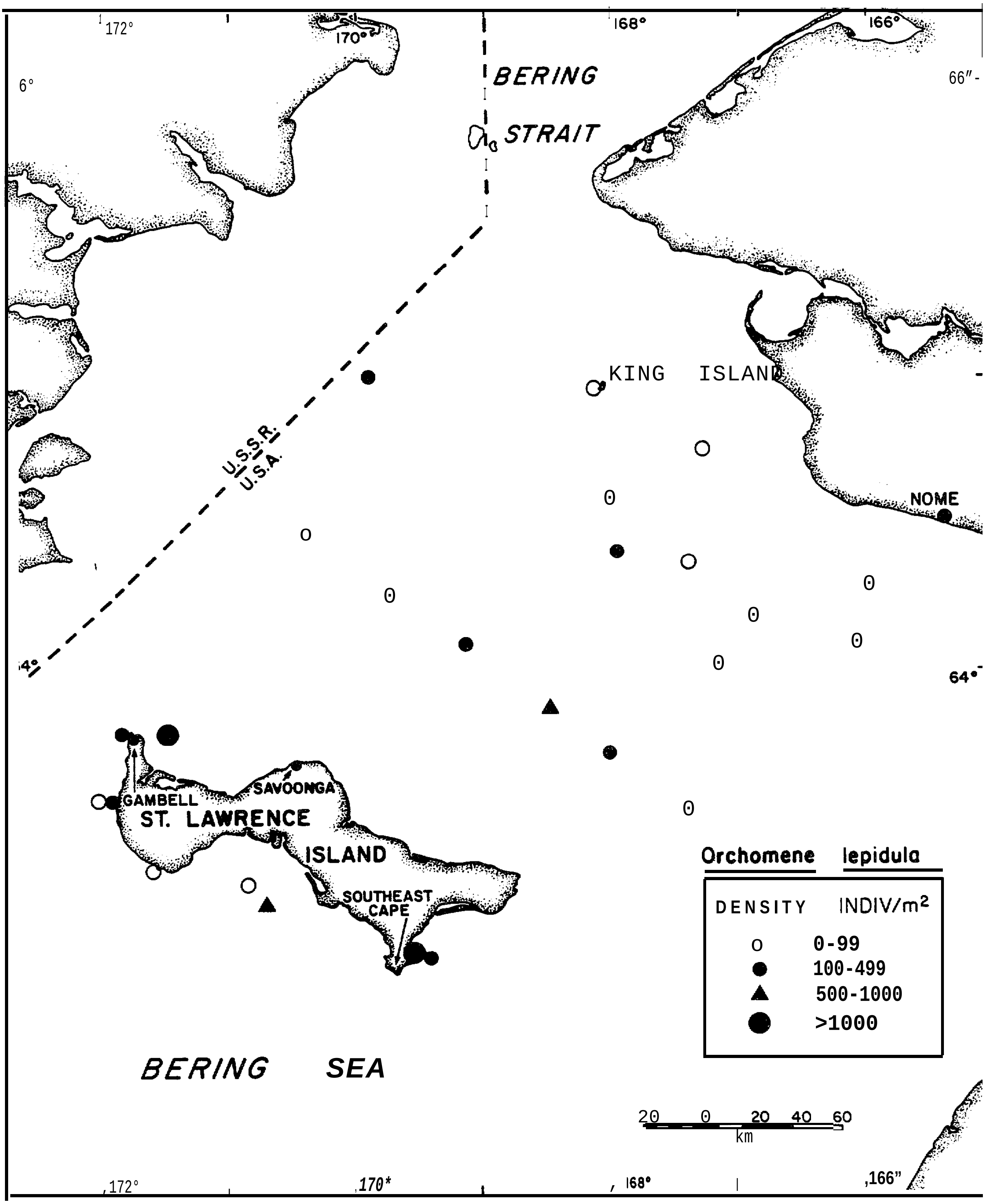
172°
170°
168°
166°
6°
66°
BERING
STRAIT
KING ISLAND
U.S.S.R.
U.S.A.
NOME
4°
64°
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST
CAPE
BERING SEA
Orchomene lepidula
DENSITY INDIV/m2
0-99
100-499
500-1000
>1000
20 0 20 40 60
km
172°
170*
168°
166”

Figure 3h.

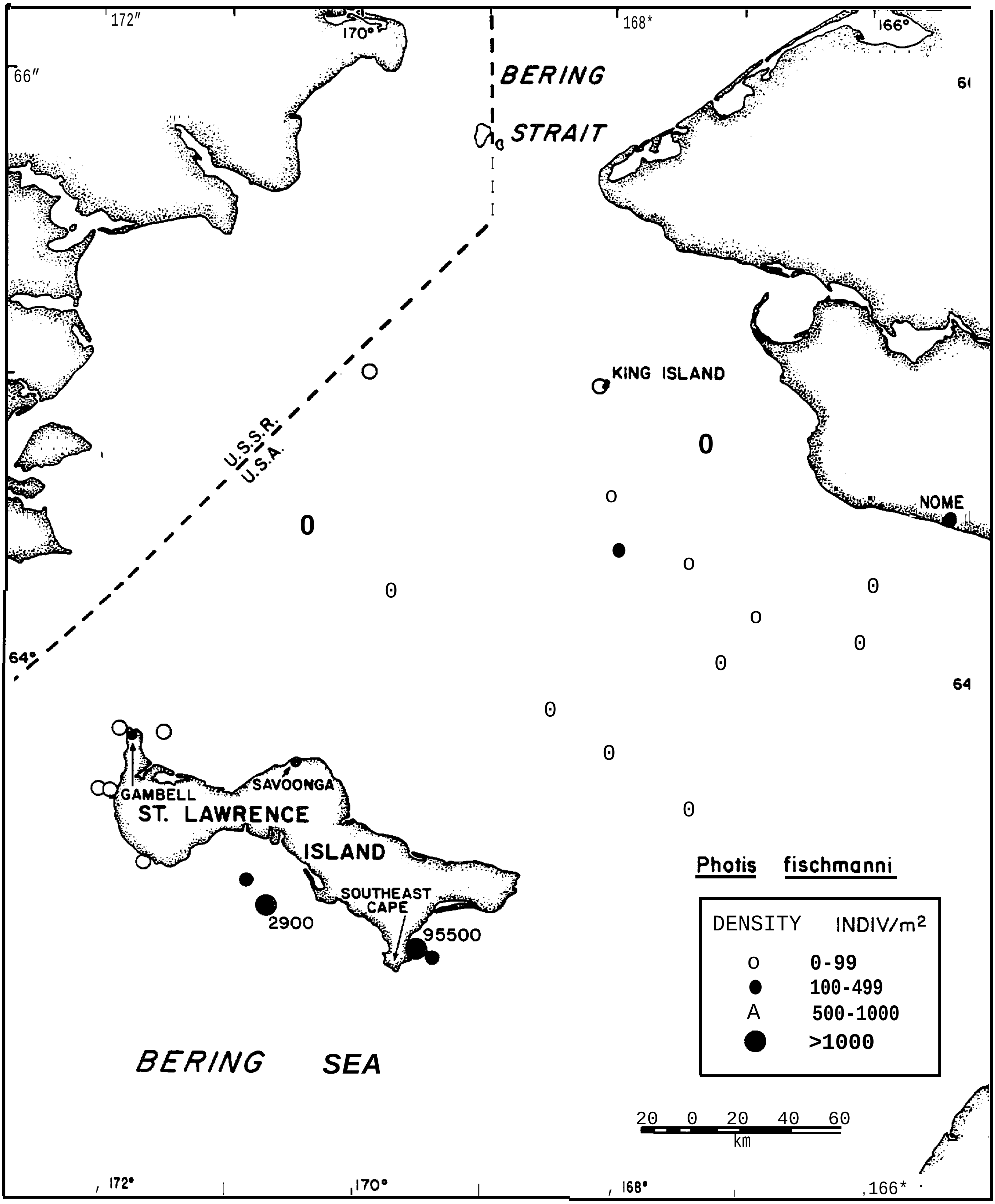
172″
170°
168*
166°
66″
BERING
STRAIT
KING ISLAND
U.S.S.R.
U.S.A.
NOME
64°
64
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST
CAPE
2900
95500
Photis fischmanni
DENSITY INDIV/m2
o 0-99
● 100-499
A 500-1000
● >1000
20 0 20 40 60
km
BERING SEA
172°
170°
168°
166*

Figure 3i.

Mean total biomass of the 37 samples from the central Chirikof Basin that were dominated by amphipods (Fig. 2) was 298.1 g/m^2--lower than the 482 ± 286 g/m^2 reported by Stoker (1978) as the mean biomass of samples taken within the ampeliscid amphipod community. However, Stoker (1978) found the highest biomass values in the northwestern part of the Chirikof Basin, an area not sampled during this study. Mean biomass of 33 samples taken by us within the area dominated by the two 'non-amphipod' communities in the eastern Chirikof Basin was 289.5 g/m2. Stoker (1978) found a mean biomass of 193 ± 111 to 265 ± 140 g/m2 in this area.

Mean densities in our samples were higher than values reported by Stoker: 9317 ± 6897 indiv/m2 vs. 3688 ± 823 indiv/m^2 for the amphipod community, and 2125 indiv/m2 in our samples VS. 340 ± 103 to 702 ± 208 indiv/m2 in Stoker's samples for other communities. Stoker's density and biomass estimates include samples from a much larger geographic area and as such are not directly comparable to values presented here.

There appeared to be considerable variation in the distribution of standing crop of the dominant amphipod species in the study area (Tables 3 and 4; Figs. 3a to 3h). One of the principal aims of the study was to define and characterize gray whale feeding areas. To this end, the following sections attempt to identify environmental conditions associated with the presence or absence of gray whale prey species.

The approach used was to quantify the abundance of the dominant amphipods in terms of various substrate conditions and depth regimes, and then use multiple regression analysis to determine if some of these environmental variables could be used as predictors of the standing crop of these animals.

All grab and airlift samples that were accompanied by measurements of the appropriate variables were used in the analyses. The environmental variables that were considered in the analysis were depth, mean grain size, sorting coefficient, organic carbon content of the sediment, caloric content of the sediment, and carbon to nitrogen ratio of the sediment. Inspection of scatter plots of the data indicated that, in some instances, a mean grain size squared term was necessary to account for non-linear relationships".

A stepwise multiple regression procedure (BMDP2R, Dixon 1981) was used to assess the relationships between the environmental variables and the standing crop of benthic animals. This technique added environmental variables to the regression equation one at a time beginning with the variable having the strongest simple correlation with animal abundance. Thereafter, environmental variables were added in decreasing order of partial correlation until no additional variable would, if included in the equation, significantly ($P<0.05$)* improve the equation's ability to predict standing crop.

Most of the environmental variables used in the analysis were correlated with one another (Table 5). Depth, the organic variables, sorting coefficient and mean grain size were all intercorrelated. The finest substrates tended to be associated with the shallowest depths, and finer substrates tended to have a higher carbon and caloric content than coarser substrates. In these circumstances it is usually impossible to determine which of the intercorrelated predictors is (or are) of direct importance to the animals.

Ampeliscid Amphipods

Ampelisca macrocephala was the dominant benthic animal in terms of both numbers and biomass in samples taken in the Chirikof Basin, off the west coast of St. Lawrence Island, and in the deeper waters near Southeast Cape (Tables 3 and 4; Fig. 3a). It was also the dominant species in terms of biomass in samples taken from the south coast of St. Lawrence Island.

The density of *Ampelisca macrocephala* varied greatly with mean grain size and sorting coefficient and less so with depth and organic composition of the substrate (Tables 6, 7 and 8). Because of an apparent non-linear relationship between mean grain size and the density of this species (Table 8), both mean grain size and its square were forced into the multiple regression equation. Both terms were significant predictors of the density

* Significance levels for individual variables in multiple regression equations in this report are the conventional ones derived directly from the F-to-delete values at the final step of the stepwise analysis. These levels generally overestimate the significance of each variable as a predictor (Hill 1979).

Table 5. Pearson product-moment correlation matrix of physical measurements taken with benthic samples from the Chirikof Basin and vicinity of St. Lawrence Island; n = 118.

	Depth (m)	Mean grain size (Φ)	Mean grain size squared (Φ^2)	Sorting coefficient	Caloric content Cal/g	Organic carbon mg/ g
Mean grain size	-0.31**					
Mean grain size squared	-0.31**	1.00**				
Sorting coefficient	0.27**	0.09 NS	0.14 NS			
Caloric content	0.24*	0.23*	0.22*	0.34***		
Organic carbon	-0.41***	0.40***	0.41***	0.11 NS	0.10 NS	
Carbon/nitrogen	-.24*	0.04 NS	0.05 NS	0.19*	0.01 NS	0.33***

Significance (two-sided) shown by asterisks; NS means not significant, $p>0.05$; * means $0.05 \geq P > 0.01$, ** means $0.01 \geq P > 0.001$ and *** means $P \leq 0.001$.

Table 6. Mean density ± s.d. (no./m^2) of 10 dominant species of benthic amphipods in samples taken in the Chirikof Basin and vicinity of St. Lawrence Island in summer 1982.

	Depth Range (m)			
	12-19	20-29	30-39	40-50
Ampelisca macrocephala	946 ± 1243	2894 * 2948	1939 ● 2249	4197 ± 4884
Byblis gaimardi	833 ± 920	90 ± 212	735 ● 1640	684 ± 1168
Ampelisca eschrichti	27*94	67 ● 181	89 ± 170	34A 52
Harpinia gurjanovae	1282 * 1732	84 * 143	104 * 190	112 * 150
Grandiphoxus acanthinus	139 * 209	155 ± 275	150 ± 252	7 ± 18
Protomedia fasciata	56 ± 148	104 * 194	814 * 2032	59 * 134
Protomedia grandimana	2511 ± 2897	•1882 * 3582	1642 * 4373	252 * 340
Photis fischmanni	83319 ± 60276	437 ± 1426	107 ± 161	22 *39
Pontoporeia f-rata	58 ± 127	152 * 394	170 * 356	5 ± 8
Orchomene lepidula	2351 ± 1876	319 * 520	132 ± 218	104 * 403
Sample size	39	37	57	17

Table 7. Mean density * s.d. (no./m[2]) of 10 dominant species of benthic amphipods in sediments of various organic characteristics. Samples were taken in the Chirikof Basin and vicinity of St. Lawrence Island during the summer of 1982.

	Caloric content (M/g) [1]			Organic carbon (mg/g[2])		Carbon/nitrogen (ratio)[1]	
Range of values	58-299	300-399	400-932	1.38-2.99	3.03-6.46	6.06-6.99	7.03-12.92
Species							
Ampelisca macrocephala	2299 * 3131	2488 * 2634	1698 * 2241	2529 * 2856	1635 ± 2561	3302 ± 3076	1284 ± 2129
Byblis gaimardi	315 * 749	719 * 1824	913 * 1026	664 ± 1419	493 ± 811	684 * 1557	526 * 854
Ampelisca eschrichti	39 * 134	129 * 198	35 ± 93	63 ± 150	58 * 148	96 ± 174	33*119
Harpinia gurjanovae	232 * 539	127 ± 199	920 * 1130	511 ± 918	250 * 502	350*622	443 ± 897
Grandiphoxus acanthinus	158 ± 240	133 ± 278	91 * 180	172 ± 273	72 ± 14	125 * 235	138 ± 237
Protomedia fasciata	597 * 1836	247 * 742	86 * 216	346 * 1549	371 * 817	78 ± 199	574 ± 1705
Protomedia grandimana	2193 ± 3433	1065 ± 4744	1750 ± 2415	1388 ± 2772	2343 * 45C8	1476 ± 3118	2000 * 3917
Photis fischmanni	9927 * 35821	152 ± 183	59115 ± 61727	22096 ± 44958	21392 * 51684	17511 ± 41506	25195 ± 51875
Pontoporeia femorata	146 * 333	143 * 386	53 * 120	94 ± 245	153 * 377	167 * 339	79 ± 212
Orchomene lepidula	379 * 852	171 * 255	1834 ± 1929	961 * 1559	438 * 995	763 * 1262	743 ± 1477
Sample size	67	39	44	90	60	66	84

1 Values expressed per unit dry sediment.

Table 8. Mean density ± s.d. (no. /m^2) of 10 dominant species of benthic amphipods in various sediment types. Samples were taken in the Chirikof Basin and vicinity of St. Lawrence Island in the summer of 1982.

Species / Sorting Coefficient (Φ)	Mean grain size (Φ)		
	2.16-3.00	3.01-3.50	3.51-4.03
Ampelisca macrocephala			
1.10-1.75	2779 ± 2716	4226 ± 3436	212 ± 219
1.76-2.59	263 ± 495	3362 * 2809	975 ± 1424
Ampelisca eschrichti			
1.10-1.75	41 *89	123 * 245	0
1.76-2.59	29 ± 63	118* 173	36 ± 108
Byblis gaimardi			
1.10-1.75	128 * 284	1113 * 2055	1140 * 1057
1.76-2.59	101 ± 126	1090 * 1297	118 * 313
Harpinia gurjanovae			
1.10-1.75	89 ± 131	423 * 763	1182 * 1306
1.76-2.59	44 ± 108	153 * 259	619 *868
Grandiphoxus acanthinus			
1.10-1.75	241 * 299	107 * 159	190 ± 232
1.76-2.59	26 ± 51	187 ± 342	17 ± 34
Protomedia fasciata			
1.10-1.75	282 ± 800	102 * 212	21 ± 63
1.76-2.59	2000 ± 3297	185 * 423	96 ± 193
Protomedia grandimana			
1.10-1.75	2702 •6226	1692 ± 2461	3309 ± 2744
1.76-2.59	438 *669	2118 * 3135	261 * 348
Pontoporeia femorata			
1.10-1.75	191 ± 417	24 ± 62	13 ± 47
1.76-2.59	4 ± 16	371 * 492	69 * 141
Photis fischmanni			
1.10-1.75	585 ± 1506	22433 ± 52310	93419 ± 67718
1.76-2.59	62 ± 128	39 ± 81	25258 ± 36560
Orchomene lepidula			
1.10-1.75	364 ± 550	619* 1127	1972 ± 2086
1.76-2.59	33 i 71	233 * 392	1304 ± 1837
Sample size			
1.10-1.75	32	29	20
1.76-2.59	17	23	29

of Ampelisca macrocephala (Table 9) and defined maximum abundance (holding other factors constant) at a mean grain size of 2.9 Φ (the cutpoint between fine and very fine sand). Mean grain size in samples where abundance of A. macrocephala exceeded 1000 indiv/m^2 averaged 3.2 ± s.d. 0.4 Φ , (n = 16). The grain size terms in the equation appeared to be quite accurate in describing the relationship between grain size and density. The equation also predicted greater abundances in well sorted substrates than in poorly sorted substrates (Table 9). After allowances for mean grain size and sorting coefficient, high density of Ampelisca macrocephala was weakly related to high caloric content. Density of A. macrocephala was higher in sediments of low organic carbon content (Table 7) than those of high organic carbon content, but this variable was correlated with grain size and was not included in the equation after grain size was considered in the analysis.

Byblis gaimardi was a significant contributor to biomass, especially in samples from the Chirikof Basin, west coast of St. Lawrence Island, and shallow water off Southeast Cape (Table 3; Fig. 3b). Both mean grain size and its square were forced into the multiple regression equation and were significant predictors of the density of this species. Holding other terms constant, the equation predicts maximum density at a mean grain size of 3.1 Φ. Mean grain size in samples where abundance exceeded 1000 indiv/m2 averaged 3.5 ± s.d. 0.2 Φ. Again the equation accurately predicted the preferred substrate. Shallow water and sediments containing a high caloric content were also significant predictors of a high density of Byblis gaimardi.

Ampelisca eschrichti was nowhere very abundant (Table 4) but is included in discussions that follow for comparison with the two common ampeliscid species. The multiple regression equation derived to explain variance in density of Ampelisca eschrichti placed much weight on the two mean grain size terms that were forced into the equation to account for an observed non-linear relationship. The equation (Table 9) predicts maximum densities of this species at a mean grain size of 2.9 Φ in poorly sorted substrates with a high carbon content and a low carbon to nitrogen ratio.

Table 9. Results of multiple regression analyses[1] of densities (no./m²) of 10 dominant amphipod species, using as predictors the physical measurements associated with samples. All samples were taken in the Chirikof Basin and vicinity of St. Lawrence Island; n = 118.

	Ampelisca macrocephala	Byblis gaimardi	Ampelisca eschrichti	Harpinia gurjanovae	Grandiphoxus acanthinus	Protomedia fasciata	Protomedia grandimana	Photis fischmanni	Pontoporeia femorata	Orchomene lepidula
Constant (Y-intercept)	-6.6692	-9.31131	-12.8585	2.6919	2.6368	2.2533	5.2761	9.6869	-7.4828	5.1891
Depth		-0.0405***		-0.0342***	-	-	-0.0379*	-0.117-		-0.06 %***
Mean grain size	7. 9337*	7. 5308**	8.8900***	0.4780 NS		-0.6922***		-0.4487 NS	5.6445**2	
Mean grain size squared	-1.3815*2	-1.1931*2	-1.5102***2	-3	-3	-3	-3	-3	-0.9438 NS	-3
Sorting coefficient	-1.4188*		0.7922***	-1.3050***	-1.6578**	0. 8484*	-1. 0073***	-2.2590***		-1.6915***
Caloric content	0.0017*	0.0033***		0.0016*		-0.0014*		0.0062***		0.0034***
Organic carbon			0. 1532*							-0.2374**
Carbon/nitrogen			-0.1341*		1. 1566***			-0. 1417**		0.0959
Multiple R	0.61 ***	0. 56***	0. 52***	0. 58***	0.59-	0.3-	0. 50***	0.85***	0. 27**	0.73***
% of variance explained	37.3	31.6	26.6	33.8	34.2	15.7	25.4	73.0	7.70	53.7
S.E. of estimate	1.15	1.10	0.78	1.06	0.91	1.20	1.11	1.04	1.00	1.00

1 Regression coefficients of each variable that entered the equation are shown, along with the constant (Y-intercept) and statistics describing the fit of the equat ion. Significance levels of the regression equation and approximate significance levels of the regression coefficients are shown by asterisks; NS means notsignificant,p>0. 05; * means 0.05>P≥0. 01. ** — 0.01≥P>0.001 and *** — P<0.001.

2 In order to account for non linear relationships, both mean grain size and mean grain size squared were forced into the equation.

3 Variable mt considered for inclusion.

Phoxocephalids and Haustoriids

Harpinia gurjanovae was most abundant in shallow water off Southeast Cape, St. Lawrence Island, and moderately abundant in other areas (Fig. 3f). Maximum densities were found in shallow water in fine, well sorted substrates with a high caloric content (Tables 6, 7, and 8). All of these variables were significant predictors of the density of this species in multiple regression analysis (Table 9).

Grandiphoxus acanthinus was rare at the deepest depths sampled and was equally abundant over other depth ranges (Table 6). It was more abundant in well sorted substrates but density did not appear to vary with mean grain size (Table 8). Multiple regression analysis predicted maximum density in well sorted substrates with a high carbon to nitrogen ratio (Table 9).

Multiple regression analysis was not very successful in explaining densities of Pontoporeia femorata. None of the variables considered in the analysis was significantly correlated with the abundance of this species (Table 10). When mean grain size and its square were forced into the equation, only 8% of variance in the density of this species was explained (Table 9).

Corophiid Amphipods

The congeners Protomedia fasciata and P. grandimana differed in the habitats of maximum density. Multiple regression analysis predicted maximum densities of P. grandimana in shallow water and in well sorted substrates. In contrast, maximum densities of P. fasciata were predicted in poorly sorted coarse substrates with a low caloric content (Table 9).

Photis fischmanni was the dominant amphipod on the shallow shelf off Southeast Cape, St. Lawrence Island (Table 5). It was common in samples taken off the south coast and relatively rare in other areas. Multiple regression analysis predicted maximum densities of this species in shallow water, in substrates that were well sorted with a high caloric content and low carbon to nitrogen ratio (Table 9). Density of P. fischmanni was positively correlated with mean grain size (Table 10), indicating that highest densities were found in fine substrates. However, after all other variables had been considered by the analysis, high densities were predicted in coarse substrates.

Lysianassid Amphipods

Orchomene lepidula was most common in shallow water near St. Lawrence Island (Table 4; Fig. 3h). Multiple regression analysis predicted maximum densities of this species in shallow water, in well sorted substrates with a high caloric content, low organic carbon content, and high carbon to nitrogen ratio.

Trophic Relationships

Feeding Habits of Amphipods

The results of analysis of gut contents of 499 amphipods are shown in Tables 11 and 12. Three hundred and forty of these amphipods had been feeding on sediment. Fewer than 100 guts contained algal material and fewer than 60 contained animal material. The species represented in Tables 11 and 12 comprise the majority of amphipods collected during the study and are thus representative of the general feeding habits of the amphipods in the region.

Four species of ampeliscid amphipod dominated the benthos of the central Chirikof Basin and areas off the west and south coasts of St. Lawrence Island and deep water off Southeast Cape. All four species were deposit feeders. The three species of Ampelisca almost exclusively consumed sediment while Byblis gaimardi appeared to be a more selective feeder. Almost all of the guts of Byblis gaimardi contained diatoms in addition to sediment (Table 11).

Photis fischmanni, the dominant benthic animal in shallow water, and Protomedia spp., common amphipods in all areas, were also sediment feeders, as were Pontoporeia femorata, Weycomedon similis and all other amphipods examined except Harpinia gurjanovae and Orchomene sp. (Tables 11 and 12).

Table 10. Pearson product-moment correlation coefficients of the density (no./m^2) of dominant amphipod species with physical measurements associated with samples taken in the Chirikof Basin and vicinity of St. Lawrence Island; n = 118.

	Ampelisca macrocephala	Byblis gaimardi	Ampelisca eschrichti	Harpinia gurjanovae	Grandiphoxus acanthinus	Protomedia fasciata	Protomedia grandimana	Photis fischmanni	Pontoporeia femorata	Orchomene lepidula
Depth	0.03 NS	-0.21*	0.30**	-0.41**	-0.31**	0.13 NS	-0.42***	-0.59***	-0.09 NS	-0.56***
Mean grain sire	-0.25*	0.17 NS	-0.24*	0.30**	-0.02 NS	-0.30**	0.10 NS	0. 18*	-0.14 NS	0.08 NS
Mean grain size squared	-0.29**	0.15 NS	-0.26**	-1					-0.16 NS	
Sorting coefficient	-0.46***	-0.13 NS	0.00 NS	-0.37***	-0.49***	0.15 NS	-0.38***	-0.46***	-0.16 NS	-0.44***
Caloric content	0.06 NS	0.40***	0.19	0.07 NS	-0.29**	-0. 18*	-0.22*	0.24*	0.03 NS	0.13 NS
Organic carbon	-0.22*	0.14 NS	-0.05 NS	0.19 NS	-0.09 NS	-0.09 NS	0.23*	0.16 NS	0.04 NS	0.06 NS
Carbon/nitrogen	-0.13 NS	0.01 NS	-0.25*	0.05 NS	0.22*	0.12 NS	0.10 NS	-0.08 NS	-0.07 NS	0.14 NS

1 Variable mt considered.

Signif icance (two-sided) shown by asterisks; NS means mt significant, p>0.05; * means 0.05≥P>0.01, ** means 0. 01>%001 and *** means P<0.001 .

Table 11. Frequency of occurrence of food items found in the guts of 11 species of amphipods collected in the central Chirikof Basin in the summer of 1982. Samples are from areas 1B, 2A, 3B, 4A, 4B, 5A and 7B.

Species	*Protomedia* sp.[1]	*Ampelisca macrocephala*	*Ampelisca eschrichti*	*Ampelisca birulai*	*Byblis gaimardi*	*Harpinia gurjanovae*	*Bathymedon* sp.[2]	*Podoceropsis* sp.	*Ischyroceros* sp.[3]	*Photis fischmanni*	*Machariomyx mulleri*
Total no. examined	74	28	7	12	30	13	11	4	3	4	1
Sediment	66	28	7	8	29	4	8	3	3	3	1
Detritus	3										
Unidentified diatoms	26	3			27	1			1		
Chaetoceros sp.	1				2						
Filamentous diatoms	1										
Unidentified dinoflagellate	1										
Peridinium sp.		1									
Tintinids	1										
Foraminifera	1										1
Filamentous material	1										
Nematodes						2					
Polychaetes						1					
Sponge						1					
Unidentified animal tissue						1					
Empty	2			4	1	7	3	1		1	

[1] Includes *P. fasciata*, *P. dulkeiti*, *P. lindhlii* and *P. microdactyla*.
[2] Includes *B. nanseni*.
[3] Includes *I. angiupes*.

Table 12. Frequency of occurrence of food items found in tte guts of 8 species of amphipods collected near St. Lawrence Island in the summer of 1982.

Area	Southeast Cape nearshore (11-14 m)				Southeast Cape offshore (22 m)				South crest (area 10D, 10E)			
Species	Photis f[redacted]	Harpinia gurjanovae	Protomedia sp.[1]	Orchomene sp.[2]	Ampelisca macrocephala	Protomedia sp.[3]	Weycomedon similis	Ampelisca eschrichti	Protomedia sp.[4]	Ampelisca macrocephala	Pontoporeia femorata	Photis fischmanni
Total no. examined	40	31	25	28	13	15	5	2	30	30	15	10
Sediment	39	1	19	16	11	15	5	1	26	24	15	8
Detritus												
Unidentified diatoms	9	2	2	1								
Pennate diatoms		5										
centric diatoms		1										
Naviculoid diatoms	1											
Chaetoceros Sp.	1											
PerMinim sp.			1									
Dinophysis sp.												
Dinobryon sp.	1											
Foramini fera			1									
Unidentified protozoa												
Identified nauplii		4										
Harpacticoid nauplii		1										
Harpacticoid copepods		5										
Amphipod remains				9								
Crustacean remains	3	1		11								
Nematodes		7										
Unidentified animal tissue		1		6								
Empty	1	12	6	3	2			1	4	6		2

1 Includes P. microdactyla.
2 Includes O. lepidula.
3 Includes P. microdactyla.
4 Includes P. epimerata and possibly P. microdactyla.

The lysianassid Orchomene sp. fed on animal material in addition to sediment. Harpinia gurjanovae appeared to be a selective carnivore; few guts contained sediment or plant material (Tables 11 and 12).

Feeding Guilds

The trophic relationships among the various components of the benthos were identified and quantified in the following manner. Animals were assigned to a feeding guild according to the nomenclature of Fauchald and Jumars (1979), using information provided by them, Stoker (1978) and Tables 11 and 12.

Wet weight was converted to carbon using data provided by Stoker (1978) . The carbon available to animals in the form of detritus, algae and meiofauna was estimated by applying the value of carbon content of sediment to the volume of sediment sampled by the grab or airlift.

A large amount of food in the form of meiofauna, algae and detritus appeared to be available to the benthic animals in all areas (Table 13). Surface deposit feeding appeared to be the most common feeding mode in all areas (Table 13). Surface deposit feeders included the ampeliscid amphipods, Photis fischmanni and the bivalve Macoma calcarea. In view of the total amount of food available in sediments, it is not surprising that biomass of this group was up to 3 times higher than that of the other primary consumers. In areas not dominated by amphipods, total biomass was lower due to the relative scarcity of surface deposit feeders.

Deposit feeders ingest substrate below the sediment surface and, in the areas studied, were represented mainly by polychaetes. This was the least common mode of feeding in all areas.

Carnivores included the isopod Tecticeps alascensis, polychaetes of the genus Nepthys and lysianassid amphipods. Some of these animals may also have been feeding on sediment; 16 of 28 specimens of Orchomene lepidula? had ingested sediment (Table 13).

Table 13. Mean biomass (g/m^2) of carbon in sediments and mean biomass according to major feeding mode of benthic animals taken in the Chirikof Basin and areas adjacent to St. Lawrence Island. Conversion of wet weight to carbon was accomplished using data provided by Stoker (1978).

	Chirikof Basin		Near St. Lawrence Island			
	Not dominated by amphipods[1]	Dominated by amphipods	West Coast	South Coast	Southeast Cape Offshore	Southeast Cape Nearshore
Carbon in sediments[2]	350	307	233	318	434	466
C/N ratio	9.0	7.0	6.7	6.7	7.8	8.5
Surface deposit feeders	2.2	11.3	11.5	10.2	13.2	10.1
Depost feeders	0.8	0.5	1.0	0.4	0.7	0.9
Filter feeders	1.2	0.7	2.7	3.0	1.9	1*0
Carnivores/scavengers	1.0	1.5	1.6	1.6	1*5	3.0
Not classified	1.5	1.0	1.6	0.7	1.2	0.9
Tot al	6.7	15.0	18.4	15.9	18.5	15.9
Sample size	38	37	11	15	10	55

1 Less than 50 g/m^2 of amphipods
2 Standardized to a sediment depth of 5 cm.

Filter feeders comprised only 5 to 19% of total biomass in various parts of the study area. In contrast, filter feeders generally dominate the benthos in other shallow areas (Jumars and Fauchald 1977). For example, in northwest Baffin Bay and Lancaster Sound in the eastern Canadian arctic, filter feeding was the dominant mode of feeding at depths <100 m (Thomson 1982); at Cape Hatt, northern Baffin Island, filter feeders, mainly bivalves, comprised 90% of standing crop at a depth of 7 m (Cross and Thomson 1981). Grain size and organic carbon content of sediments in Lancaster Sound and northern Baffin Bay were similar to those found in the Chirikof Basin.

Stoker (1978) believes that filter feeding bivalves were under-represented in his samples which, like many of ours, were taken with a Van Veen grab. However, we also obtained few bivalves when operating the airlift, and bivalve siphons were not conspicuous when we were diving or observing the seafloor with the video camera. A heavy suspended sediment load was observed during all dives and video tows. It is possible that these massive amounts of sediment precluded filter feeding by bivalves. Another factor preventing the establishment of filter feeders may be competition for space. Brenchley (1982) has shown that animal tubes restrict burrowing activities of bivalves and polychaetes. The dominant surface deposit feeders were all tubicolous amphipods. Their prodigious numbers, closely packed tubes covering the entire seafloor, and apparent ability to recolonize quickly (Thomson and Martin, this report) may prevent other groups from establishing themselves.

Productivity of Amphipods

Samples for the estimation of secondary productivity were taken in 15 m depth off Southeast Cape, St. Lawrence Island, during July and September 1982 and during January, March and May 1983. Only *Photis fischmanni* and *Ampelisca macrocephala* were taken in sufficient quantities during all periods for the estimation of secondary productivity.

Ampelisca macrocephala

Ampelisca macrocephala is a large tubicolous ampeliscid amphipod that may reach 32 mm in total length. Ovigerous females were found in the Chirikof Basin in July and September. At this time, eggs were in early stages of development; those most developed showed only leg buds. These ovigerous females were 21 to 29 mm in length. Mean number of eggs per female was 18 ± 6 (n = 18). The eggs were large (1.2 x 1.5 mm) and weighed 1.2 to 1.3 mg wet weight (0.31-0.39 mg dry weight). Females with oostigites in formation were found off Southeast Cape in July. In September, large females were rare in samples taken off Southeast Cape. Ovigerous females were also taken in the March and May samples. In May, ovigerous females were 14 to 16 mm in length. The eggs were not well developed but had eye spots.

Examination of the length frequency histograms for *Ampelisca macrocephala* from Southeast Cape (Fig. 4) shows two periods of release of young. Individuals 3 mm in length were abundant in the samples taken in May but absent in March (Fig. 4). Individuals 2 to 4 mm in length were common in January and rare in September. The ovigerous females observed during summer apparently released young in fall.

The following interpretation has been placed on the life history of *Ampelisca macrocephala* at Southeast Cape. Young released in spring at a length of 3 mm were 4 to 5 mm in length by July and 5 mm in September. They reached 7 to 8 mm in January, 9 to 10 mm in March and May, and were 10 to 13 mm in length the following July. Some matured at 15 mm the following spring and may also have spawned in fall. The 7 and 8 mm individuals found in the July samples were hatched the previous fall, reach 9 mm in September, 10 mm in January, 12 mm in March, and 13 to 14 mm in May; they may have spawned in the fall at 15 mm and/or the following spring at 18 mm. Life span is about 2.5 years in this area.

The growth rate of *Ampelisca macrocephala* in the northern Bering Sea is similar to that of other northern and arctic amphipods (Table 14). Growth is about 6 mm per year.

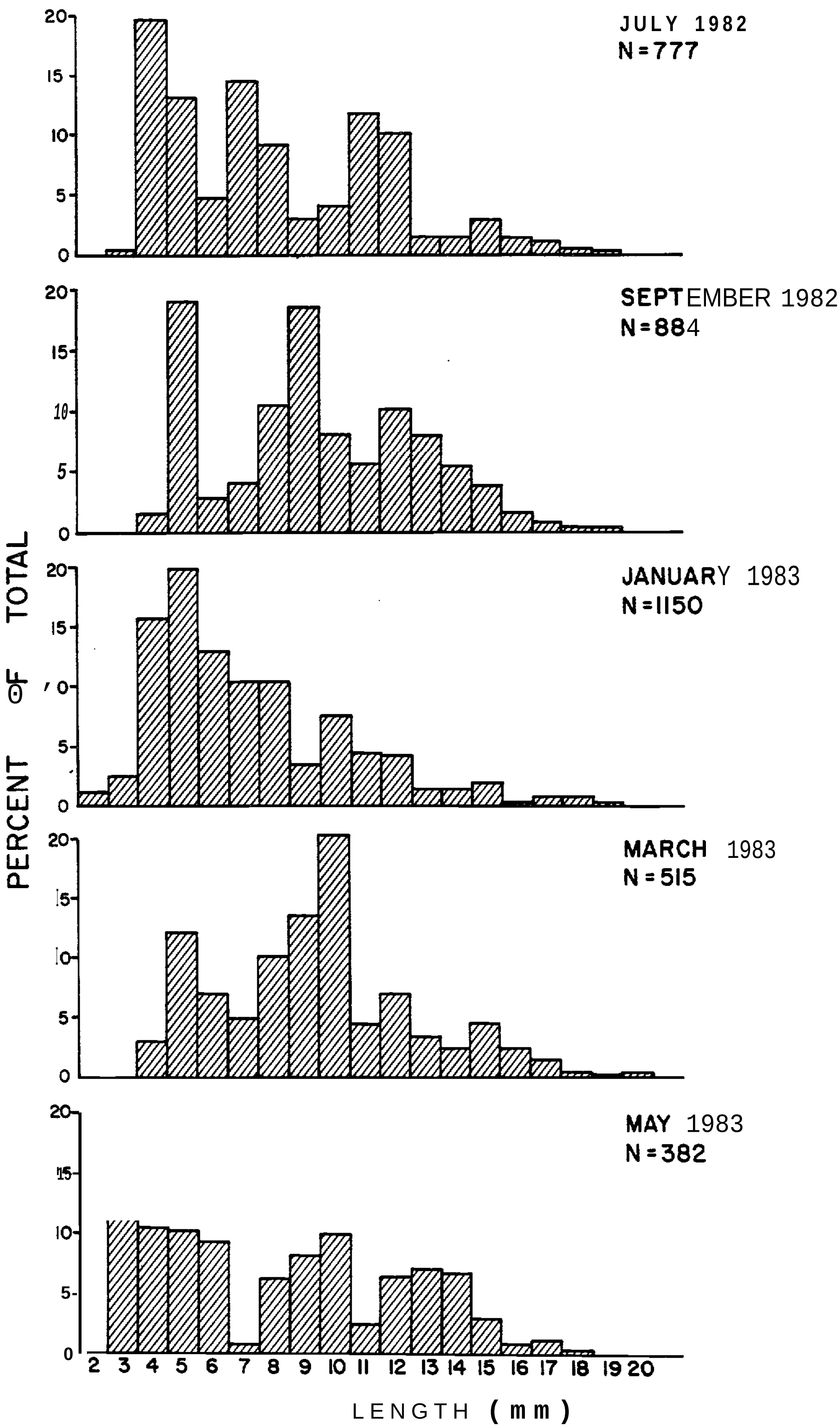

Figure 4. Length frequency histograms for **Ampelisca macrocephala** collected near Southeast Cape, St. Lawrence Island, in 1982 and 1983.

Table 14. Growth rates of arctic and temperate amphipods. All values in mm.

	Length at hatching	Growth over 1st year	Length at 1 year	Growth over 2nd year	Length at 2 years	Reference
Arctic Canada						
Gammarus setosus	3	4.5	7-8	7*5	14-16	Steele 1961 ; Cross 1982
Onisimus litoralis	3	9	12	6.5	16+	Steele 1961; Roy 1978; Cross 1982
Weyprechtia pinguis	3-4	9.5	11-14	12.5	19-24	Steele 1961 ; Cross 1982
Temperate Atlantic						
Ampelisca macrocephala	3	7*5	10-11		16.5	Kanneworff 1%5
Ampelisca brevicornis	2	10	12			Klein et al. 1975
Bering Sea						
Photis fischmanni	1.4	5.5	6-7			This report
Ampelisca macrocephala	3	6	8-10	6	15	This report

Dry weight was regressed against length and used to compare condition of the animals in July and January, and to generate a length-weight equation for use in computation of productivity. Examination of the data and residuals showed that the length vs. dry weight relationship of *Ampelisca macrocephala* was well described by a power curve (length and weight were both log transformed). Analysis of covariance (Dixon 1981) showed that differences in slopes of the regression lines were nonsignificant for animals collected in summer and winter ($F = 1.93$, $P = 0.17$, $df = 1, 62$). After accounting for length, differences in mean weights of animals 4 to 18 mm in length taken in July and January were nonsignificant ($F = 3.81$, $P = 0.056$).

There was a difference in the caloric content of animals taken in winter and summer. Mean caloric content of animals was 3674 ± 436 cal/g dry weight in JUly and 2136 ● 584 cal/g in January. The mean difference was 1538 cal/g dry weight or about 0.16 g lipid/g dry weight (1 g lipid = 9540 cal) assuming that all of the loss was due to lipid utilization.

The regression of length on weight for all animals collected in July and January was highly significant ($r = 0.98$, $P = 0.0000$, $n = 71$). The equation dry weight = $0.00197\ (\text{length})^{3.02681}$ explained 96% of the variance of dry weight on length. This equation was used to estimate mean dry weight of the various categories of individuals listed in Table 15.

Productivity was estimated using the cohort summation method (Crisp 1971). Mean length was estimated for each cohort shown in Figure 4. Mean dry weight of individuals was estimated from length using the above equation. Several cohorts were present during each sampling period, and productivity was computed separately for each one (Table 15). The May to July productivity estimate is less precise because it necessitated comparing data from May 1983 with July 1982. Inter-year differences in growth rates could be substantial.

Total productivity of *A. macrocephala* for the ten month period between July 1982 and May 1983 was 3.8 g/m^2 dry weight and mean standing crop was 2.9 ± 1.0 g/m^2. Productivity to biomass ratio was 1.3. The May 1983 and July 1982 data were used to estimate productivity from May to July; this yielded a

Table 15. Computation of productivity estimate for Ampelisca macrocephala from Southeast Cape, St. Lawrence Island, by cohort summation of population growth. Biomass is expressed as dry weight.

Date	Spring Cohorts					Fall Cohorts				
	Mean length (mm)	Indiv. dry wt. (mg)	Mean density (no./m²)	Standing crop (g/m²)	Productivity[1] (g/m²)	Mean length (mm)	Indiv. dry wt. (mg)	Mean density (no./m²)	Standing crop (g/m²)	Productivity[1] (g/n?)
Hatched Spring 19S2						Hatched Fall 1982				
July 198?	4.5	0.19	826	0.154	(0. 157)[2]					
Sept 1982	5.0	0.26	239	0.061	0.037	3.0	0.05	Not sampled		
Jan 19S3	7.3	0.81	775	0.626	a279	4.6	0.20	1210	a242	(0.182)[2]
March 1983	9.2	1.63	612	00995	a569	5.4	0.32	300	0.096	0.091
my 19s3	9.1	1.58	201	0.318		597	0.38	115	0.044	0.012
Hatched Spring 1981						Hatched Fall 1981				
JUly 1982	11.2	2.95	664	1.%9	(0.433)[3]	7.4	0.84	641	0.539	(o. 174)[3]
Sept 1982	12.4	4.01	254	1.020	0.487	8.8	1.42	492	0.700	0.329
Jan 1983	14.4	6.31	114	0.720	0.423	10.7	2957	464	1. 192	0.3m
March 1983	15. 1	7.29	107	0.780	a 108	12.3	3.92	175	0.686	0.431
May 1983	1607	9.83	20	0. 198	0.165	13.1	4.74	193	0.915	0.151
Hatched Spring 1980						Hatched Fall 1980				
July 1982	18.3	13.05	18	a235	(0.0(0)[3]	15.3	7.59	167	1.268	(0.513?
Sept 1982			0			15.2	7.44	99	0.737	
Jsn 1983						18.2	12.84	47	0.603	0.394
March 1983						18.1	12.62	36	0.454	
Hatched May 19S3										
May 1983	3.6	0.10	251	0.024						

[1] Productivity = Weight increment per animal over the period x mean density over the period.
[2] Minimum estimate assuming no mortality between hatching and indicated tire; weight of newly hatched individual estimated from extrapolation of length-weight regression.
[3] May to July productivity estimated from individual weight gain and standing crop difference between previous and following years' cohort (see text).

productivity estimate of 1.5 g/m2 for a total annual productivity to biomass ratio of 1.8.

Photis fischmanni

Some females of *Photis fischmanni* 4 to 6 mm in length were ovigerous in January. Eggs were 0.3 mm in diameter with ill-formed embryos. In May 1983 females 2 to 7 mm in length were brooding and/or had just released young 1.3 to 1.5 mm in length.

Thus the 2 mm individuals that formed the greatest proportion of this species in samples taken in July 1983 (Fig. 5) had most likely been released in May. This cohort grew 1 mm in the period July to September and formed the spawning population for the fall. Ovigerous or brooding females were not taken in September; however, fall-winter spawning is indicated by the presence of 2 mm individuals in January samples and oostigite formation in July. Animals hatched in the fall reached 2 to 3 mm in length by January, at which time females were ovigerous, and reached 3 to 4 mm in May. The rate of growth proposed here of 0.5 mm/month is consistent with growth rates of other northern amphipod species (Table 14). *Photis fischmanni* appears to require six months to reach maturity, lives one year and may spawn twice.

Productivity was calculated by cohort summation (Table 16). Total productivity from July 1982 to May 1983 as estimated by this method was 24.97 g/m2 and mean biomass was 8.158 g/m^2. Productivity to biomass ratio for the ten-month period was 3.1. Data from May 1983 and July 1982 yielded a productivity value of 5.42 g/m^2 for the period May to July. Total annual productivity was 30.39 g/m2 and annual productivity to biomass ratio was 3.7.

DISCUSSION

Interrelationships Among Species

The ten amphipod species discussed in the preceding section accounted for 95% of the density of all amphipods taken in the study area. In most of the areas studied, amphipods were abundant and totally dominated the benthos. Within the narrow range of depths and bottom conditions that we

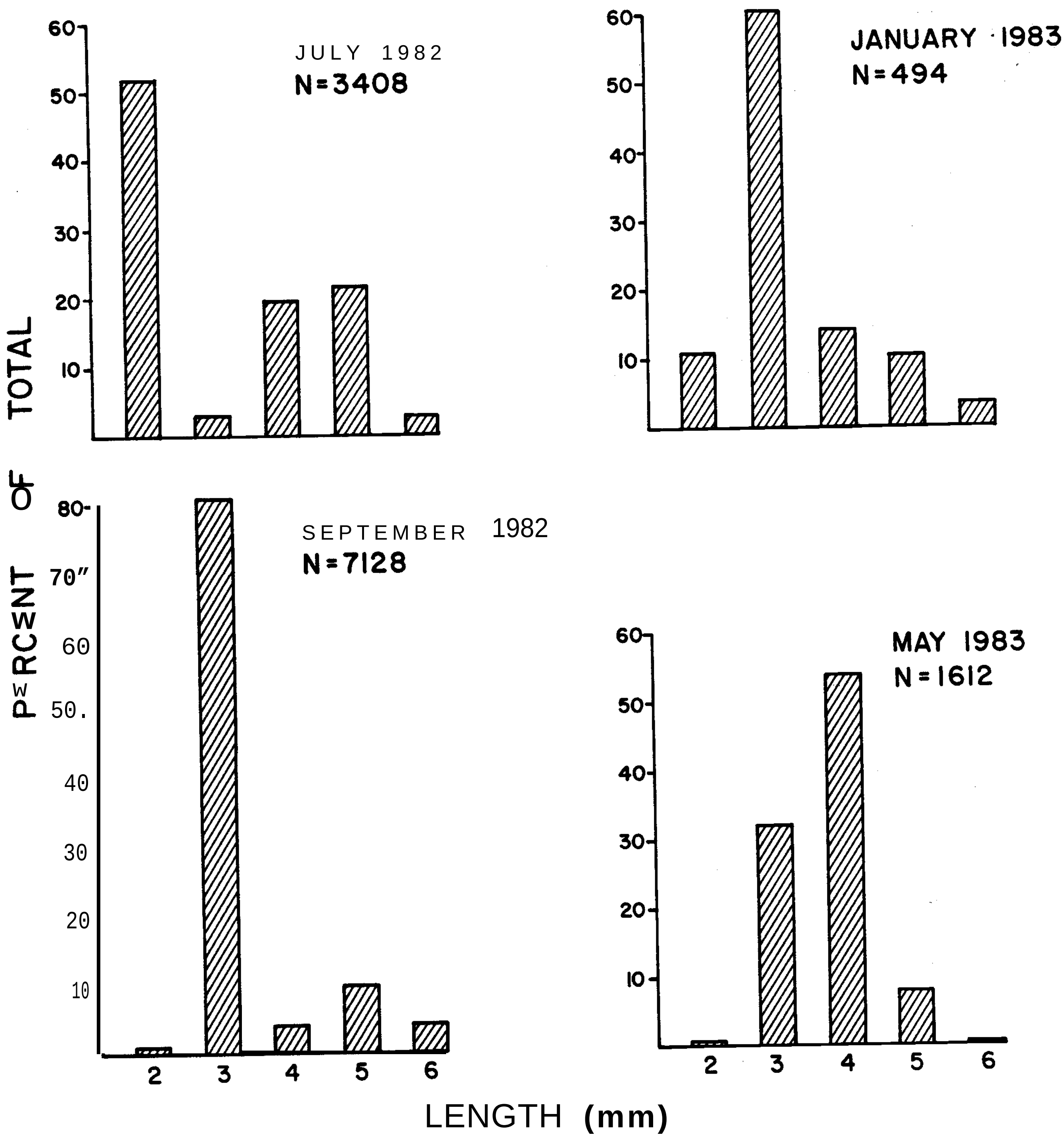

Figure 5. Length frequency histograms for **Photis fischmanni** collected near Southeast Cape, St. Lawrence Island, in 1982 and 1983.

Table 16. Computation of productivity estimate for Photis fischmanni from Southeast Cape, St. Lawrence Island, by cohort summation of population growth. Biomass is expressed as dry weight.

Date	Spring Cohorts						Fall Cohorts				
	Mean length (mm)	Indiv. dry wt. (w)	Mean density (no./m^2)	Standing crop (g/m^2)	Productivity[1] (g/m^2)		Mean length (inn)	Indiv. dry wt. (mg)	Mean density (no./m^2)	Standing crop (g/m^2)	Productivity[1] (g/m^2)
Hatched Spring 1983											
May 1983	1.4	0.004	26020								
Hatched Spring 1982						Hatched Fall 1982					
July 1982	2.05	0.01	26797	0.268	(0.158)[2]						
Sept 1982	3.02	0.($	108635	8.691	4.740						
							1.4	0.004	Not sampled		
Jan 1983	4.64	0.37	609	0.225	15.840		2.85	0.06	3223	0.193	(0.18))[3]
May 1983	5.16	0.47	3360	1.579	0.198		3.62	0.17	305%	5.201	1.850
						Hatched Fall 1981					
July 1982							4.64	a 37	22035	8.153	(5.263)[2]
Sept 1982							5.28	0.48	17335	8.321	2.165

[1] Productivity = Mean density between sampling periods x weight increment per individual between sampling periods.
[2] Extrapolated between May 1983 and July 1982.
[3] Assumes no mortality between hatching and indicated period.

considered, each of these species appeared to differ from the others in terms of habitat selection and utilization. In cases where species showed somewhat similar habitat preferences, e.g. Photis fischmanni and Protomedia grandimana, there were spatial differences in location of maximum densities (Table 17). These spatial differences most likely reflect differences in environmental conditions that were not considered in the analyses.

Orchomene lepidula, Harpinia gurjanovae, Protomedia grandimana, Byblis gaimardi and Photis fischmanni were all abundant in shallow water. Byblis gaimardi appeared to be a selective deposit feeder, whereas Photis fischmanni was not. Protomedia grandimana was also a shallow water non-selective deposit feeder; however, it was most abundant off the south coast of St. Lawrence Island. The other shallow water species were relatively rare in this area. Orchomene lepidula fed on substrate and crustacea. Harpinia gurjanovae fed on crustacea and meiofauna.

Ampelisca macrocephala appeared to be the most successful amphipod species in the study area. Its habitat appeared to be only slightly different from that of its congener A. eschrichti. A. eschrichti was nowhere very abundant. Protomedia fasciata was also a non-selective deposit feeder, not apparently restricted to any particular depth. Unlike Ampelisca macrocephala, this species was most abundant in poorly sorted substrates having a low caloric content (Table 17).

There appears to be little niche overlap among the most common amphipod species in the study area.

In the Chirikof Basin, gray whales appear to feed only in areas with a high biomass of amphipods (Thomson and Martin, this report). Areas of the Chirikof Basin that had a high biomass of amphipods were dominated by large (lengths to 30 mm) ampeliscid amphipods (Table 18). Areas that had a low biomass of amphipods in samples were dominated by other taxa and the most abundant amphipods were smaller (to 15 mm) species such as Protomedia and Ischyrocerus (Table 18). Areas contiguous to St. Lawrence Island showed a high density of both ampeliscid amphipods and other amphipod species. Thus, gray whale feeding grounds in the Chirikof Basin are dominated by large

Table 17. Summary of habitat preferences and food habits of the 10 dominant amphipod species found in the Chirikof Basin and near St. Lawrence Island.

	Substrate							
	Grain size	Sorting	Caloric content	Carbon content	C/N ratio	Depth	Feeding	Location of maximum density
Ampelisca macrocephala	medium (2.9 Φ)	well sorted	high				sediment, non-selective	Least abundant SE Cape nearshore
Ampelisca eschrichti	medium (2.9 Φ)	poorly sorted		high	low		sediment, non-selective	SE Cape offshore
Byblis gaimardi	medium (3.1 Φ)		high			shallow	sediment, selective	West coast, St. Lawrence Island
Photis fischmanni	coarse	well sorted	high		low	shallow	sediment	SE Cape nearshore
Protomedia grandimana		well sorted				shallow	sediment	South coast, St. Lawrence Island
Protomedia fasciata	coarse	poorly sorted	low				sediment	Chirikof Basin
Harpinia gurjanovae	fine	well sorted	high			shallow	carnivorous	SE Cape nearshore
Grandiphoxus acanthinus		well sorted			high		not examined	None
Pontoporeia femorata	medium (3 Φ)						sediment	South coast, SE Cape offshore
Orchomene lepidula		well sorted	high	low	high	shallow	sediment/carnivorous	SE Cape nearshore

Table 18. Percent of total amphipod density contributed by the dominant species at stations with a similar biomass of amphipods in the Chirikof Basin. Percentages are shown only where the indicated specks are dominant.

Range of Amphipod Biomass Station	*Ampelisca macrocephala*	*Ampelisca eschrichti*	*Ampelisca birulai*	*Byblis gaimardi*	*Protomedia fasciata*	*Protomedia grandimana*	*Ischyrocerus* sp.	*Photis fischmanni*	*Harpinia gurjanovae*
0-10 g/m^2									
1A				22	25	18			
1B	35						25	10	
4A					25	68			
4B						48			19
4C						91			
5B						43			
7A						55	15		
10-100 g/m^2									
3A					71	11			
3B					30	15	7		
2B	55			9	13	10			
3C	12				11	46			
>100 g/m^2									
2A	51		16	21					
5A	90								
6A	49					10			
6B	80	5							
7B	47			23					

amphipods. Smaller species appear to be excluded by habitat requirements and/or competition. Over most of their feeding range in the study area, gray whales are presented with a concentrated food source in the form of large amphipods.

Productivity

Differences in productivity among the species listed in Table 19 are due primarily to differences in life cycle. Generally, longer lived species will have a lower productivity than short lived species (Birklund 1977; Wildish and Peer 1981). The productivity of Photis fischmanni is similar to that of Ampelisca brevicornis and Pontoporeia femorata. All three species have a life span of one year. Corophium insidiosum produces 5-5.6 generations per year (Casablanca 1975) and has a very high productivity. The relatively low productivity of Ampelisca macrocephala in the Bering Sea is a reflection of its long life span.

One of the aims of this study was to determine the amount of food available to gray whales and food consumption by gray whales in relation to food availability. The mean biomass of amphipods in all areas utilized by gray whales in the Chirikof Basin was 132.8 ± 96.5 g/m2 (n = 37, includes 0.3 g/m2 of amphipod parts that could not be identified, Thomson and Martin, this report). Most of the biomass was accounted for by animals that reach a length of more than 20 mm (Table 20).

Application of the annual productivity to biomass ratio of 1.8 determined for Ampelisca macrocephala to the biomass of these large amphipods (124.9 g/m^2) yields a productivity of 224.8 g/m^2. Application of the productivity to biomass ratio of 3.7 determined for Photis fischmanni to the smallest class of amphipods yields a productivity of 7.4 g/m^2. Productivity of an intermediate-sized amphipod was not determined, so a productivity to biomass ratio intermediate between that of large and small amphipods (2.75) was used. In this manner, productivity of the intermediate size class of amphipods was estimated at 15.4 g/m2. Total productivity of the 132.5 g/m^2 of amphipods listed above was thus estimated at 246.6 g/m^2. The annual productivity to biomass ratio of all amphipods in the Chirikof Basin was

Table 19. Productivity of benthic amphipod species, the benthos as a whole, and the zooplankton from the temperate Atlantic and Bering Sea.

Location/species	Productivity/ Biomass ratio	Time span considered	Reference
Temperate Atlantic			
Pontoporeia femorata	3.6-4.8	1 year	Wildish and Peer 1981
Corophium insidiosum	2-5	5 months	Birklund 1977
Corophium volutator	3-4	15 months	Birklund 1977
Corophium insidiosum	12-19.5	1 year	Casablanca 1975
Ampelisca brevicornis	3.4-4.4	1 year	Klein et al. 1975
Ampelisca sp.	5	1 year	Sanders 1956
Ampelisca brevicornis	3.4	1 year	Sheader 1977
Zooplankton (North Sea)	7	1 year	Crisp 1975
Benthos (North Sea)	3	1 year	Crisp 1975
Northern Bering Sea			
Photis fischmanni	3.7	1 year	This report
Ampelisca macrocephala	1.8	1 year	This report
Zooplankton	4.2	1 year	Ikeda and Motoda 1979
Macoma calcarea	0.3	1 year	Stoker 1978

Table 20. Mean biomass of amphipod species according to maximum size attained in that part of the Chirikof Basin dominated by amphipods.

Small <10 mm	g/m^2	Intermediate 10-20 mm	g/m^2	Large >20 mm	g/m^2
Phoxocephalids	1.3	Boeckosimus plautus	0.3	Ampelisca birulai	1.8
Ischyrocerus sp.	0.1	Hippomedon granulosus	0.2	A. eschrichti	14.4
Photis fischmanni	0.3	Melita spp.	0.1	A. macrocephala	85.5
Corophium sp.	0.3	Orchomene lepidula	0.7	Byblis gaimardi	19.7
		Pontoporeia femorata	1.3	Anonyx nugax	1.2
		Protomedia spp.	2.5	Lembos arcticus	1.9
		Others	0.5	Wecomedon similis	0.4
Total	2.0		5.6		124.9

estimated to be 1.9 in 1982. This estimate was used by Thomson and Martin (this report) to assess the food available to gray whales relative to their requirements in the Chirikof Basin.

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Appendix Table 1. Summary of samples collected and work performed in the Chirikof Basin near St. Lawrence Island in July and September 1982.

Area	Benthic samples Station (no. samples)[1]	No. of sediment samples[4]	Amphipod feeding No. animals	Video tows Tow no. (h)
Central Basin				
1A	407(5)V	1		
1B	263(5)V	1	17	
4A	283(5)V	1	27	
4B	292(5)V	1	15	
4C	417(3)V	1		
3A	269(5)V	1		
3B	276(5)V	1	39	
3C	423(5)V	1		
2A	246(5)V	1	36	
2B	257 (2)V	1		
5A	232(5)V	1	15	
5B	240(5)V	1		
6A	219(5)V	1		
6B	225(5)V	1		
7A	199(5)V	1		
7B	207 (5)V	1	43	
St. Lawrence Island				
South Coast				
10C	438(5)V			111(.75)
10D	446(5)V			113(.5)
Boxer Bay				
10E	455(5)V		45	115(.18)
West Coast				
8A				l(l)
8B				3(1.9)
8C nearshore	101 (5)V			7(1)
off shore	92(5)V			11(1)
8D	113(4)V			14(1.9)
8E	125(5)A		45	
southeast cape				
9A off shore	136(5)V		46	16(1.7)
	179(5)V			19(2.1)
nearshore	152(8)[2]A		171	
	158(15)A			
	166(30)A			
	464(30)[2]A			
	475(10)[2]A			
	464(30)[3]P			

1 V.Van Veen Grab, A = Diver-operated airlift, P = Ponar Grab.
2 50% of samples taken inside and 50% taken outside f urrows.
3 Winter sampling in January, March and May 1983.
4 Grain size, caloric content, carbon and nitrogen content.

Appendix Table 2. Level of effort and numbers of samples collected and analyzed from the Chirikof Basin and the vicinity of St. Lawrence Island in July and September 1982.

Days on site		31
Days worked		24*
Video tows	No. tows	27
	Hours towed	26
Dives	No.	40
	Diver hours	39.5
Benthic Samples	Van Veen Grab	114
	Airlift Samples	98
	Ponar grab (winter)	30
	Total	242
Sediment samples	Grain size	38
	Caloric content	43
	Carbon nitrogen content	32
	Chlorophyll content	10
	Surface detritus	19
Amphipods	Stomach contents (no. animals)	499
	Caloric value	30

* 7 days were lost due to bad weather in September.