FEEDING ECOLOGY OF GRAY WHALES
IN THE CHIRIKOF BASIN

by

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ABSTRACT

In July and September 1982, morphology, size and distribution of bottom features made in the Chirikof Basin and near St. Lawrence Island by feeding gray whales were investigated with side-scan sonar and by divers. Distribution and abundance of gray whale prey species and physical characteristics of the substrate associated with the features were also investigated.

Within the American Chirikof Basin, gray whales fed extensively only in areas that had a high biomass of amphipods and a substrate composed of fine sand with little gravel. Within their foraging grounds, the percent of bottom disturbed and mean size of feeding features was higher in shallow water than in deeper water, and density of feeding features was positively correlated with biomass of amphipods.

Whales apparently fad either by suction furrowing of the bottom to a depth of 2 cm or stationary suctioning of shallow pits to a depth of 10 cm. These features encompassed mean areas of 18 m2 and 13 m2, respectively. The whales removed amphipods but. little else. Amphipods 5 mm or less in length may not be retained by the baleen but these comprise less than 5% of biomass of amphipods.

Daily consumption of amphipods was estimated in two ways--from behavioral data and characteristics of feeding features, and on the basis of theoretical energy requirements. (1) Whales performing 198 feeding dives per

day in July and 164/d in September (Würsig et al. , this report) would consume an average 321 kg/d wet weight if feeding on average densities of amphipods (133 g/m2), and 678 kg/d if they selectively fed in areas containing 250 g/m2 of amphipods. The latter biomass is equivalent to the mean biomass in the 25% of benthic samples containing the most benthos. Evidence is presented showing that gray whales may select areas with high amphipod biomass in which to feed. (2) Estimated energy requirements for active metabolism and food storage for winter are similar, ranging from 445 kg/d assuming no energy storage for migration to 763 kg/d assuming that all energy needed for migration is stored during summer. About 2500 gray whales are estimated to summer in the Chirikof Basin, and an additional 9000 may migrate through it. Assuming that consumption is 650 kg/d/whale, whales resident in and migrating through the Chirikof Basin would consume about 7.5% of the standing crop of benthic amphipods each year, or about 4% of their productivity. However, since the whales apparently select areas with a higher than average biomass of amphipods in which to feed and apparently must do so in order to meet energetic requirements, not all of the apparent feeding habitat in the Chirikof Basin is of use to the whales. The major consideration, with regards to industrial development, would be exclusion of whales from areas of prime feeding habitat.

INTRODUCTION

The present population of gray whales is estimated to be about 17,600 to 18,000 animals with most of these summering in the Bering Sea and areas to the north (Reilly 1981; Reilly et al. 1983; Rugh in press). During their stay on these summer foraging grounds, the whales must store enough energy to carry them through their stay on their winter grounds off Baja California and for all or at least part of their long southward and northward migrations.

The gray whale is the only baleen whale to feed primarily on benthic animals. In northern seas, benthic amphipods form the principal part of the diet of gray whales (see Nerini in press for a review of feeding ecology).

This chapter presents information on the amount of food consumed per dive by gray whales and integrates these results with observations of feeding behavior presented by Würsig et al. (this report) to estimate the daily rate of food consumption. This estimate is compared to estimates derived through consideration of the energetic requirements of gray whales. These estimates are, in turn, integrated with estimates of the abundance of whales (Miller, this report) and the abundance, distribution and productivity of principal prey species (Thomson, this report) to yield an estimate of the impact that these whales have on their food resources and to assess the carrying capacity of their summer habitat in the Chirikof Basin.

MATERIALS AND METHODS

Study Design

Sampling was conducted from the NOAA ships DISCOVERER (September) and MILLER FREEMAN (July). Sixteen stations were occupied in the Chirikof Basin and 12 stations in the vicinity of St. Lawrence Island (Figs. 1 to 4). At each station, side-scan sonar tows were made to detect the presence of bottom features made by feeding gray whales. Benthic samples were taken at each station to provide descriptions of the quantity and quality of benthic animals present, the mean grain size, and the caloric, carbon and nitrogen

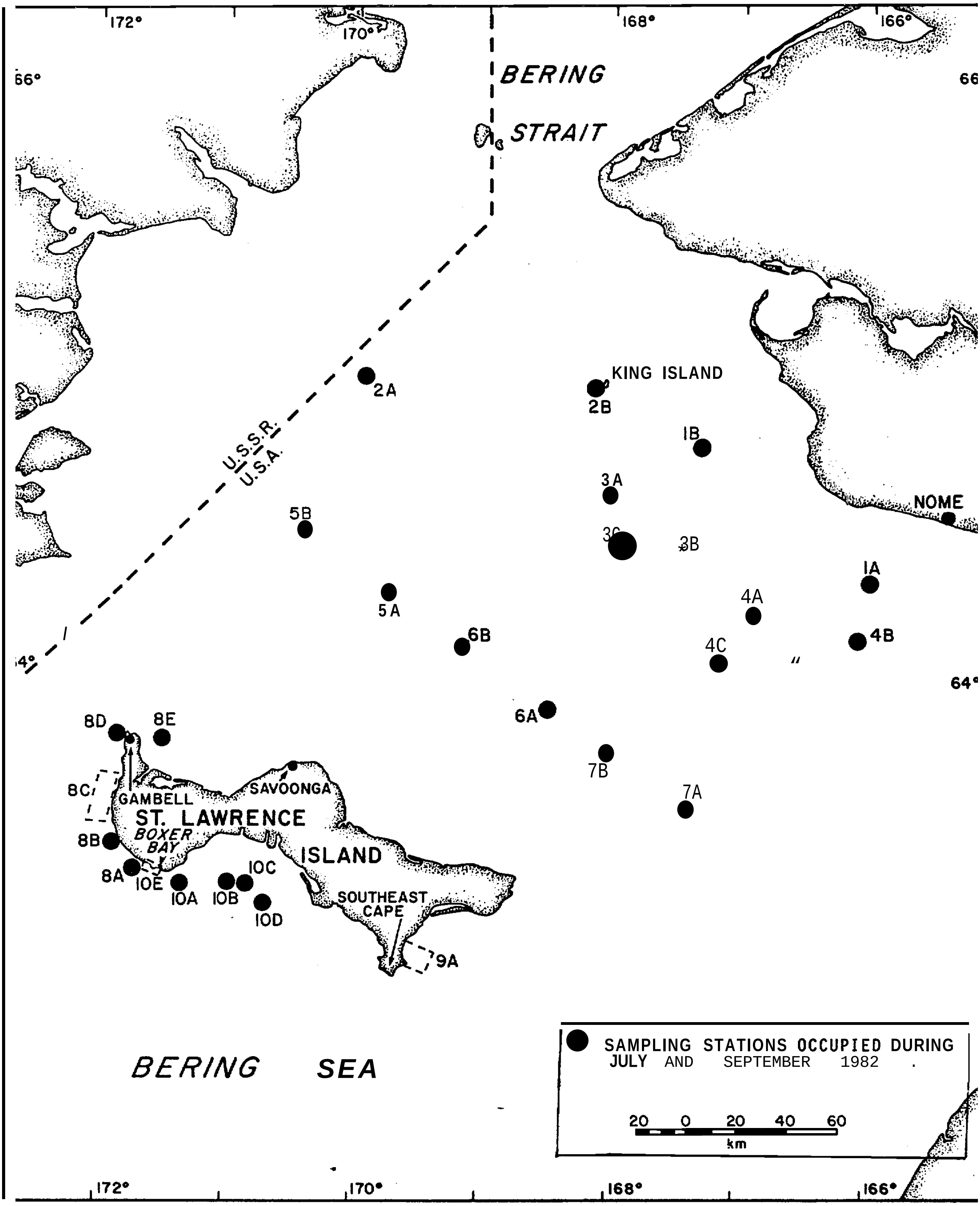


FIGURE 1. Sampling stations in the Chirikof Basin and off *St.* Lawrence Island occupied during July and September 1982.

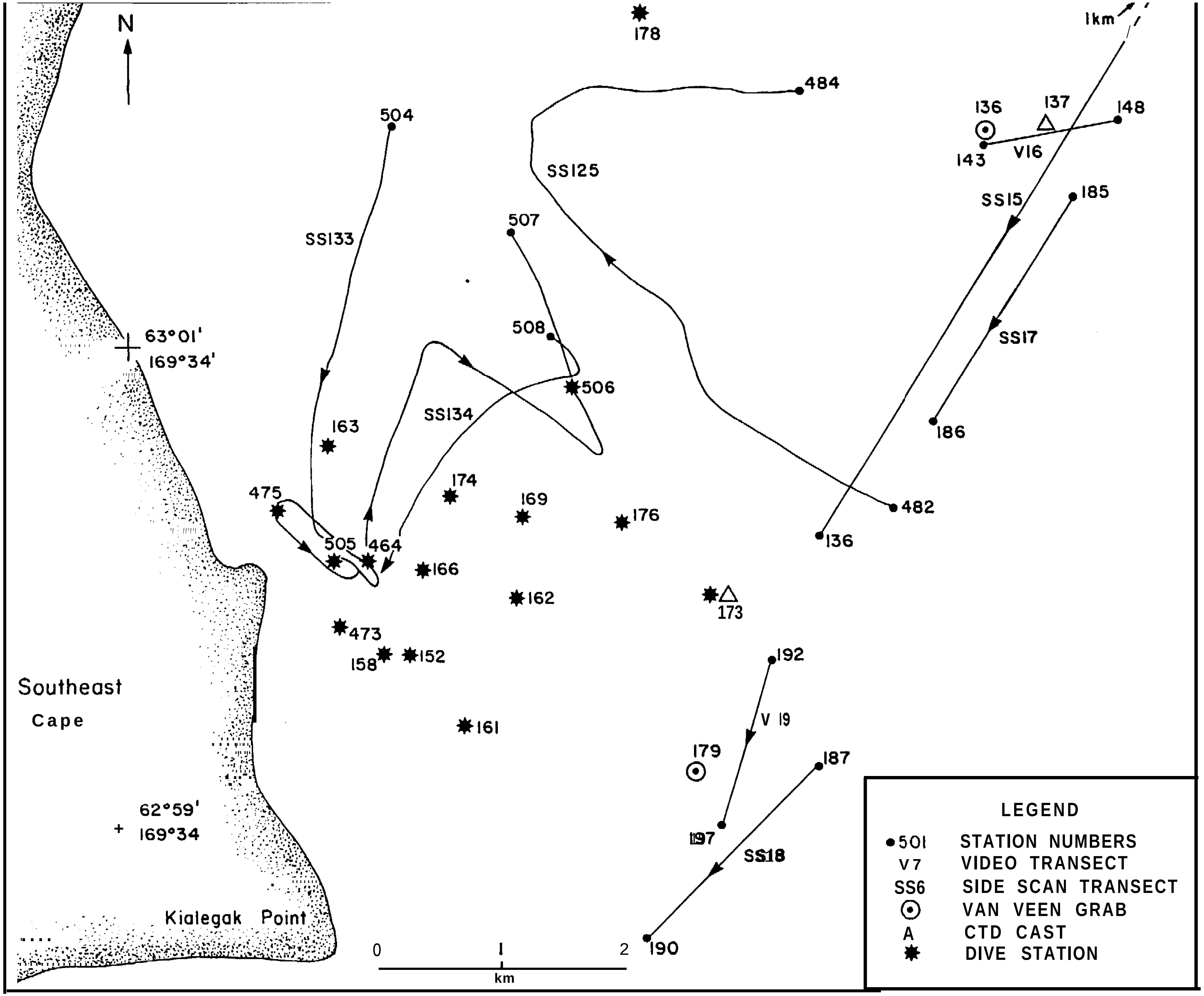


FIGURE 2. Sampling locations off Southeast Cape, St. Lawrence Island

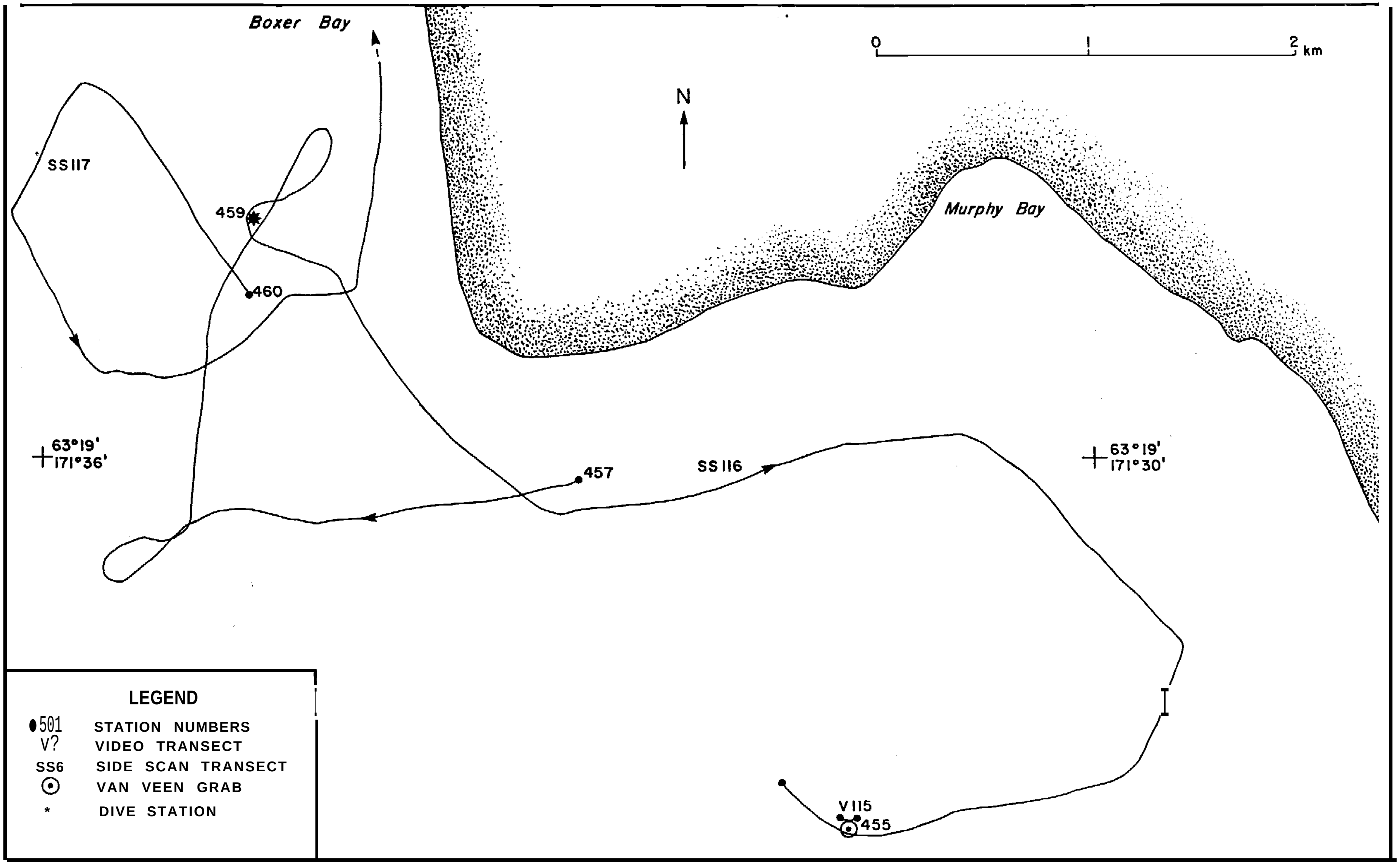


FIGURE 3. Sampling locations in Boxer Bay, St. Lawrence Island,

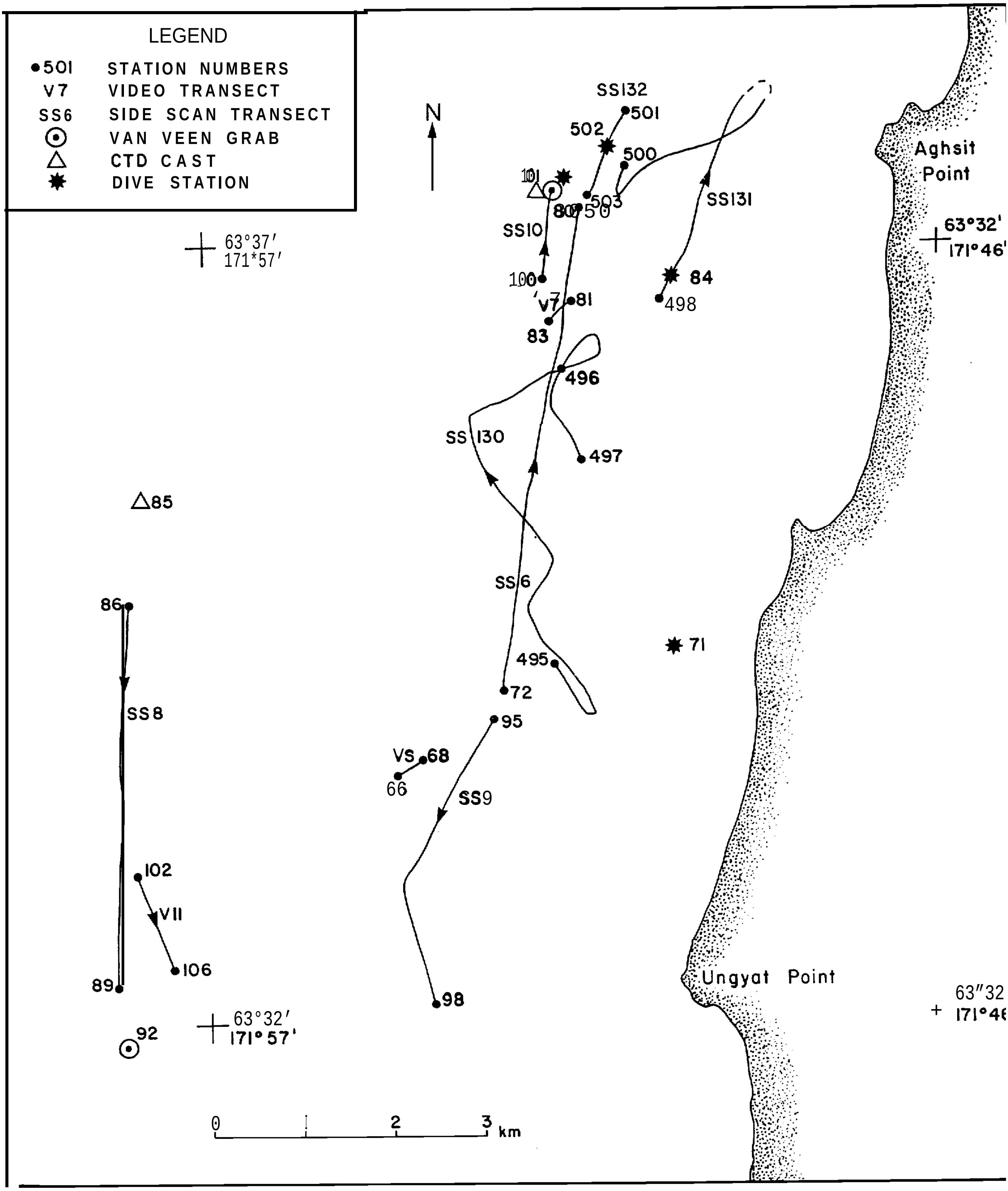


FIGURE 4. Sampling location in area 8c off the west coast of St. Lawrence Island.

content of the substrate. A video camera was also towed in an attempt to recognize bottom features indicative of feeding and provide greater coverage for descriptions of benthic habitat. Observations of the feeding behavior and distribution of whales were also made at each station (Würsig et al., Miller this report). In shallow water, divers investigated and sampled features made by feeding whales.

The types and amounts of work performed in each area are summarized in Table 1. Details of procedures and methods used in benthic sampling with grab, airlift and video camera are described by Thomson (this report).

Table 1. Level of effort and work performed in the Chirikof Basin and nearshore areas off St. Lawrence Island in July and September 1982.

			St. Lawrence Island			
		Chirikof Basin	West Coast	South Coast	Southeast Cape	Total
stations Occupied		16	4	5	3	28
side-scan sonar	- No. tows	16	9	6	8	39
	- km	37.1	30.7	29.7	66.9	164.4
Benthic Samples	- van Veen grab samples	75	14	15	10	114
	- Airlift samples				93	93
	- Sediment samples	16	2	3	16	37
Diving Operations	- No. dives		7	1	32	40
	- Diver hours		4.8	1	33.7	39.5

Side-Scan Sonar

The side- scan sonar was generally towed from the ships. In shallow water it was deployed from a small boat. When towed from the small boat an anchor and float were used to mark areas showing evidence of feeding activity by gray whales. A Klein Associates 500 kHz side-scan sonar with a Model 521 two channel recorder was used routinely. At five stations an EG and G Model 259-4 100 kHz side-scan sonar unit was used instead of the 500 kHz unit.

Comparison of features observed on the bottom by divers and features detected by the side-scan sonar indicates that hard objects as thin as 2 cm (light anchor chain) were resolved, as were soft objects as small as 5 cm (mounds and depressions).

The side-scan unit routinely was towed for 30 min at each station. In shallow nearshore areas tows were of two or more hours duration. These long tows were used to look for and mark specific features and areas to be investigated by divers.

The ship's position, speed, heading, and water depth were recorded for each tow. The side-scan record was marked at 2-rein intervals. Later, the total number of depressions in the bottom attributable to feeding activities of gray whales was recorded for 1 or 2-rein segments, coded and entered into a computer.

From each of 18 transects, we digitized the feature boundaries from five 1- or 2-rein segments of the side-scan chart record. Segments ware l-rein long when many bottom features were evident, and 2-rein long when few were evident. The digitized feature shapes were then corrected for ship speed and height of the sonar above bottom, and feature areas were computed. This was done with a Hewlett Packard HP9874A digitizer in conjunction with an HP9845B computer. Communication between machines was accomplished with a system 45 1/0 ROM and an HP-IB interface. Digitizing and data management software was developed by LGL for this project. The area was calculated from the digitized data using a modified trapezoid rule (see Loomis 1975). The plotting was completed on a HP-9872A line plotter. Because of the irregularities of digitizing, a 3-point spatial. smoothing filter was applied to the data (see Riply 1981). Only recordings made by the 500 kHz unit were digitized or used to estimate size of feeding features. Limitations of the side-scan sonar for this kind of work are discussed by Johnson et al. (1983).

Temperature

Temperature measurements were made with a Plessy Environmental Systems Model 9041 CTD.

Underwater Observations and Sampling

A team of two divers investigated bottom features in areas where whales were observed to be feeding and in areas marked by a small boat towing the side-scan sonar. Dimensions and morphology of features were measured and recorded in waterproof notebooks. Faunal observations were also made and recorded during a debriefing session after each dive. Features and the surrounding area were photographed with a Nikonos camera and strobe. Five diver-operated airlift samples were taken inside and five outside each of five features. Samples of the substrate were also taken for later analysis of grain size, caloric content, and carbon and nitrogen content. Details of airlift sampling, processing of benthic samples, and laboratory methods are described by Thomson (this report).

Plankton Tows

Eight horizontal plankton tows were made with a 1/2 m #6 mesh net deployed from the ship's launch. These tows were made through the mud plumes emanating from the mouths of feeding gray whales.

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 AND DISCUSSION

Description and Distribution of Gray Whale Feeding Features

Morphology and Size of Bottom Features Made by a Feeding Whale

Nerini (in press) discussus the feeding mechanisms of gray whales. They apparently may feed in two different ways. Gigi, a captive gray whale, rolled on her side and--with her head 10-20 cm above the bottom--cleared a 30-50 cm wide swath through the squid lying on the bottom (Ray and Schevill 1974). Hudnall (1981 cited in Nerini in press) also describes a gray whale feeding on its side and sweeping along the bottom, in this case leaving depressions approximately the size of its head. Nerini (in press) believes that feeding whales suck up the surface layer of sediment leaving a series of oblong mouth-sized depressions. She describes these types of features from the Chirikof Basin.

In the following section we describe two different types of features resulting from gray whale feeding: pits and furrows. The pits were as described by Nerini (in press). Furrows were apparently made as described by Ray and Schevill (1974) with the whale sucking while in motion and leaving gaps when expelling sediment. A feeding event is defined as the disturbance made on the bottom by one whale on one dive, and usually consists of a series of features made on the bottom by the whale. As discussed below, a furrowing feeding event may be made up of a series of furrows.

Furrows.--In 13 m of water off Southeast Cape, St. Lawrence Island, a float and anchor marked a location where two whales had been feeding continuously for 2 h in July. In July, whales made approximately 198 feeding dives/day (Würsig et al., this report). This would represent approximately 33 dives in the small area investigated during the two hour period. The whales may also have been feeding before and after the period of observation. A dive was made 6 h after the float was dropped. The sea floor at this location was marred by long narrow furrows, often with short gaps between visible continuations of the feature. Although shallow, these furrows were easily recognized because of the disruption to the “mat*’ of amphipod tubes that covered the bottom. Density of furrows was so high that it was not possible to follow an individual feeding event composed of these furrows for any great distance. It was possible to isolate and measure 27 discrete portions of furrows but it was not possible to determine how many of these were made during one feeding dive. Discrete portions of the furrows (features) were separated from other furrows by short gaps. Mean length of all furrows measured, from one gap to the next, was 4.9 ± s.d. 3.7 m (n = 27). Mean width was 47.6 ± 34 cm. Depth of all features was 1 to 2 cm. It was possible to follow one feature (furrows and gaps) for 14 m and another for 13.5 m. None of the others could be followed this far, largely because of overlap between feeding features. Gaps between continuations of furrows were 25-50 cm wide.

The side-scan sonar records made in July did show what appeared to be complete furrows in areas not heavily utilized by whales. It was not possible to distinguish individual furrows in areas heavily utilized by whales. The furrows recorded by the side-scan sonar also showed gaps, and the furrows were between 25 and 50 cm in width (Fig. 5a).

The mean total length of the seven isolated furrows was 46 ● s.d 12 m (Table 2.) This distance is consistent with Wursig et al.'s (this volume) surface observations of mean horizontal distance traveled underwater by a feeding whale in July: 100 ± s.d. 46 m (n = 24). The mean furrow length not including gaps was 41 ± 10 m. Mead width of furrows measured by divers off Southeast Cape, St. Lawrence Island, in July (42.6 ± 34.1 cm) was used to calculate the mean area encompassed by these furrow. Mean area was 18 ± 5 m^2 for the seven furrows.

Table 2. Total length, total length of gaps and area encompassed by gray whales' feeding furrows recorded by side-scan sonar in the Chirikof Basin. Mean width of furrows recorded by divers was used to compute area.

Station	Total length (m)	Total length of gaps (m)	Furrow length (m)	Area (m^2)
2A	67	7	60	26
2A	54	15	39	17
2A	49	0	49	21
2A	38	4	34	14
2B	41	3	38	16
2B	37	0	37	16
2B	34	3	31	13

Pits.--Pits are defined here as shallow depressions in the sea floor. These were noted by divers and recorded by side-scan sonar in most areas investigated. Again, density of pits was so high in the shallow waters off Southeast Cape that isolation of single feeding events by divers was impossible. It was possible to measure individual features composed of a series of pits and individual pits.

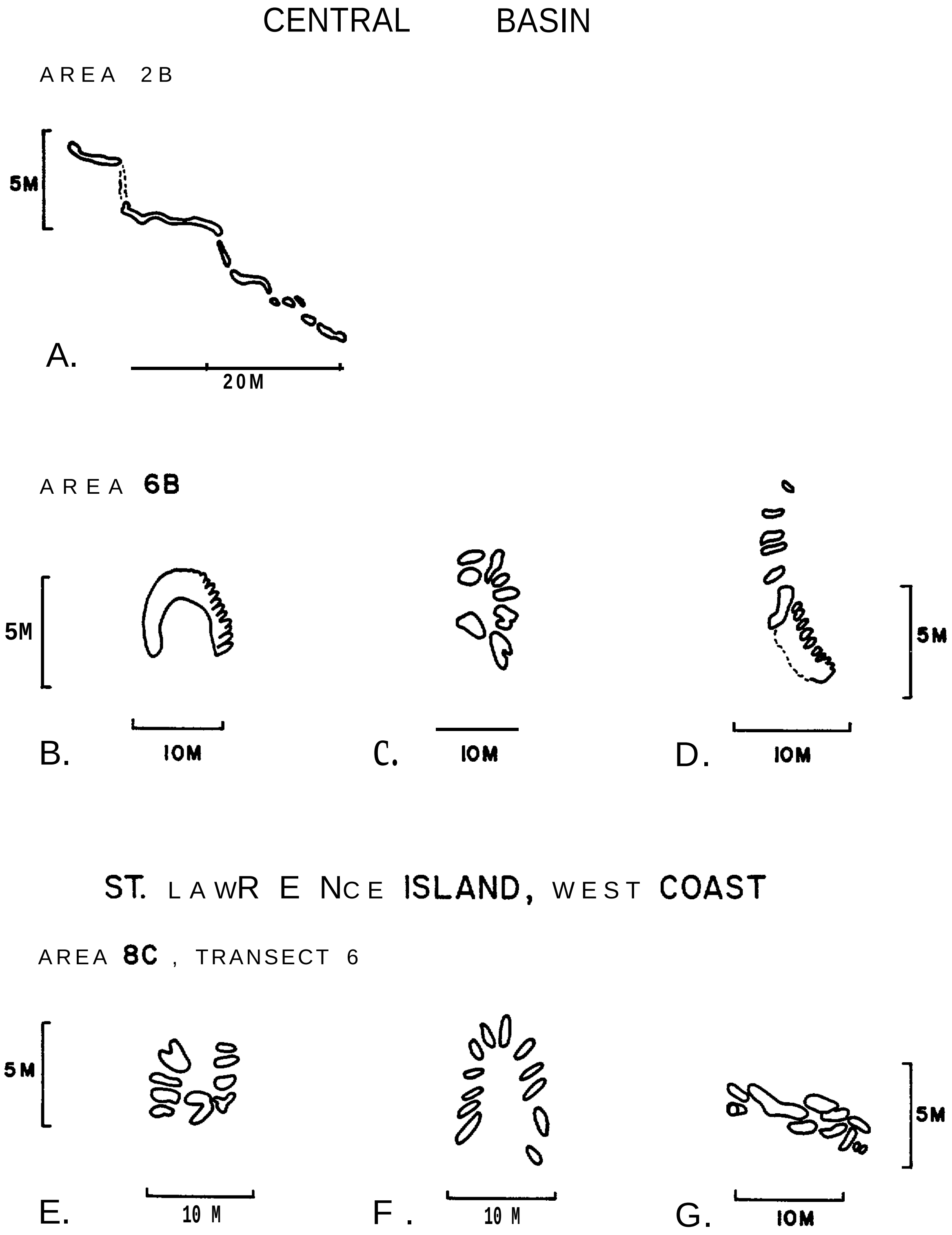


FIGURE 5. Individual bottom features recorded by 500 kHz side scan sonar and attributed to feeding activities of gray whales.

Individual isolated feeding events were recorded elsewhere by side-scan sonar (Figs. 5b to 5g). The whale's mode of feeding in this case was apparently as described by Nerini (in press). While on its side, the whale appears to have taken individual suction 'bites' of the substrate. These ‘bites^t may be regularly spaced in a semicircle, random in a small area, something between the previous two, or so close together that individual 'bites' are not recognizable (Figs. 5b to 5g). Mean total area of these is given in Table 3.

Table 3. Mean area of gray whale ‘bites’ into substrate at six feeding-feature areas in the Central Basin and off the west coast of St. Lawrence Island (see Fig. 5).

Feature No.[1]	Total Area (m^2)	No. 'Bites'	Mean Area of 'Bite' (m^2)
B	17.0		
C	11.0	9	1*2
D	10*2	52	0.8
E	12.4	10	1.2
F	11.3	12	0.9
G	15.5	10[2]	1.2[1]

[1] See Figure 5.

[2] The largest pits are not included in the calculation.

Mean total area of individual feeding features was 12.9 + s.d. 2.7 m^2 (n = 6) and mean area of individual ‘bites^t that could be resolved was 1.08 m^2 (n = 46) with a range of 0.75 to 2 m^2.

In September, divers measured 49 features in the heavily pitted region off Southeast Cape (Fig. 6). Although features up to 28.5 m^2 in area were recorded, mean area of all features was 2.9 ± s.d. 5.5 m^2 (n = 49). At this time depth of all features was on the order of 10 cm. The features were close to each other, and often only a few centimetres separated them. Many features appeared to cross and merge with each other. The divers *were* unable to identify individual feeding events.

In September over the shallow waters off Southeast Cape, some features noted on the side-scan record could be identified as individual feeding events. Some showed elevations within the feature similar to ‘coalesced bites' observed in deeper water. Mean area of eight of these features was

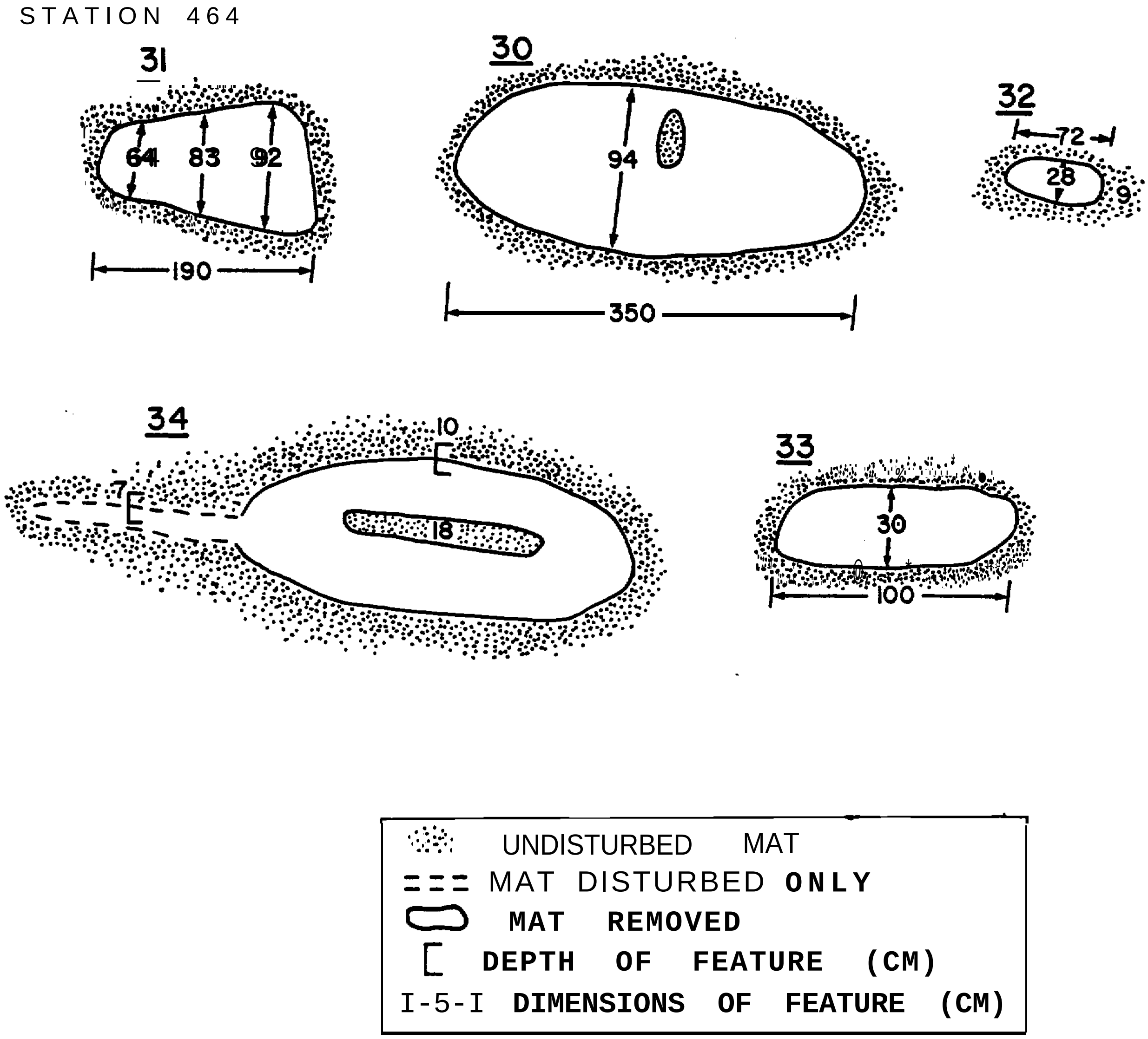


FIGURE 6. Features observed by divers off Southeast Cape, St. Lawrence Island, at depths 11 to 13 m in September 1982.

STATION 475

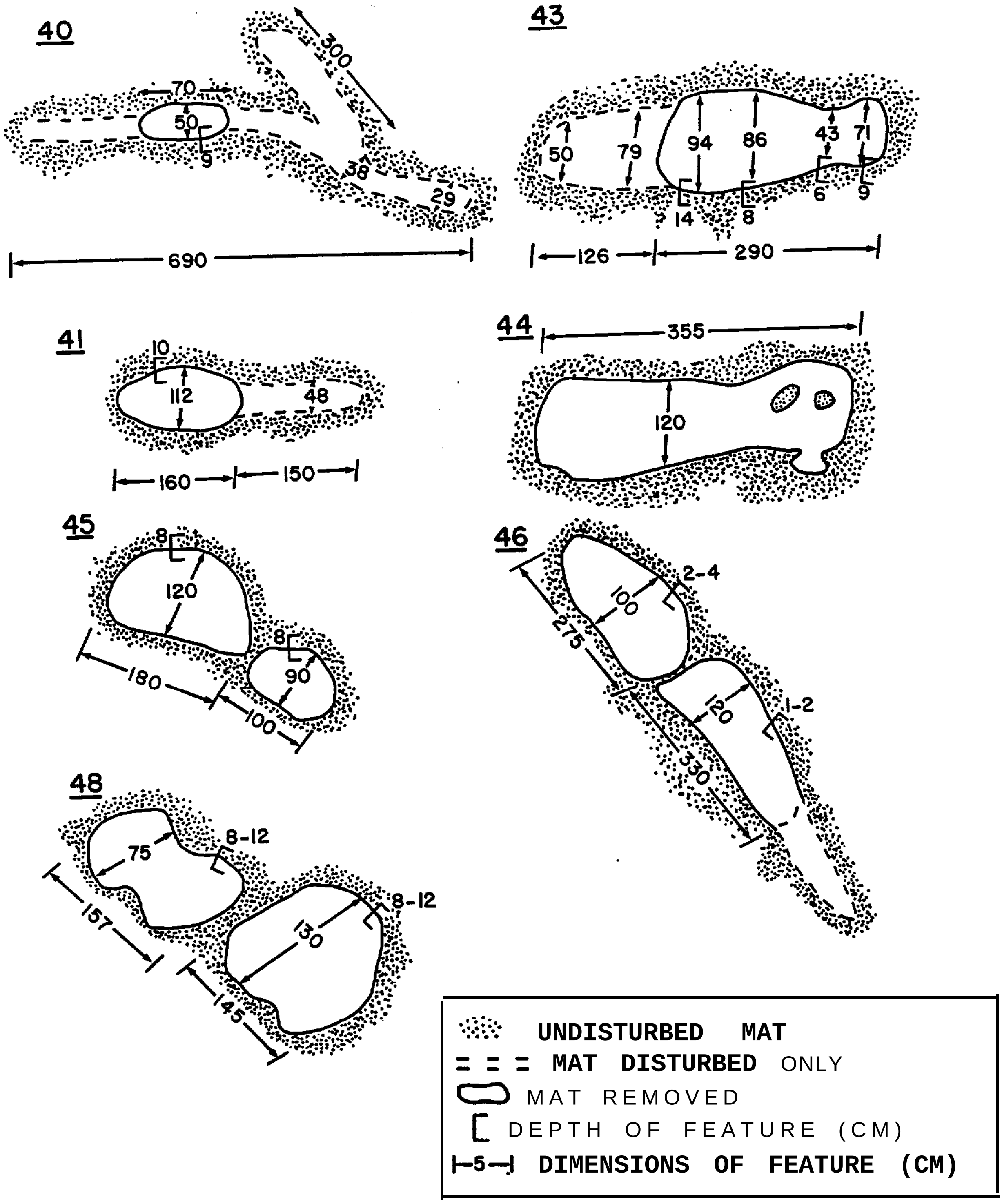
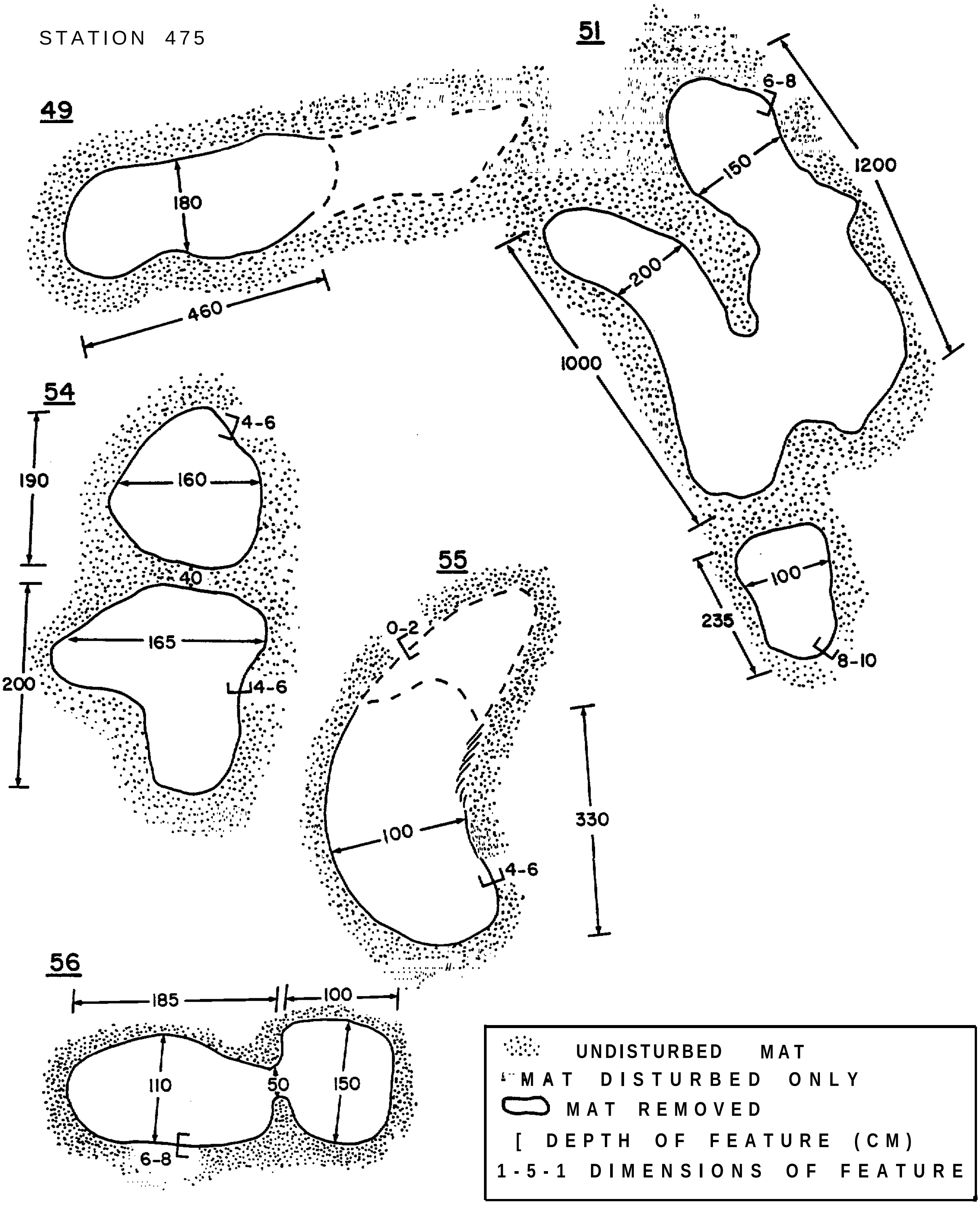


FIGURE 6. Continued



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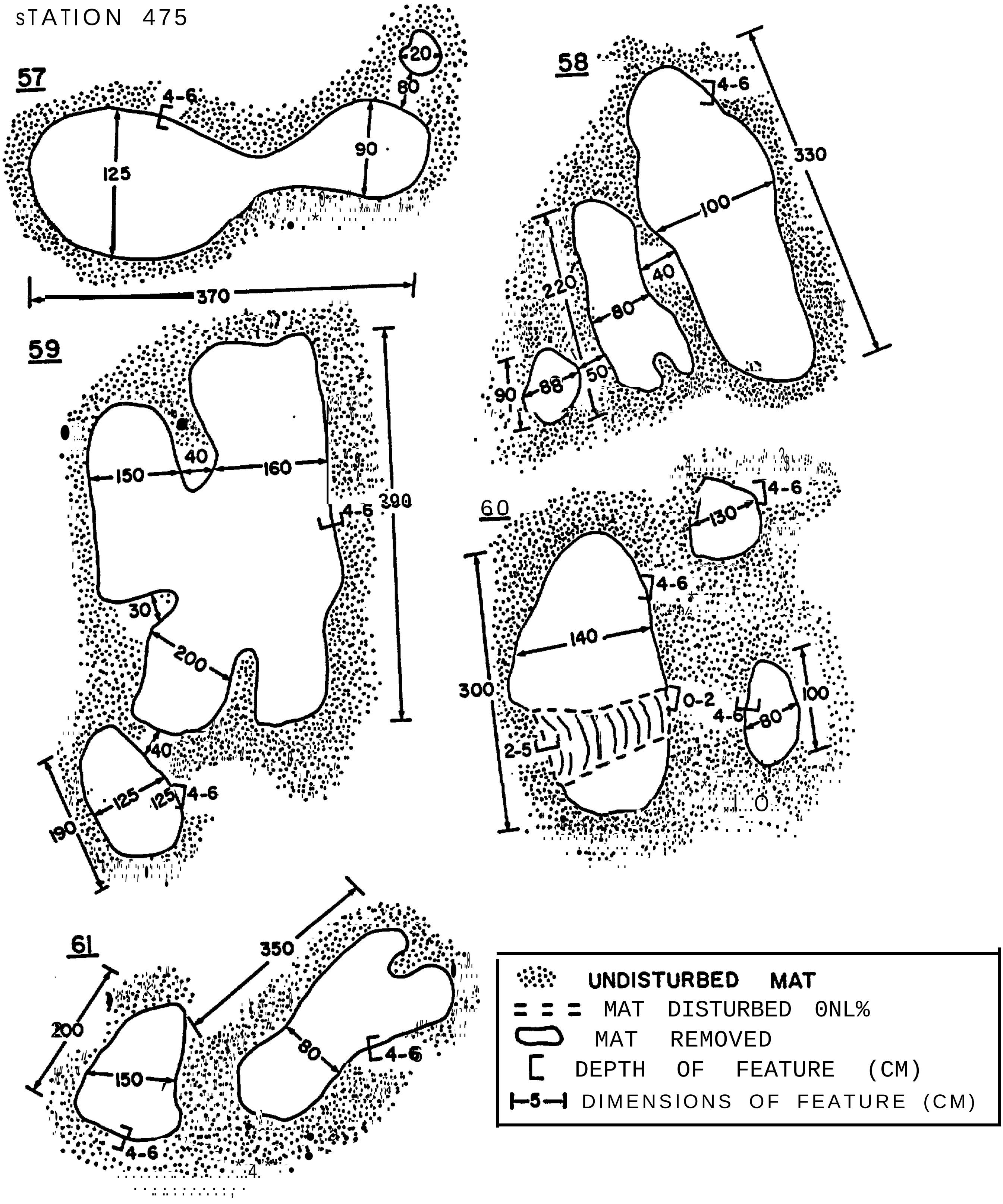

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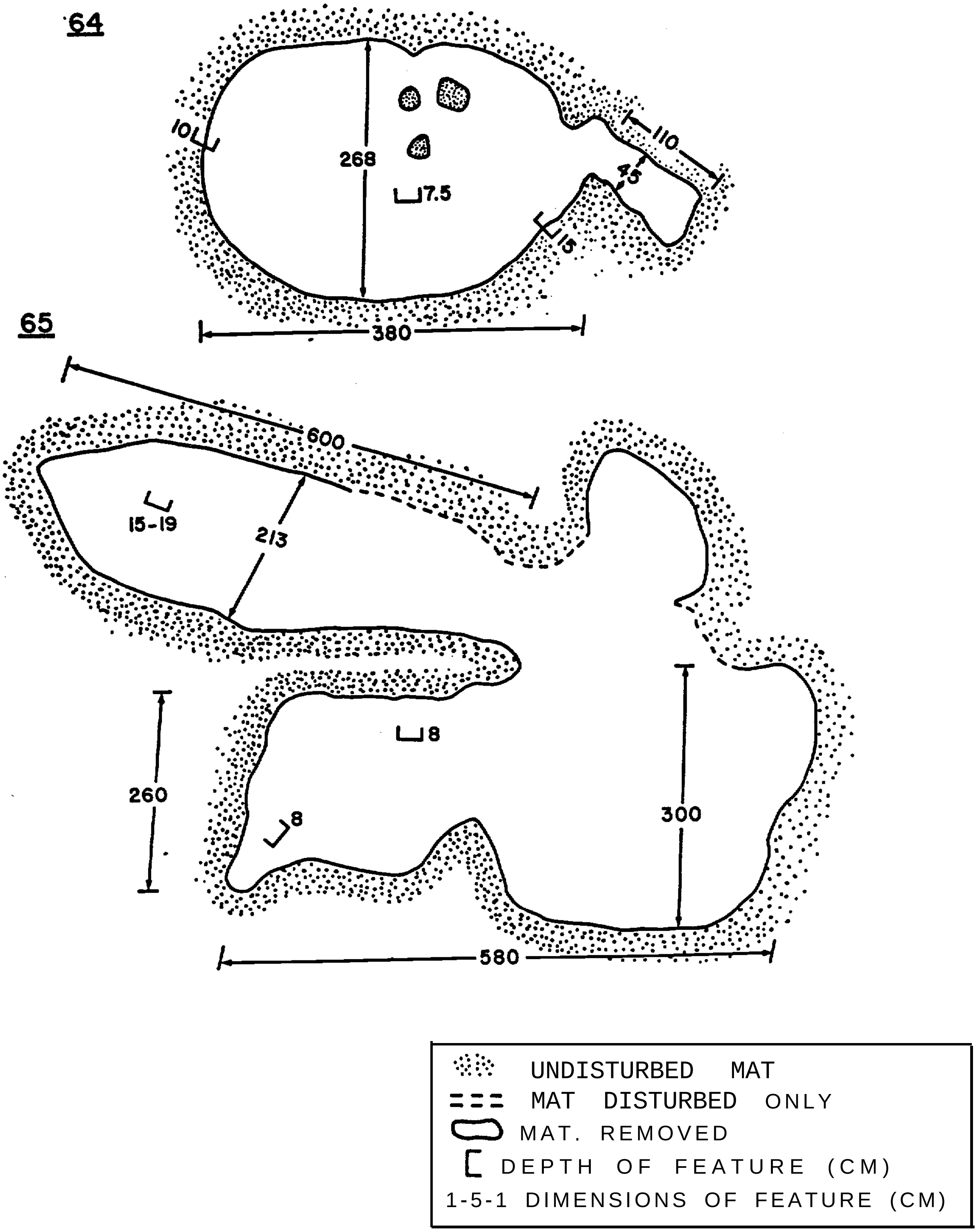

Figure 6. Continued

16.9 ± s.d. 3.3 m^2. At this time, however, most feeding features were so concentrated that individual feeding events were not discernible. This was especially evident on transect 133 made in 11 to 13 m off Southeast Cape in September (Fig. 7). As the area of intense pitting was approached, apparent size of features became larger (Table 4).

Table 4. Mean size of whale 'bite' feeding-feature areas in relation to 'percent of bottom affected for five segments along transect 133 (see Fig. 7).

Segment No.	% of Bottom Affected	Mean ± s.d. feature area (m^2)
A	2.2	4.3* 2.0
B	9.4	7.4* 3.6
C	36.4	20.7* 34.7
D	36.4	34.7 *38.3
E	26.9	15.5* 13.9

The large apparent size of some of the features in the heavily pitted areas was due to the difficulty in recognizing pit boundaries on the side-scan record. There was a large discrepancy between the size of features recorded by divers and by the side-scan sonar (Figs. 8 and 9). Inspection of the seabed by divers revealed that the feeding features made by the whales were convoluted, overlapped and resembled a maze. To further complicate the patterns, some whales had also been feeding within other features. Divers were able to determine feature boundaries and measure them. They were not able to identify the entire feeding event. Very poor visibility ensured random selection of transect line direction and features for measurement on the transect. During digitization, location of individual feature boundaries on the side-scan sonar record within these heavily pitted areas was extremely difficult and grossly overestimated mean feature size. Estimates of feature size made by divers were more realistic. Areas showing heavy feeding activity were easily recognizable and thus the estimate of percentage of bottom disturbed may be quite accurate.

Examination of the side-scan record indicated that the nearshore areas off Southeast Cape showing this heavy pitting encompassed about 12 km^2. Eighteen percent of the seabed was affected or about 2,300,000 m^2. If a whale cleared 15.5 m^2 per dive and made between 164 and 198 feeding dives

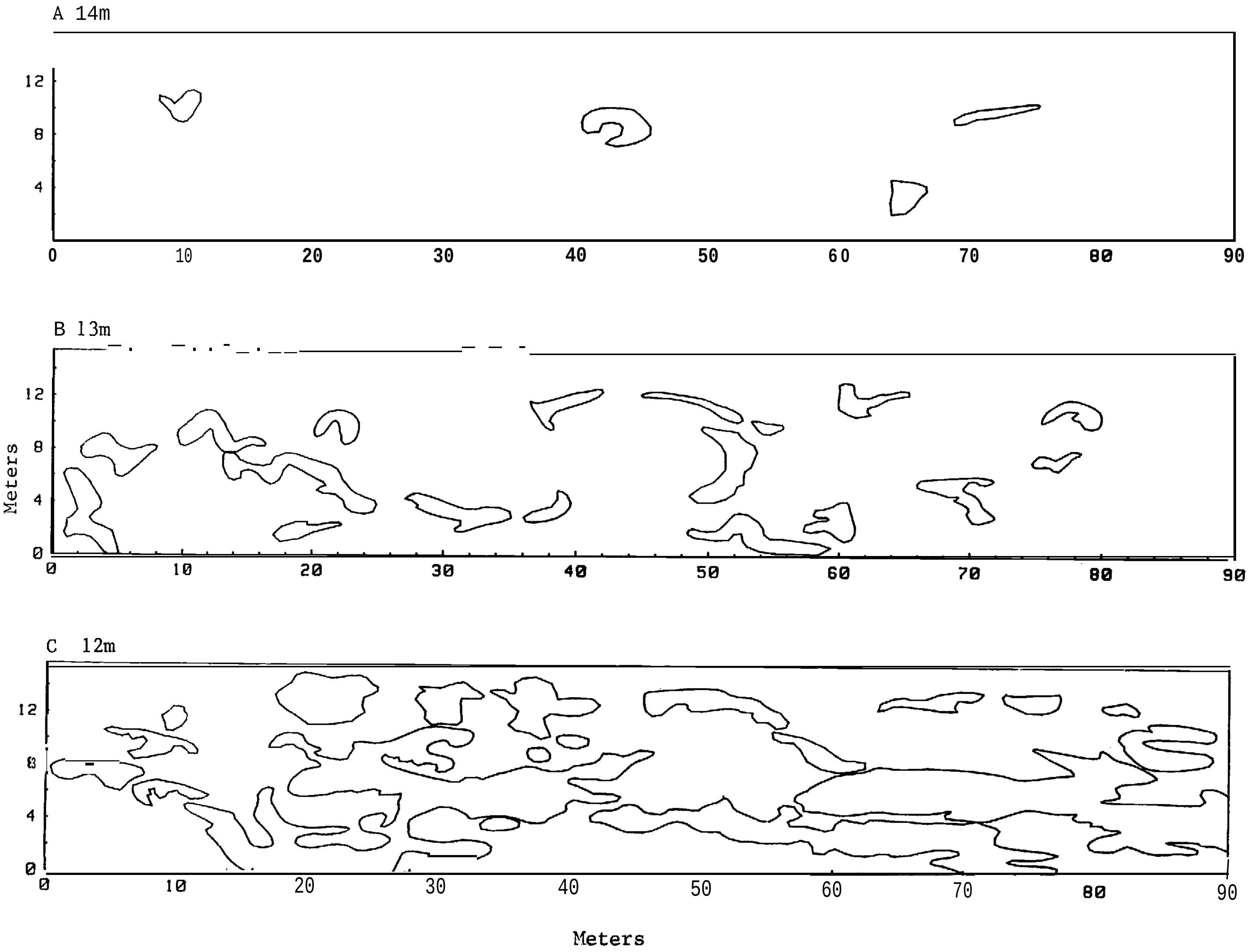

FIGURE 7. Corrected digit ized side scan sonar records from transect 133 off Southeast Cape, St. Lawrence Island, in September 1982. The water depth is shown for each segment.

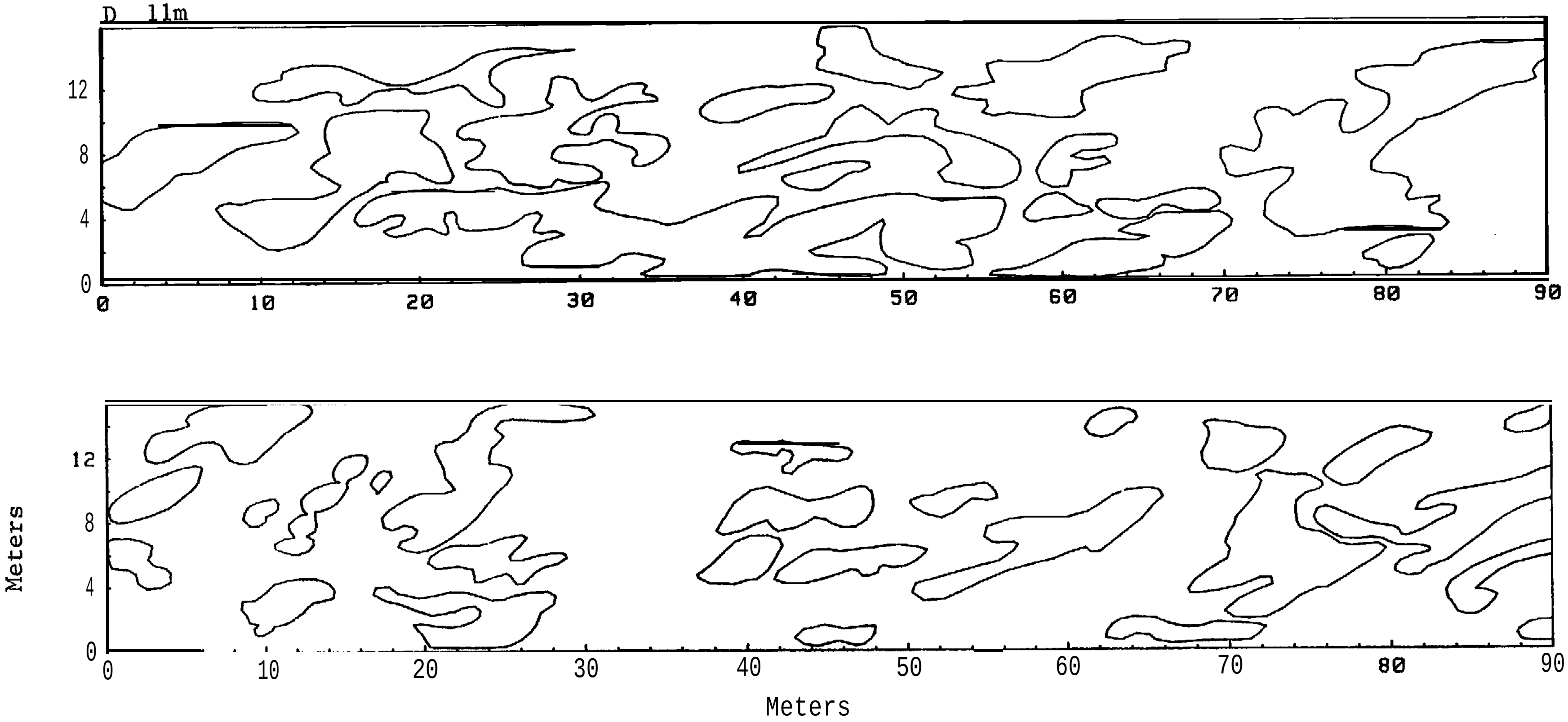

FIGURE 7. Continued

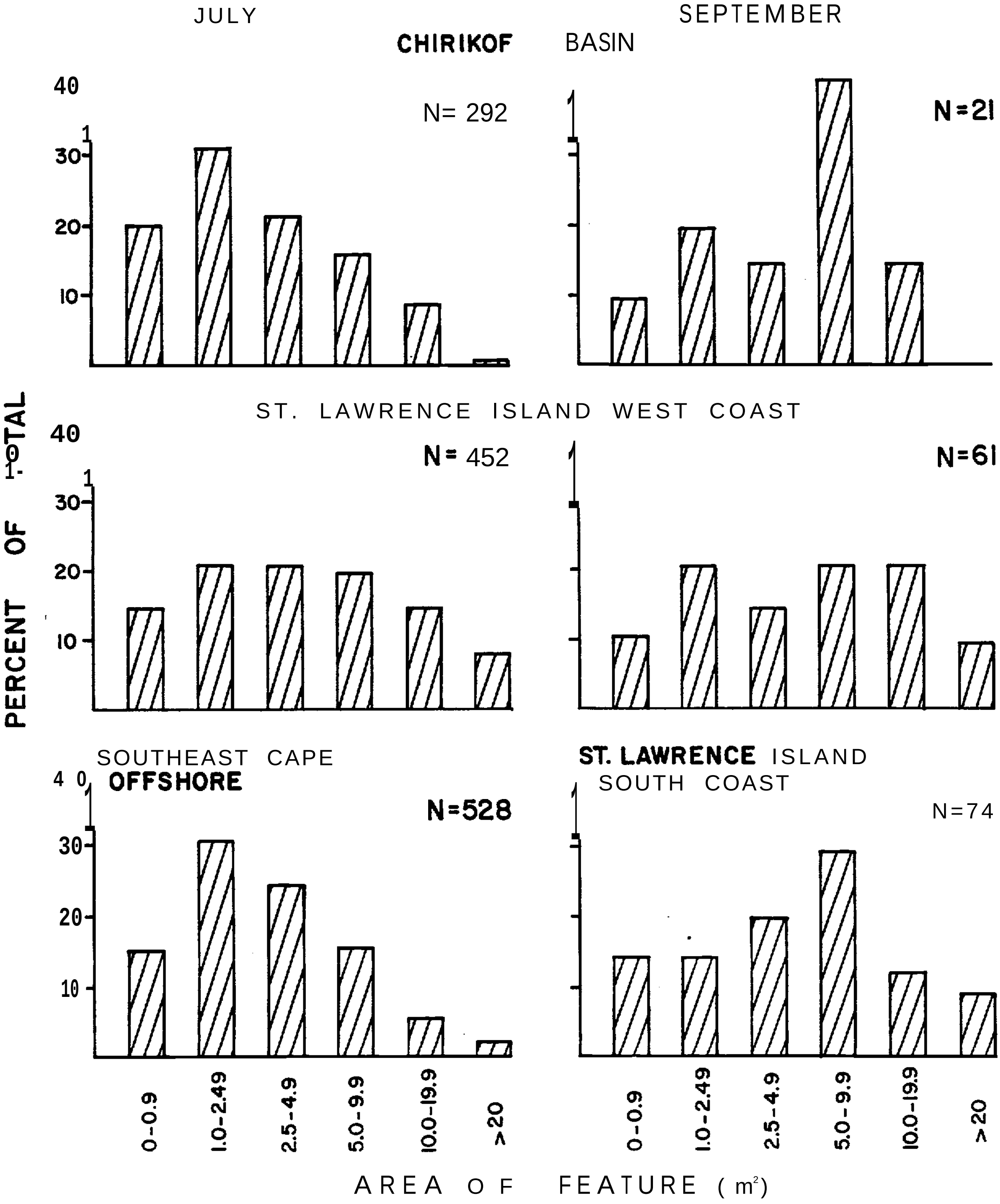

FIGURE 8. Size frequency distributions of the area of bottom features recorded by side-scan sonar and attributed to feeding activities of gray whales. Areas were calculated from digitized side scan records and were corrected for ship speed and height of tow fish above the bottom.

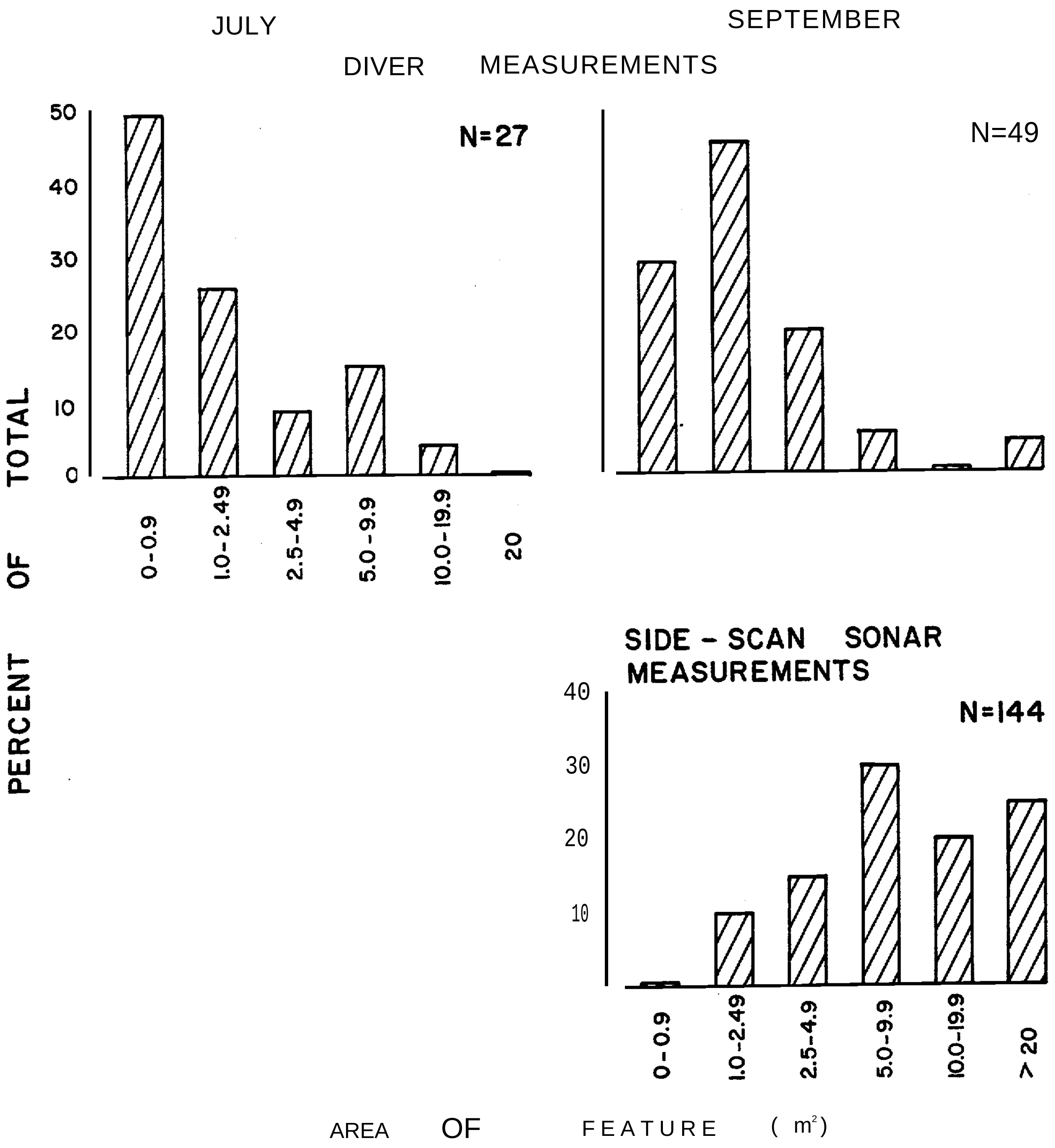

FIGURE 9. Size frequency distributions of the area of bottom features recorded by side-scan sonar or measured by divers and attributed to feeding activities of gray whales in nearshore waters off Southeast Cape, St. Lawrence Island. Measurements of features on side scan data were made on digitized corrected data.

per day (Würsig et al., this report), then only 820 whale-days or nine whales in the area from the beginning of July to the end of September were required to account for the disturbance to the seabed that was observed. About 40 whales were observed off Southeast Cape in July and twenty in September (Miller, this report) .

In summary, mean area of furrows was 18 ± s.d. 5 m^2. Mean area of pit type feeding events in deep water was 13 ● s.d. 3 m^2 and mean area of pit type feeding events in shallow water may be on the order of 17 ± 3 m^2. In all areas examined, pits were slightly more numerous than furrows (8.0/1000 m2 vs. 6.5/1000 m^2, n = 350). We do not know how many feeding events are represented by each of these types of features. A mean area of 15.5 m2 (the mean of recognizable pits and furrows) will be used as the area of a feeding event in later computations.

The size frequency distribution of features recorded in July in deeper waters not investigated by divers was similar to that recorded off Southeast Cape by divers (Figs. 8 and 9). In the central basin and offshore waters off Southeast Cape approximately one-half of the features were less than 2.5 m2 in area and as such were within the size range of individual 'bites'. The larger features could include coalesced 'bites' and long stretches of furrow that could not be resolved into smaller units.

Seasonal Comparisons.--Feeding feature size tended to increase in September (Fig. 8). In July, the modal size class in the Chirikof Basin and offshore from Southeast Cape was 1 to 2.5 m^2. In September, modal size in the Chirikof Basin and along the south coast of St. Lawrence Island was 5 to 10 m^2. This difference is also evident in the larger mean size of features recorded for September vs. July (Table 3).

Distribution of Features

In most areas, there appeared to be a mixture of small and large pits and furrows (Figs. 10 to 14). The distribution of bottom features recorded via side-scan sonar and attributed to the feeding activity of gray whales is shown on Figure 15, and their density and mean size in various areas are

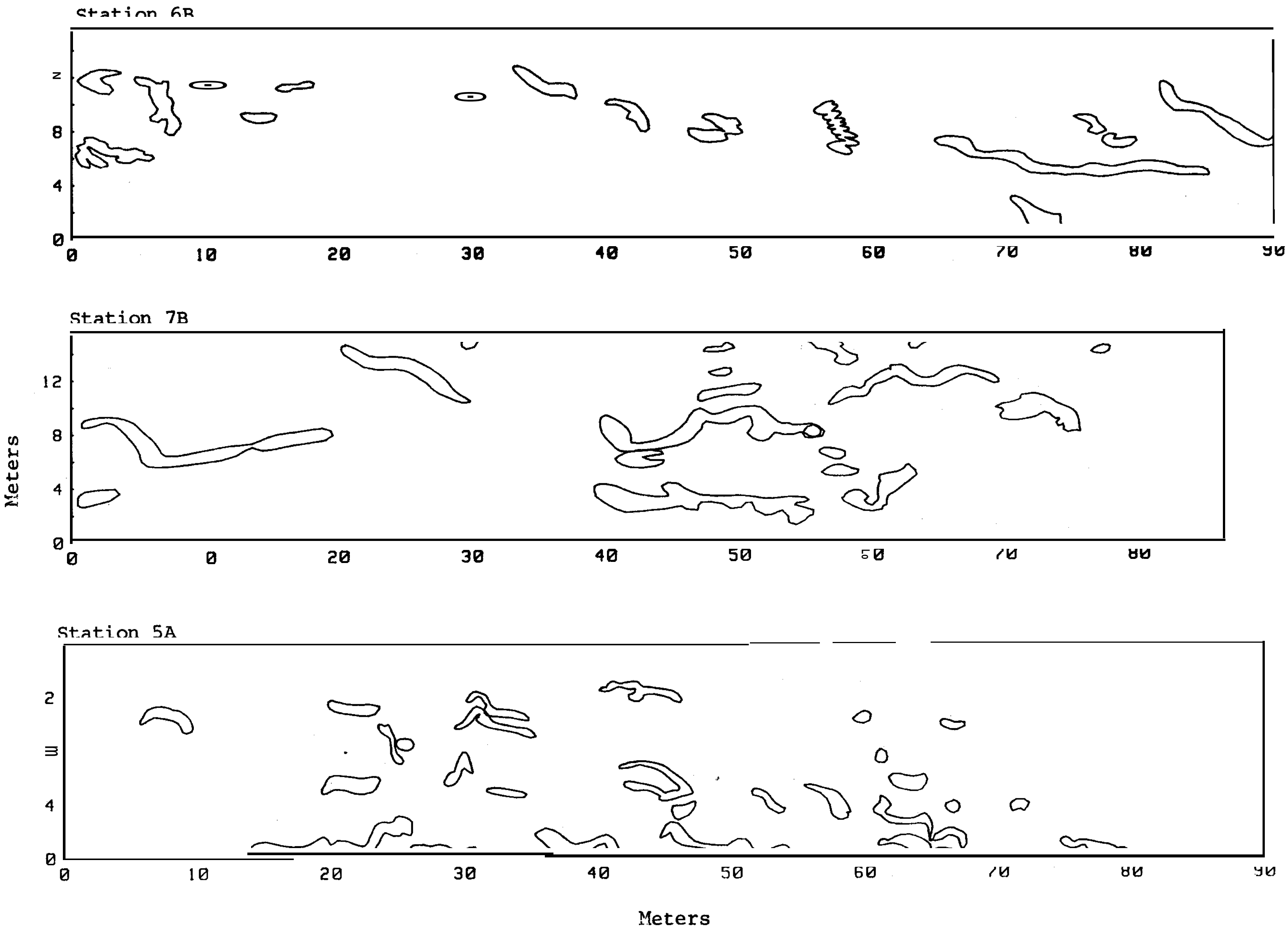

FIGURE 10. Corrected digitized side-scan sonar records from the Chirikof Basin taken in July 1982 at depths of 33 to 41 m.

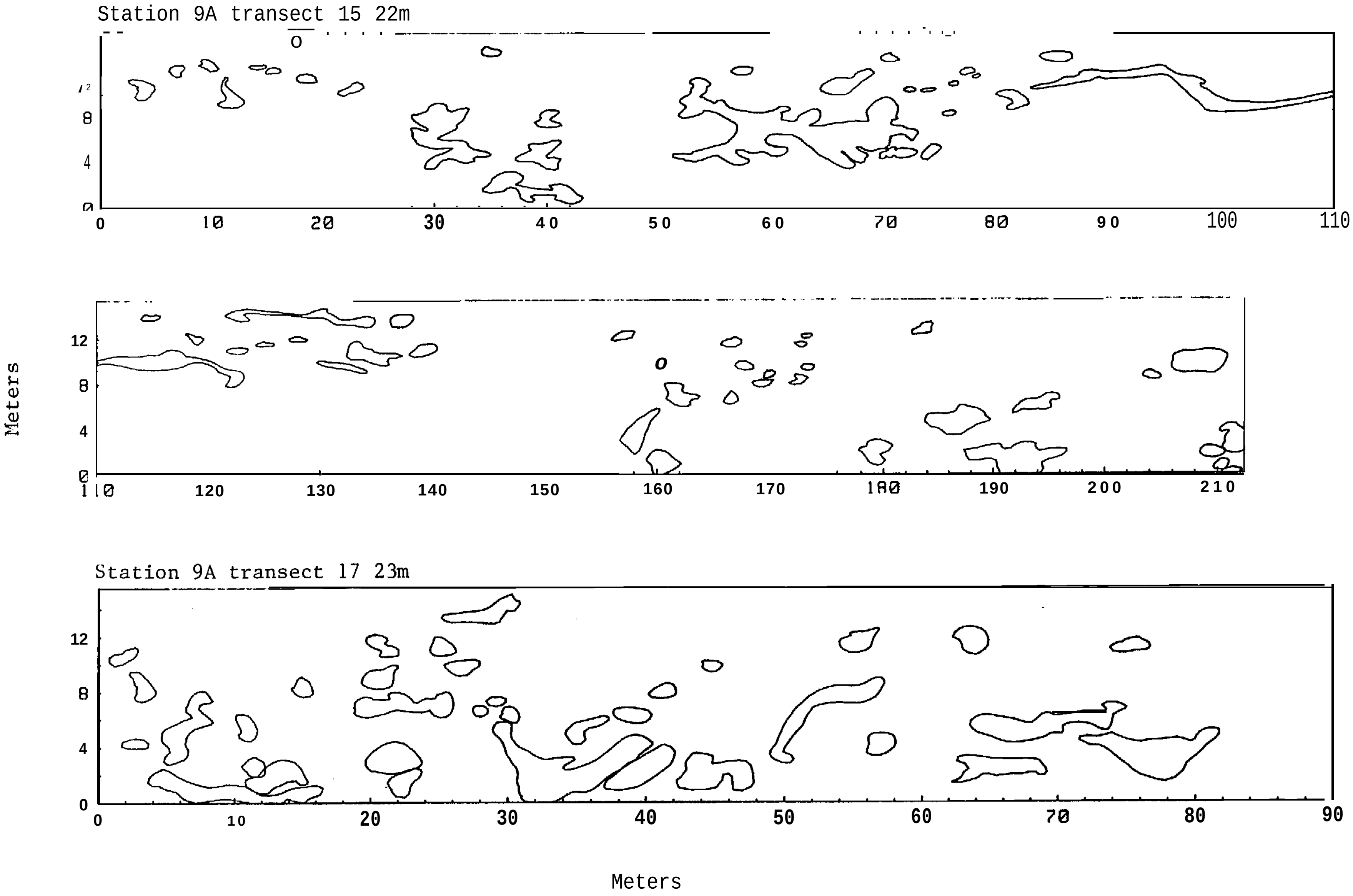

FIGURE 11. Corrected digitized side - scan sonar records from offshore waters off Southeast Cape, St . Lawrence Island taken in July 1982.

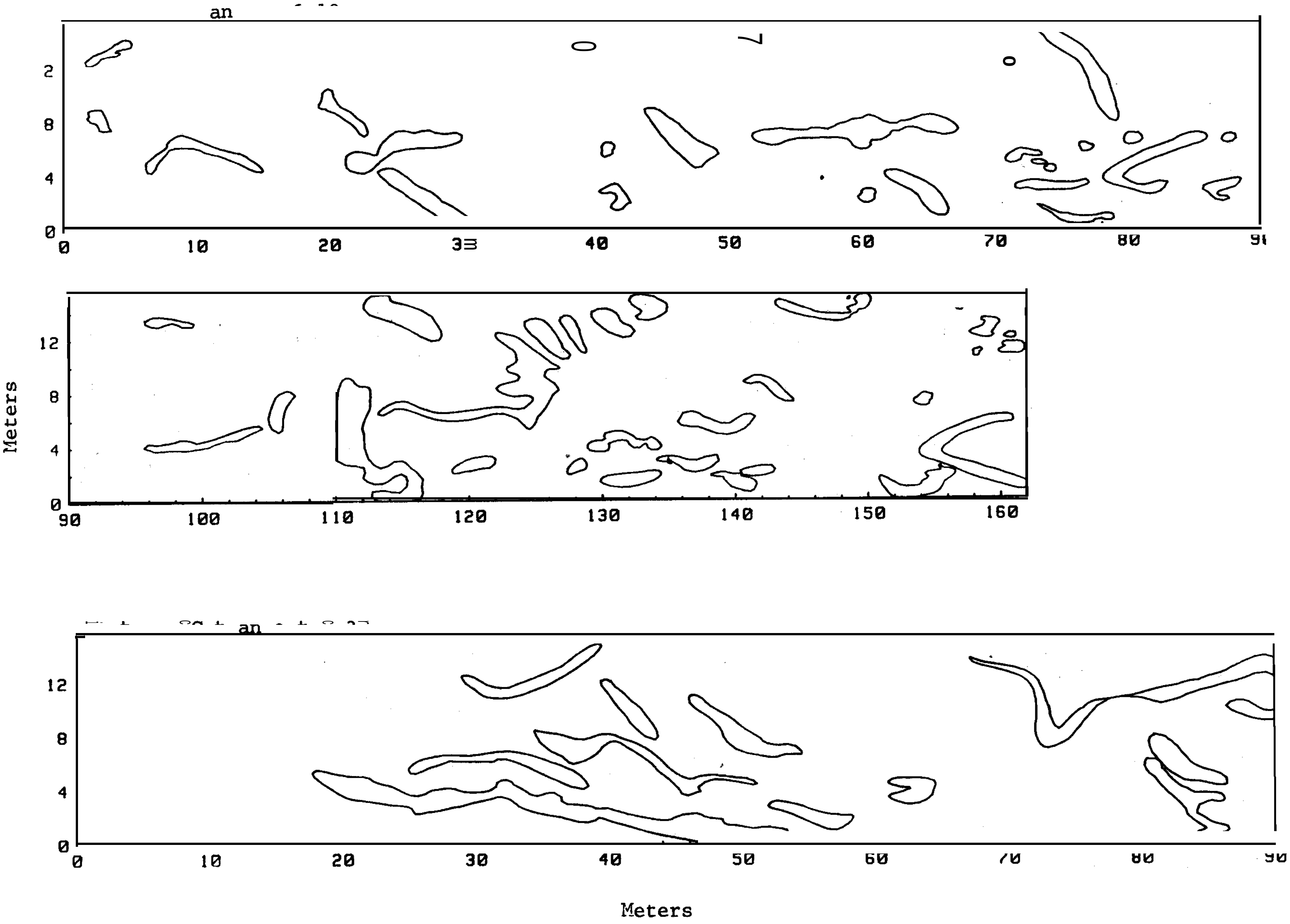

FIGURE 12. Corrected digitized side-scan sonar records from the west coast of St. Lawrence Island taken in July 1982.

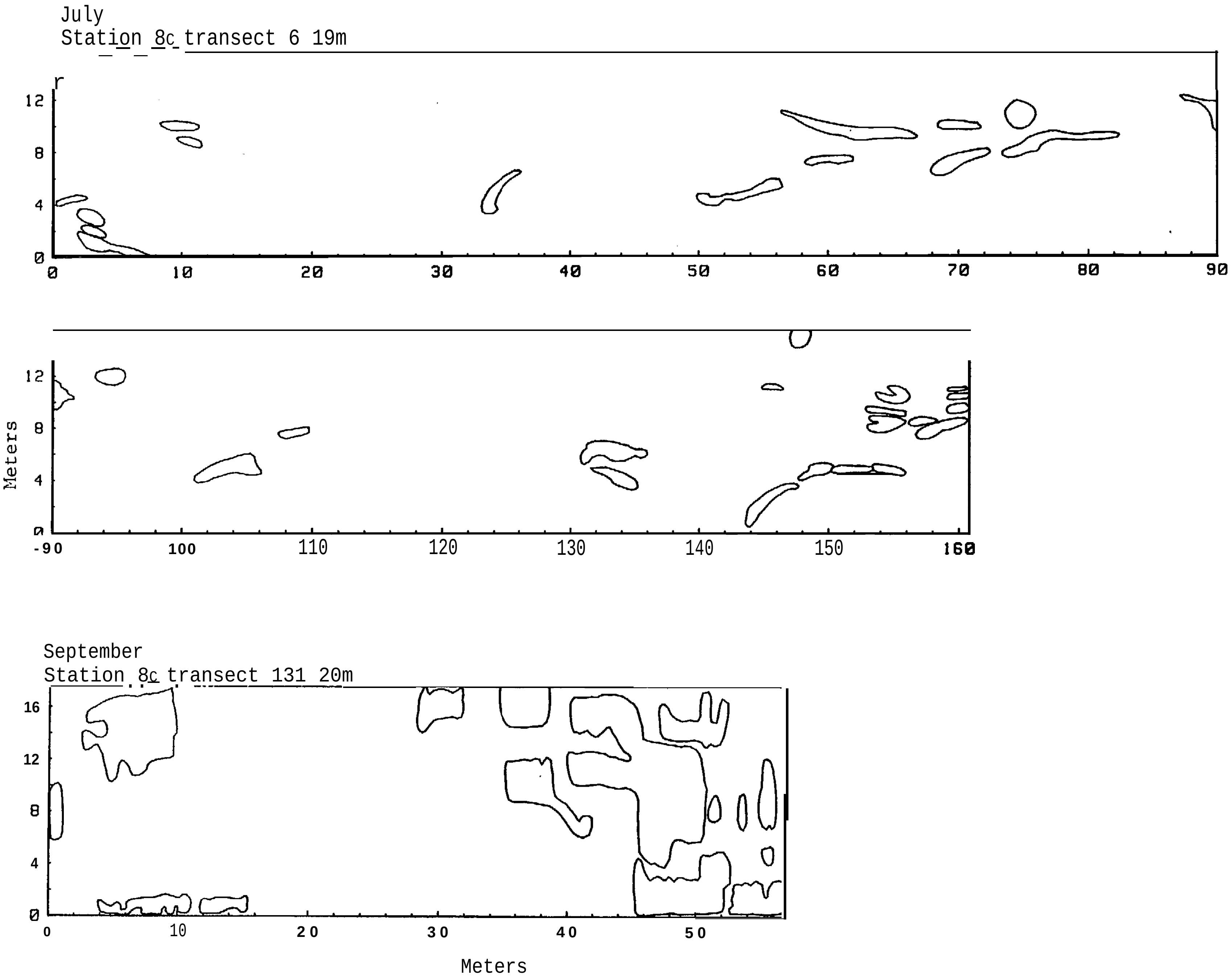

FIGURE 13. Corrected digitized side-scan sonar records from the west coast of St. Lawrence **Island** taken in July and September 1982.

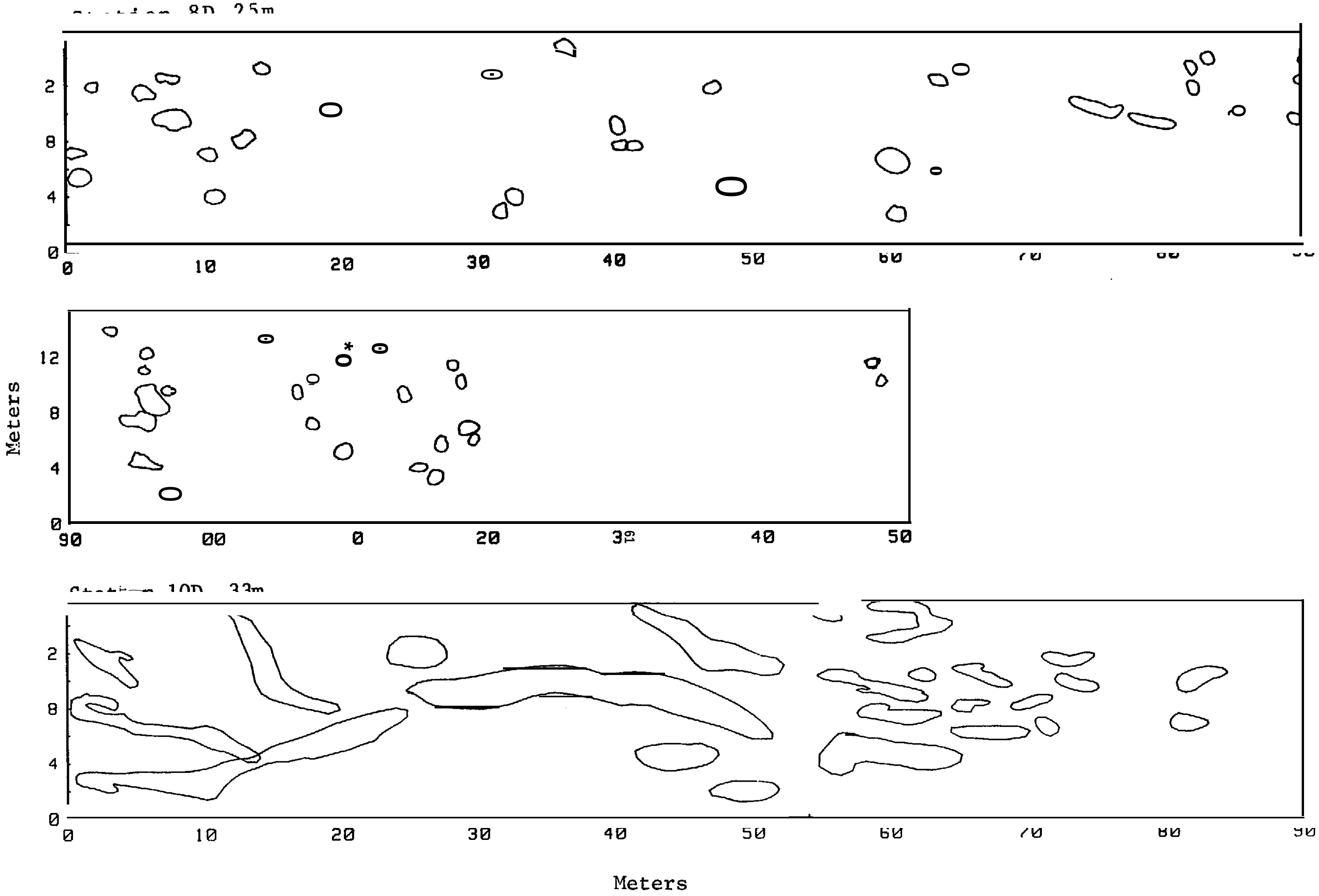

FIGURE 14. Corrected digitized side-scan sonar records from Station 8D off the west coast of St. Lawrence Island in July and from Station 10D off the south coast of St. Lawrence Island in September.

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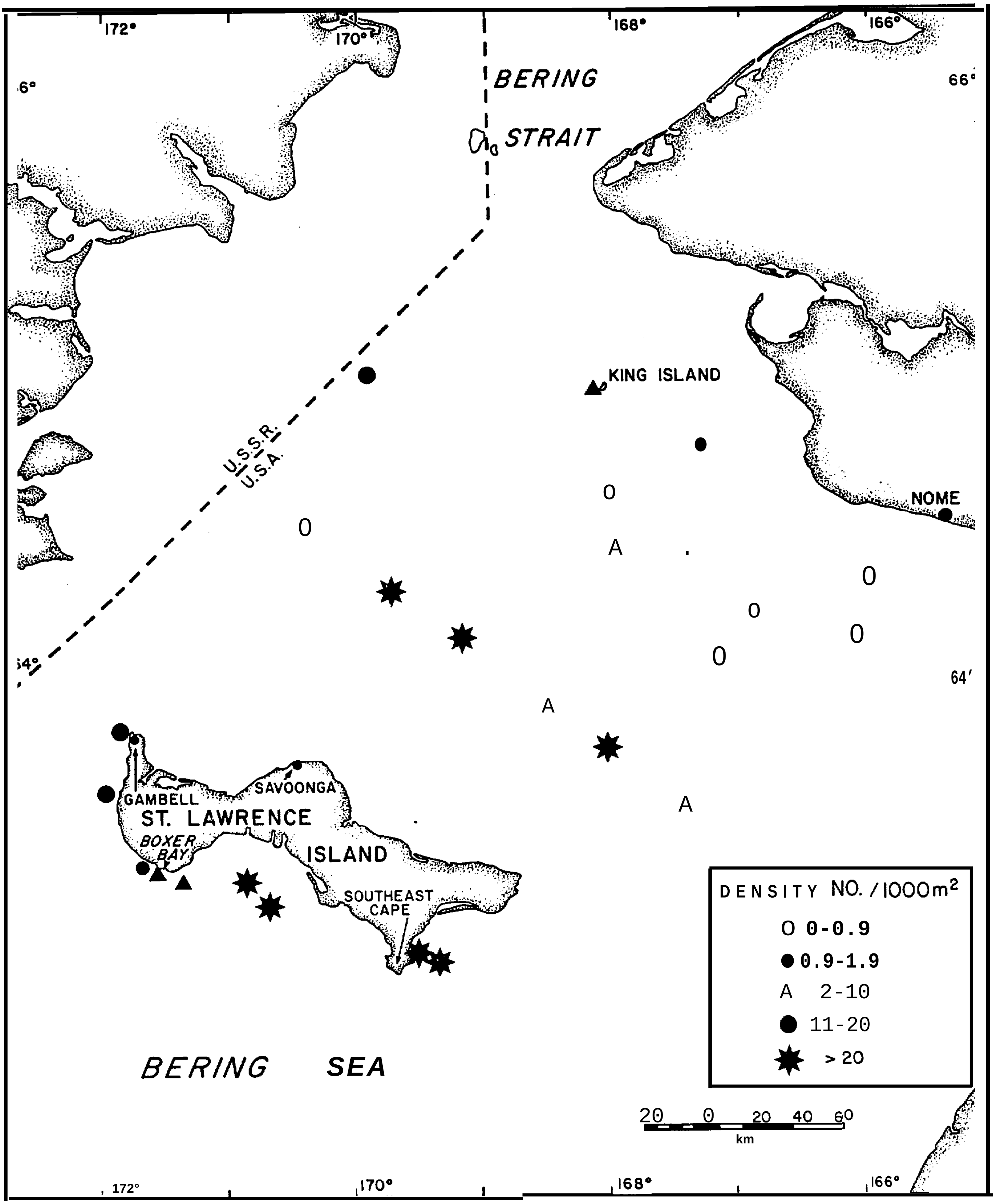

FIGURE 15. Density of individual identifiable bottom features attributed to feeding activities of gray whales, as recorded via side-scan sonar in the Chirikof Basin and near St. Lawrence Island in July and September 1982.

Table 5. Mean area (± s.d.) of features measured via corrected digitized side-scan sonar and by divers in July and September of 1982. Bottom features were atributed to the feeding activity of gray whales. The number of features measured is shown in parentheses.

Area	July	September
Chirikof Basin	3.9 ± 4.1 (292)	6.1 ± 4.5 (21)
St. Lawrence Island[1]		
west coast[1]	7.0 ± 9.0 (452)	8.8 ± 11.7 (61)
south coast[1]		8.3 ± 11.0 (74)
Southeast Cape (offshore)[1]	5.0 ± 8.3 (528)	
Southeast Cape (nearshore)[1]		17.8 ± 26.4 (144)
Southeast Cape (nearshore)[2]	2,3 ± 3.1 (27)	2.9 ± 5.5 (49)

[1] From side-scan sonar.

[2] Diver measurement.

shown in Table 6. It was possible to identify three categories of areas on the basis of the side-scan record:

1. The northeastern region and the west central region (Station 5B; Fig. 15) of the Chirikof Basin are used very little or not at all by gray whales. Mean density of features was only 0.01 ± s.d. 0.03/1000 m^2 in the 174,000 m^2 that were examined.
2. The north central region of the basin appears to be used only sparsely by Mean density of features was 0.60 ± 0.45/1000 m^2 ‘he ‘hales.
3. The central portion of the Chirikof Basin and all of the areas around St. Lawrence Island that were examined (Fig. 15) appear to be used extensively by gray whales. Mean density of features was greater than 10/1000 m^2 for all of these areas (Table 4).

Of the various category areas examined, the proportion of seabed affected by the whales was lowest in the deep waters of the central basin and highest in the shallow waters off Southeast Cape (Table 6.) This apparent inverse relationship between depth and percent of the seabed affected by whales was statistically significant ($r = -0.32$, $0.01 > p > 0.001$, $n = 82$).

Table 6. Mean density (no. /m*) 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

Mean area of the features was also greater in the shallow water off Southeast Cape than in deeper water (Table 6). The relationship of this variable to water depth was also statistically significant ($r = -0.32$, $0.01>p>0.001$, $n= 82$).

Comparison with Gray Whale Distribution

The distribution of feeding features on the sea floor as revealed by side-scan sonar closely parallels the distribution of whales as observed during shipboard transects (Table 7). A high density of feeding features on the bottom was generally accompanied by large numbers of whales sighted at the surface at or near side-scan sonar stations (Table 7). No whales were sighted at any of the stations where the sonar revealed one or fewer feeding features per 1000 m^2 on the bottom. Only at Station 7A were there a moderate number of feeding features but no observations of whales.

The correlation between number of feeding features on the sea floor and number of whales observed at the stations was significant ($r = 0.53$, $0.05>p>0.01$, $n = 20$).

Distribution of feeding features on the sea floor also parallels distribution of whales as shown by aerial surveys. Miller (this report) found high densities of whales off Southeast Cape and the west coast of St. Lawrence Island and in the central and northwestern portions of the Chirikof Basin. He observed few whales in areas that showed few or no feeding features on the sea floor. Aerial surveys conducted by Ljungblad et al. (1982, 1983) showed a similar distribution of whales.

Characteristics of Gray Whale Feeding Areas

There were striking biological and physical differences between areas that were heavily utilized as feeding grounds by gray whales and those that were only lightly utilized or not utilized at all (Table 8). The most obvious difference between the three types of areas was in the biomass of amphipods. Biomass of amphipods in areas where side-scan sonar showed many features attributable to feeding gray whales was an order of magnitude greater than in areas with a paucity of features, and almost two orders of

Table 7. Number of bottom features attributed to the feeding activities of gray ties as recorded via side scan sonar and numbers of whales observed via shipboard transects in 20 areas in the Chirikof Basin and near St. Lawrence Island.

Area	No. features/1000 m^2 mean ± s.d	(N)	No. Whales[1] Sighted at Station	Remarks
St. Lawrence Island				
West coast	14 * 10	(66)	65	
South coast	24 * 17	(36)	20	
Boxer Bay	10 ± 3	(5)[2]	15	
Southeast Cape	26 ± 16	(87)	40	
Chirikof Basin				
7A	8 ± 4	(10)	0	
7B	16 ±10	(13)	10 (15)[3]	
6A	3 ± 1	(12)	0 (2)[3]	4 between 7B and 6A
6B	22*4	(12)	4 (20)[3]	16 between 6A and B
5A	31 ± 8	(6)	1	
5B	0	(11)	0	
2A	13 ± 9	(8)	8	~100 across international boundary from 2A
2B	5*10	(9)	4	
1B	1 ± 1	(5)	0	
3A	(.).5 ± 0.5	(5)	0	
3B	0.1 * 0.1	(5)	0	
3C	8 ± 5	(13)	2	
1A	0	(10)	0	
4A	0	(10)	0	
4B	0.1 ± 0.1	(4)	0	
4C	0	(19)	0	

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[1] Fran Miller (this report).

[2] Includes only transects within Boxer Bay.

[3] Parenthetical values include whales sighted nearby.

Table 8 .Physical and biological characteristics of stations where the side-scan sonar record showed no, few, and many features attributed to feeding activity of gray whales. The mean, standard deviation and sample size (in parentheses) are shown.

	Chirikof Basin			All Areas**
	No Features (0-0.08/1000 n?)*	Few Features (0.14-1.23/1000 m^2)	Many Features (3.49-30.81/1000 m^2)	(3.4$%2%%%)
Mean grain size (Φ)	3.82 * 0.25 (4) 2.74 (1)	2.37 * 0.23 (3)	3.23 * 0.30 (8)	3.14 ± 0.32 (17)
Sorting coefficient (Φ)	2.19 ± 0.44 (5)	2.02 ± 0.11 (3)	1.79 * 0.38 (8)	1*64 ± 0032 (17)
Caloric content (Ccl/g)	328 ± 94 (5)	241 * 60 (3)	464 * 292 (7)	372 * 237 (15)
Carbon/nitrogen ratio	9.2 •1.1 (5)	8.6 * 3.3 (3)	7.0 •1.0 (8)	7.3 •1.0 (is)
Carbon content (mg/g)	3.9 * 1.3 (5)	2.4 * 0.8 (3)	2.9 * 0.5 (7)	3.1 * o.8 (15)
Biomass of amphipods (g/m^2)	3.2 * 4.0 (23)	13.7 ± 12.9 (15)	. 132.8* 96.5 (37)	148.3 * 81.1 (93)
Total benthic biomass (g/m^2)	179.9 (23)	128.1 ± 131.2 (15)	262.8 * 146.3 (37)	280.4 * 131.9 (93)
Dominant species (% of total biomass)	Macoma calcarea (25) Serripes groenlandicus (15) Sand dollar (12) Chirodota (11) Nephtys spp. (5) Pelonaia corrugata (4)	Macoma calcarea (16) Yoldia hyperborea (7) Astarte spp. (7) Nephtys spp. (6)	Ampelisca macrocephala (33) Macoma calcarea (12) Byblis gaimardi (7) Sand dollar (7) Ampelisca eschrichti (5)	Ampelisca macrocephala (23) Macoma calcarea (14) Photis fischmanni (12) Byblis gaimardi (5) Yoldia myalis (4) Nephtys spp. (4) Ampelisca eschrichti (3)

* Range of mean no. features/1000 m^2 for stations in the category.

** Includes stations in the Central Basin as per Table 4 and stations near St. Lawrence Island.

magnitude greater than in areas showing no features. The correlation between log transformed biomass of amphipods in random samples taken in the vicinity of side scan tows and log transformed density of features attributable to feeding activities of gray whales was significant ($r = 0.75$, $p<0.001$, $n = 131$).

Bivalves, echinoderms, and polychaetes were the dominant benthic organisms in areas that showed few or no feeding features on the side-scan record. Ampeliscid amphipods and the corophiid amphipod *Photis fischmanni* accounted for 42 to 45% of the benthic biomass in samples taken from areas showing a large number of gray whale feeding features on the side-scan record (compare Figure 15, this chapter and Figures 2 and 3 in Thomson, this report).

The distribution of gray whales as shown by aerial surveys and shipboard observations (Miller, this report; Ljungblad et al. 1982, 1983) also corresponds closely to the area of the Chirikof Basin occupied by dense concentrations of ampeliscid amphipods (Stoker 1981: Fig. 62.2).

In all areas examined, the mean grain size of samples associated with side-scan records showing many gray whale feeding features was 3.1 ± s.d. 0.3 (Table 8). That value is within the range of mean grain sizes (2.9-3.5) preferred by the ampeliscid amphipods inhabiting the Chirikof Basin (Stoker 1978; Thomson, this report).

Areas with many whale feeding features also showed less heterogeneity of substrate than areas with few or no features on the side-scan record (the sorting coefficient was smaller, Table 8).

There was much less gravel (particle size >2.0 mm) in areas showing many features (0.2 ± s.d. 0.5% of dry sediment weight, n = 16) than in areas showing few or no gray whale feeding features (4.6 + 6.8%, n = 8). Although gravel has been reported in the stomachs of gray whales (Zimushko and Ivashin 1980), it must interfere with feeding activities. A whale clearing 15 m^2 of sea bottom to a depth of 2 cm, given a mean gravel concentration of 4.6%, could ingest 37 kg of gravel at each feeding, as opposed to about 2 kg when mean gravel concentration is 0.2%. This difference in amount of gravel to be handled could be quite important, considering that the whales made between 164 and 198 feeding dives per day (Würsig et al., this report).

The mat community described by Thomson (this report) was characteristic of feeding areas on the shallow shelf off Southeast Cape, St. Lawrence Island. Presence of this cohesive layer allowed feeding whales to leave a long-lasting record of their feeding activities on the bottom. This mat layer may be characteristic of all portions of the study area utilized by foraging gray whales. As discussed by Thomson (this report), animal tubes were the most striking feature of this mat. Biomass of these tubes, less sediment and animals, was 1470 + s.d. 812 g/m^2 (n = 14) in July and 771 ± 395 g/m^2 (n = 20) in September in the shallow waters off Southeast Cape. Along the south coast of St. Lawrence Island, biomass was 210 ± 103 g/m^2 (n = 15) and in the areas of the central basin utilized by whales it ranged between 242 ± 92 (n = 5) and 476 ± 217 (n = 5) g/m^2.

Food Removal by Gray Whales

Effects on Benthic Animals

In July and September, in the shallow waters off Southeast Cape, St. Lawrence Island, airlift samples were taken both inside and outside bottom features attributed to the feeding activities of gray whales.

At depths of 10-15 m on the shallow shelf off Southeast Cape, St. Lawrence Island, the bottom was covered by a 'mat' of animal tubes. This 'mat' consolidated the surface layer of sediment, imparting it with a cohesive gelatinous nature. Sediments were very fine sand. Amphipods accounted for 65% of the total biomass of 297.8 ± 144.9 g/m^2 (n = 34) and 98% of the total density (110,262 ± 56,084 indiv./m^2) of benthic animals in this area. Polychaetes and bivalves accounted for 13% and 10% of benthic biomass, respectively. The amphipod *Photis fischmanni* was the dominant benthic animal in terms of both biomass (42% of total) and density (87% of total). The ampeliscid amphipods *Ampelisca macrocephala* and *Byblis gaimardi* and the bivalve *Macoma calcarea* were also important contributors to biomass.

In July, a float and marker were placed within a group of two whales that were observed to be feeding for at least 2 h. The two whales, made at least 33 dives and showed concrete evidence of feeding (mud plumes, mud streaming from mouths). The bottom features were investigated 6 h after the float was dropped, but we have no way of knowing absolutely that the whales made the feature that was investigated or when the feature was made. Mean length of furrow determined above was 41 m. Over 1000 m of furrows could have been made in the 2 h of observation. In all, 27 features were measured and/or photographed and benthic sampling was carried out inside and outside one feature. Biomass of benthic animals inside the feature was 221 g/m^2, about 40 g/m2 higher than outside. Yoldia myalis, a burrowing bivalve, was common (50 ± 21 g/m^2) in four samples taken within the feature and rare in four samples taken outside (<1 g/m^2) the feature. The furrow was likely over a high density patch of this species. If the bivalve Yoldia is excluded from consideration, the biomass within the feature was 171 g/m^2--equivalent to the biomass outside (182 g/m^2). It is not known how much of the biomass in the feature remained after the whale fed and how much immigrated subsequently.

The isopod Tecticeps alascensis was more abundant within the feature than outside. Analysis of stomach contents of this isopod showed that it had been feeding primarily on amphipods (Table 9). It seems likely that this isopod immigrated into the feature to take advantage of the sea bed that had been traumatized by a feeding gray whale. Carnivorous (Fauchald and Jumars 1979) nephtiid polychaetes were also more abundant within the feature (Table 11), and may also have quickly immigrated into it for the same reason.

The ampeliscid amphipod Ampelisca macrocephala was also more abundant within the feature than outside. In fact its biomass within the feature was higher than in other samples taken at similar depths away from areas that had been utilized by whales (Table 11). Photis fischmanni showed a markedly lower biomass within the feature (Table 11). Synidotea picta, another isopod, was more abundant within the feature than outside, as were the amphipods Protomedia grandimana and Dyopedes arcticus.

Table ‘9. Frequency of occurrence of food items found in the guts of 43 specimens of the isopod *Tecticeps alascensis* taken at depths of 10 to 15 m in the nearshore waters off the southeast cape of St. Lawrence Island in the summer of 1982.

Food Item	Frequency of Occurrence
Amphipods	
Unidentified amphipods	9
Ampeliscidae	3
Ampelisca eschrichti	1
Haustoriidae	1
Euhaustorius sp.	2
Lysianassidae	2
Orchomene sp.	1
Protomedeia sp.	10
Photis sp.[1]	7
Corophium sp.	3
Other taxa	
Foraminifera	1
Gastropoda	2
Animal tissue	2
Sediment	9
Empty	9

[1] Includes *P. fischmanni*.

In September, four features of indeterminate age were investigated; results were similar to those from July (Table 11). Within features, biomass of *Photis fischmanni* was lower than outside features, and biomass of *Ampelisca macrocephala*, isopods and nephtiid polychaetes was higher than outside features. Differences in mean individual weight for *Photis fischmanni* from samples taken inside and outside feeding features were negligible.

Table 10. Mean individual wet weight of the amphipod *Photis fischmanni* from samples taken inside and outaide feeding features in the vicinity of Southesat Cape, St. Lawrence Island.

	Mean individual wet wt[1] (mg) ± s.d. (sample size)	
Month	Inside feature	Outside feature
July	1.34 ± 0.80 (3)	1.72 ± 0.69 (4)
August	1.34 ± 0.76 (12)	1.16*0.42 (15)

[1] Only samples containing more than 100 individuals were used. Values are biomass in sample/ no. individuals in sample,

Table 11, Mean biomass (g/m^2 * s.d.) of major taxa and dominant species from samples taken inside and outside bottom features attributed to the feeding activity of gray whales and from samples taken of the upper 2 cm and upper 10-15 cm of substrate. All samples were taken off Southeast Cape, St. Lawrence Island, by diver operated airlift.

Taxon	n=	July Inside 4	July Outside 4	September Inside 20	September Outside 20	surface 2 cm of mat 30	samples taken to 10-15 cm into mud 10
Total. biomass		221 ± 69	182 ± 41	256 * 131	263 * 128	207 * 102	412 * 138
Amphipods		104 * 62	159 * 42	130 * 70	206 * 73	147 * 77	184 ± 78
Polychaetes		12 * 11	3*2	46 ± 63	18 ± 25	7 ± 8	94*73
Isopods		23 ± 12	3*3	43*29	5*7	15 * 18	3 ± 10
Bivalves		53 * 19	6*11	24 ± 67	26 ± 76	16 ± 38	44*45
Amphipods							
Photis fischmanni		27 * 27	106 *43	34 ± 42	150 *65	73 ± 69	81 ● 49
Protomedia grandimana		5*5	1 ± 2	31 ± 28	19 * 13	10 * 11	7 ± 21
Ampelisca macrocephala		44 ± 27	12 ± 7	20 * 20	6 ± 7	21 * 16	21 * 13
Byblis gaimardi		2 ± 2	4*4	11 * 10	8 ± 6	4*5	<1
Anonyx nugax		8 ± 7	16 ± 9	12*8	4*3	8 ± 16	26*9
Orchomene lepidula		4*4	6*4	5*3	7*6	6 ± 6	8 ± 6
Pyopedes arcticus		7 ± 10	2 ± 2	0 ± 0	0 ± 1	15 * 14	33 * 16
Some Other Taxa							
Tecticeps alascensis (I)		17*7	0 ± 1	33 * 28	4*7	11 * 15	<1
Synidotea picta (I)		5 ± 6	2 ± 3	8 ± 8	1 ± 2	3*5	3*10
Nephtys spp. (P)		8 ± 9	<1	39 * 61	12 * 21	2 ± 2	28*29
Macoma calcarea (B)		1 ± 2	<1	15 ± 63	18 ± 77	1 ± 1	13 ± 18
Yoldia myalis (B)		50*21	<1	6*13	7*12	4*21	16*38

I isopod, P polychaete, B bivalve.

Based on the length-weight relationship of P. fischmanni (Thomson, this report), all of the mean weights shown above correspond to a 4 mm individual. There were also no apparent differences in the size frequency distributions of Ampelisca macrocephala taken from inside and outside feeding features in September (Fig. 16). Recolonization by these species appears to involve the general population rather than specific size groups.

It is interesting that total biomass of polychaetes exclusive of Nephtys spp. was similar inside and outside the feeding features. Stomach contents of gray whales taken in Russian waters indicate that they feed almost exclusively on amphipods (Zimushko and Ivashin 1980; Bogoslovskaya et al. 1982; Blokhin and Pavlyuchkov 1983; Yablokov and Bogoslovskaya in press). Other animals are rare in stomach contents. It is also worth noting that amphipods accounted for 78 to 87% of total biomass in samples taken outside but immediately adjacent to furrows, but only 44% of total benthic biomass of samples taken 800 m from feeding features in July. Thus, the whales had been feeding in areas with a high biomass of amphipods and low biomass of other taxa. In July, whales were feeding on the top 2 cm of the 'mat' layer. Samples taken to a depth of 2 cm in the 'mat' layer contained a large biomass of amphipods and low biomass of other taxa (Table 11). The whales were selecting for amphipods both during selection of feeding sites and by processing only the top 2 cm of the substrate,

In these shallow waters off Southeast Cape, density of Photis fischmanni alone in areas where whales were feeding was over 100,000 animals/m^2. Density of Ampelisca macrocephala was only 1/5 of that in deeper (>20 m) water where density of all animals was only 10,000/m^2. There was a significant negative correlation between densities of A. macrocephala and P. fischmanni, considering all samples taken within, outside and away from the furrowa found in shallow water off Southeast Cape ($r = -0.329$, $p<0.001$, $n = 86$). A high density of P. fischmanni was accompanied by a low density of A. macrocephala. Competition for space with P. fischmanni may be a factor that limits the abundance of A. macrocephala in this region.

In other regions, ampeliscid amphipods are opportunistic recolonizes of disturbed areas (Mills 1967). During this study, we observed that disturbance of the seabed by divers or the underwater video frame caused

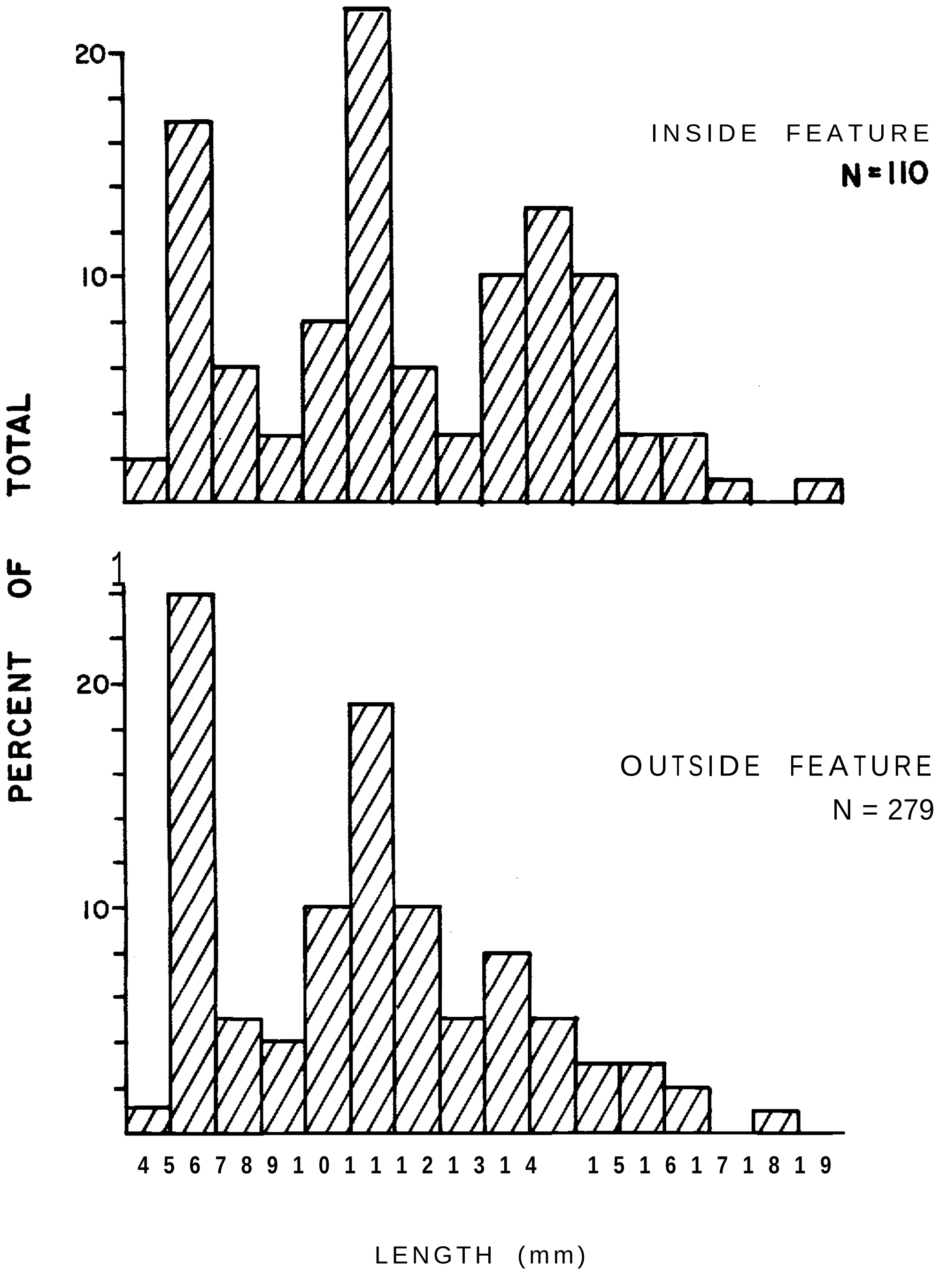

FIGURE 16. Length frequency distributions of Ampelisca macrocephala from airlift samples taken inside and outside a bottom feature attributed to feeding activities of a gray whale in shallow water off Southeast Cape, St. Lawrence Island, in September.

ampeliscids to leave their tubes and begin swimming about. Because of the high density of Photis tubes, ampeliscids disturbed by whales may not be able to settle again until they find a relatively depauperate substrate. Ampeliscids disturbed by a feeding whale would find a suitable habitat within the fresh furrow. When whales fed in these shallow areas they reduced the density of P. fischmanni within features and may have allowed Ampelisca macrocephala to recolonize the furrow.

Nerini et al. (1980) estimated relative ages of pits through examination of the densities of Ampelisca macrocephala and other species. In the following paragraph, we have used the same methodology to estimate relative furrow age. 'Twenty-four samples each were taken within and outside five furrows. The density of Photis fischmanni in all of these samples was negatively correlated with the density of both the isopod Tecticeps alaskiensis ($r = 0.416$, $0.01<p>0.001$, $n = 48$) and the ampeliscid amphipod A. macrocephala ($r = -0.446$, $p<0.001$, $n = 48$). There was no correlation between densities of A. macrocephala and T. alaskiensis ($r = 0.06$, $p<0.05$, $n = 48$).

We estimated the relative ages of furrows by comparing the numbers of animals and biomass of amphipod tubes found in samples taken inside as a percentage of those taken outside the furrows that were sampled.

In Table 12, we have estimated the relative ages of features by assuming that those with the lowest biomass of tubes and density of amphipods relative to biomass *and* density outside were the freshest features.

Table 12. Estimated relative ages of gray whale feeding features based on numbers of amphipods and biomass of amphpod tubes.

		No. Samples	Photis fischmanni	Ampelisca macrocephala	Tecticeps alaskiensis	Animal Tubes*
Age	Station	Inside/Outside	% in/out[1]	% in/out	% in/out	% in/out
fresh	464a	5/5	5	83	1387	5
↓	464b	5/5	10	1168	0	43
	464c	5/5	22	2123	2909	54
	152	4/4	33	501	2900	49
Old	475	5/5	54	1	543	157

* Based on g/m^2.

[1] Mean density inside the feature expressed as percentage of mean density outside feature.

It would appear that when a furrow is first created it is denuded. The above table also shows that the scavenging amphipod Tecticeps alaskiensis is the first to colonize. Ampelisca macrocephala is relatively quick to colonize the area but its relative density decreases as Photis fischmanni re-establishes itself. If so, then the furrow at station 154, which was sampled in July in an area where whales had been observed to be feeding, was either an older furrow or reflected the effect of a different mode of feeding. As previously mentioned, in July the whales were apparently skimming the bottom and leaving furrows 2 cm deep while in September they were making pits 10 cm deep. Furrowing may be a less effective method of feeding.

There are some differences between these results and those of Nerini et al. (1980), Nerini and Oliver (1983), and Nerini (in press). Features we sampled off Southeast Cape were on average 2.9 m^2 in area and were 2-10 cm deep. Pits examined and sampled by Nerini were smaller (1.8 m^2) and deeper (19 cm). They found a reduction in density of Ampelisca macrocephala inside features. However, Nerini et al. (1980) were sampling in deeper water, where A. macrocephala was the dominant organism and Photis fischmanni was rare. Competition for space in the bottom may have been minimal as only a total 6000-12,000 animals/m^2 were present. Decreased competition for space in deeper water may have allowed ampeliscids to settle anywhere on the bottom. The smaller deeper pits found by Nerini et al. (1980) may, in fact, have been avoided by ampeliscids because they prefer areas with a substantial current (Sanders 1956). Length-frequencies of Ampelisca macrocephala sampled inside and outside furrows in September by ourselves are identical to Nerini et al.'s (1980; Fig. 13) results from the fall.

Feeding gray whales apparently have little effect on burrowing polychaetes and bivalves and a large effect on surface-dwelling forms such as amphipods and isopods. Recolonization by the latter groups is extremely rapid. Scavenging isopods, polychaetes and perhaps lysianassid amphipods may move into denuded areas to take advantage of damaged animals, Other species such as Ampelisca macrocephala and Photis fischmanni appear quick to respond to newly available substrate.

Effects on Physical Characteristics of the Substrate

Foraging gray whales cause a disruption of the surface 'mat' layer that overlays the sea bed in the shallow waters off Southeast Cape, St. Lawrence Island. This 'mat' is composed of dense concentrations of amphipod tubes and it is the presence of these tubes that give the surface layer its discrete and cohesive nature. Disruption of this 'mat' by feeding whales is not total. In July, biomass of the animal tubes and other organic matter not including animals was 937 ± s.d. 116 g/m^2 (n = 4) outside feeding features and 465 ± 315 (n = 4) g/m^2 inside features. In September biomass of this material was 795 ± 405 g/m^2 (n = 18) outside feeding features and 282 ± 256 g/m^2 (n = 18) inside. It should be noted that some of the tubes inside features may have been constructed by recently immigrated animals.

Mean grain size within the 'mat' layer averaged 3.4 ± s.d. 0.2 Φ (n = 4) outside of the features and 3.6 * 0.1 Φ (n = 4) inside features. Mean sorting coefficient was 1.4 ± 0.3 Φ (n = 4) inside features and 1.5 ± 0.2 Φ (n = 4) outside features. The feeding activity of the whales or subsequent erosion, (if any) of features does not appear to affect sediment characteristics. The presence of animal tubes within features may prevent or at least retard erosion of features.

Food Available to Gray Whales

In the shallow waters off Southeast Cape in July, gray whales were apparently feeding on the upper 2 cm of the 'mat' that covered the bottom. Airlift samples taken to a sediment depth of 2 cm indicated that a total biomass of 207 * 102 g/m^2 wet weight was available *to* the whales. Amphipods, especially Photis fischmanni and Ampelisca macrocephala, accounted for 71% of this biomass. At the feeding feature sampled in July, 159 g/m^2 of amphipods were available to the whales.

Amphipod biomass estimates from deeper waters of the Chirikof Basin and areas adjacent to St. Lawrence Island are given in Table 13.

Table 13. Estimates of **amphipod** biomass in Chirikof Basin and the St. Lawrence Island areas.

	mean **± s.d.**	(sample size)
Central **Chirikof Basin**[1]	133 ● 97	(37)
St. Lawrence Island		
south coast	120* 49	(15)
west coast	130 *50	(16)
Southeast Cape (offshore)	139 * 52	
Southeast Cape (nearshore)	194 ± 78	(34)

[1] Only samples from areas utilized by gray whales are included.

Other baleen whales appear to seek out and feed in dense concentrations of **zooplankton** (e.g., **Brodie** et al. 1978; **Griffiths** and Buchanan 1982). As previously noted, over the study area as a whole there was a strong correlation between biomass of **amphipods** and number of feeding features. When all of the areas not used by whales are excluded from the computations, the correlation between log transformed percent of sea floor disturbed and log transformed mean biomass of **amphipods** was 0.69 ($0.01>p>0.001$, n = 17). This relationship **would** indicate that, within their feeding grounds, whales are selectively feeding in areas of high **amphipod** density. This relationship explains differences in gray whale feeding activities among stations that were 10's of km apart and we have no data on small scale distribution of feeding features in relation to biomass of amphipods.

Mean biomass of **amphipods** in all samples taken in areas utilized by feeding gray whales was 148 ± 81 g/m^2 (n = 93). The frequency distribution of biomass in the samples shows that 49% of samples contained a biomass of amphipods greater than the mean (Table 9).

Table 14. **Frequency** distribution (%) of **amphipod** biomass in 93 samples taken within that portion of the study area utilized by gray whales.

Range of **Amphipod** Biomass (g/m*)							
o-49	50-99	100-149	150-199	200-249	250-299	300-349	>350
9%	20%	22%	24%	15%	6%	3%	1%

Food Retention Efficiency of Gray Whales

Not all animals may be retained by the baleen when the whale is feeding. Johnson et al. (1983) discuss the available conflicting evidence. Amphipods as small as 4 mm have been found in gray whale fecal material, but baleen separation of gray whales may allow animals of sizes less than 4 mm to escape.

Eight horizontal plankton tows were taken through mud plumes emanating from feeding gray whales. These tows were taken at a water depth of 20 m between grab stations 138 and 179 off Southeast Cape, St. Lawrence Island (Fig. 2). A control tow taken away from mud plumes contained no benthic animals. Species composition of the benthic amphipods recovered from tows through mud plumes (Table 10) reflects the species composition on the bottom at nearby grab stations. Ampelisca macrocephala was the dominant benthic species both in tows (Table 15) and in the grabs (Thomson, this report). Protomedia spp. were next in order of abundance both in tows and grabs. Unlike the situation on the shallow (10-15 m) shelf, Photis fischmanni and Byblis gaimardi were rare in these deeper water grab samples. These two species were also rare in the plankton towa through mud plumes.

A comparison of the sizes of Ampelisca macrocephala recovered from plankton tows through mud plumes with those taken in nearby benthic samples (Fig. 17) shows a preponderance of 4 and 5 mm individuals in the plankton tows (81%). These two size classes comprised 23% of the population on the bottom at Station 138 (Fig. 17). This evidence suggests that some individuals smaller than 6 mm are not retained by the whale. However, individuals less than 6 mm comprise only 3.2% of the wet weight biomass of A. macrocephala on the bottom. Ampelisca macrocephala, A. eschrichti and Byblis gaimardi, animals similar in size, were the dominant animals in areas heavily utilized by the whales (Table 8). Whales feeding on these species would retain most of the biomass, assuming that individuals greater or equal to 6 mm in length are retained. Protomedia spp. and Dyopedes arcticus were also abundant in plankton tows and may not have been retained by the whales. However, both of these animals are small, and together they comprised only

Table 15. Number of benthic animals found in eight surface plankton tows taken through mud plumes emanating from feeding gray whales off Southeast Cape, St. Lawrence Island, in July.

Taxon	Tow Number 1	2	3	4	5-8[a]	Total
Amphipods						
Ampelisca macrocephala	8	8	8	10	29	63
Byblis gaimardi	1				1	2
Photis fischmanni				1	3	4
Ischyrocerus sp.	1		1	1	3	6
Pontoporeia femorata	1	1	1		5	8
Protomedia sp.	6	2		3	13	24
Dyopedes arcticus	1		6	2	4	13
Atylis sp.	1					1
Orchomene sp.		1			2	3
Lembos arcticus		1				1
Grandiphoxus acanthinus					1	1
Boekosimus plautus			1			1
Podoceros sp.			4	1		5
Orchomene lepidula			1	1		2
Other Taxa						
Cumacea			1		1	2
Polychaeta			1			1

[a] Four tows combined.

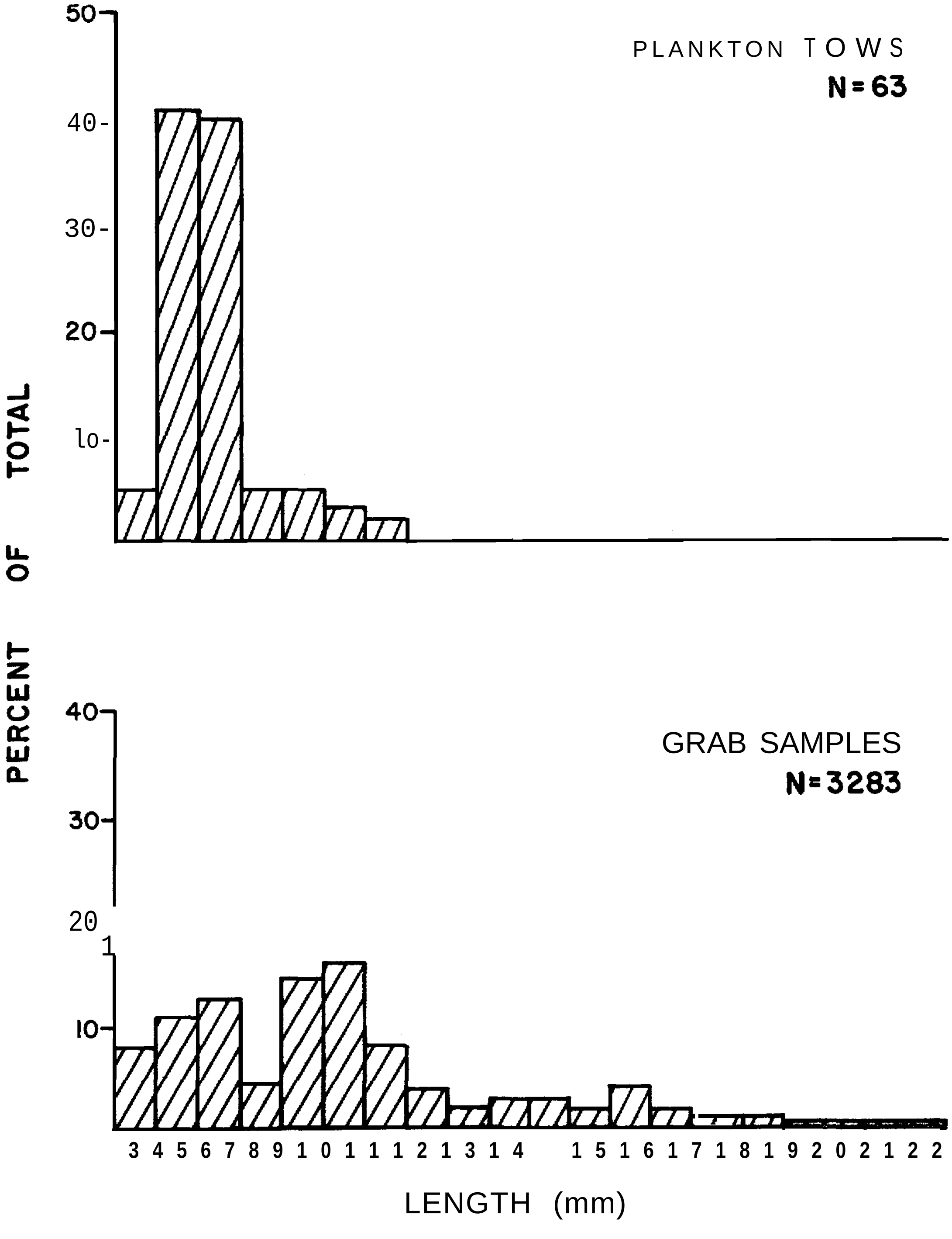

FIGURE 17. Length frequency distributions of _**Ampelisca macrocephala**_ from (a) plankton tows taken in July through mud plumes emanating from feeding gray whales, and (b) **benthic** grab samples. Grab samples were taken off Southeast Cape, St. Lawrence Island, near the location of plankton tows.

6.5% of the biomass of amphipods found on the bottom in the area where the towa were made.

When all benthic species collected in the plankton tows are combined, individuals of 5 mm or less comprised 71 % of the total number of animals collected in the tows. In benthic grab samples taken nearby, 39% of the 3744 amphipods taken were 5 mm or less in length. We estimated biomass of amphipods by length categories by applying the length vs. dry weight relationship developed for Photis fischmanni (Thomson, this report) to approximate the length weight relationship for small animals and that of Ampelisca macrocephala (Thomson, this report) to large animals. Animals of size 5 mm or less in these samples comprised only 4.3% of total amphipod biomass. The percent total amphipod biomasses contributed by six other size categories are shown in Table 16.

Table 16. Length to dry weight relationships for six size categories of amphipods.

	% of Total Dry Weight Biomass of Amphipods					
Size Range (mm)	2-5	6-10	11-15	16-20	21-25	26-29
% Total	4.4%	18.1	21*2	12.9	24.8	18.5

Thus , at water depths of more than 20 m, over 75% of the total amphipod biomass is contributed by amphipods greater than 10 mm in length. Even if none of the amphipods of size 5 mm or less are retained by the baleen, the loss would be less than 5% of total amphipod biomass.

The shallow water benthos off Southeast Cape was dominated by the small amphipod Photis fischmanni. In July and August 40-60% of the biomass was represented by amphipods less than 5 mm in length. Feeding efficiency may be lower in this region. However, we do not know what proportion of these small amphipods is retained by the whale. Oliver et al. (1983) found large numbers of amphipods less than 5 mm in length in gray whale feces collected in the vicinity of St. Lawrence Island.

Utilization of the Chirikof Basin By Gray Whales

Migration

The theoretical estimation of food consumption by gray whales while on their summer feeding grounds requires some knowledge of their migration patterns and food consumption while migrating. Migrating animals may consistently swim at a speed of 7.2 km/h (Sumich 1983). Other authors cited in Rugh and Braham (1979) have calculated travel rates of 7 *to* 10.2 km/h. Rugh and Braham estimated that gray whales travel at a mean speed of 4.3 km/h between Point Loma, California, and Unimak Pass in the Aleutian Islands. Würsig et al. (this report) calculated a mean forward speed of 2 km/h for feeding whales. It is not surprising that feeding whales move at a slower speed than traveling whales.

Oliver et al. (1984) and Darling (in press) found *'pockets'* of suitable habitat along the Vancouver Island coast and Darling speculates that these may be found along migration routes between California and Alaska. If the whales feed while traveling through these 'pockets', or stop to feed there and then quickly traverse the regions between 'pockets' as they do off Vancouver Island and in Russian waters (see Darling in press), then mean speed of travel will be reduced,

Gray whales depart Russian waters in mid October to November, arriving at Unimak Pass during the last two weeks of November and the first three weeks of December (Rugh and Braham 1979; Yablokov and Bogoslovskaya (in press). If the whales depart the Siberian coast on the first of November and arrive at Unimak Pass on 22 November (the date of peak passage; Rugh and (in Braham (1979)) then a mean speed of 1.7 km/h is required to cover the 864 km coastal. migration route outlined by Braham (in press) between the Bering Strait and Unimak Pass. This is less than the forward speed of a feeding whale.

Between Unimak Pass and Point Loma mean speed of migrating whales is 4.3 km/h (Rugh and Braham 1979), slow enough to allow feeding, given the traveling speeds cited above. The timing of movements past Vancouver Island

and Oregon (Herzing and Mate 1981; Darling in press) indicates that traveling speeds are similar between Unimak Pass and Vancouver Island and between Vancouver Island and California.

Northbound whales travel at a slower rate than southbound whales (Rugh and Braham 1979). The main pulse of northbound migrants passes California during the first week of March (Dohl et al. 1981). They reach Oregon by mid March and pass Vancouver Island during the last two weeks in March. Mean speed would have to be about 4 to 6 km/h during this time. By June animals are found between Unimak Pass and the Bering Strait. To arrive off St. Lawrence Island by the first of June, the whales traveling the coastal route would have to average only 2.2 km/h during this Bering Sea portion of their journey. Braham (in press) has observed these northbound whales to be feeding extensively in Bristol Bay and north of the Alaskan Peninsula. Migrating animals also feed sporadically off Vancouver Island in spring (C)liver et al. 1984; Darling in press).

Nerini (in press) has reviewed the question of feeding during the migrations and found some evidence for feeding all along the route, including feeding in offshore waters of Baja California. However, the only confirmed intensive feeding is from the northern part of the range, and the evidence suggests a lack of feeding activity off California (Nerini in press).

For the purposes of the following energetic computations, we consider a mature male gray whale that spends 62 days on its winter grounds (Rice and Wolman 1971). It departs on 12 March and arrives at Vancouver Island on 28 March. It passes through Unimak Pass on 19 May and arrives at St. Lawrence Island on 1 June. The whale spends 150 days on the summer feeding grounds in the Chirikof Basin, departing on 1 November. Unimak Pass is reached on 22 November and Point Loma, California, on 11 January. Alternative calculations will be made below assuming different rates of feeding while migrating.

Animals that summer in the American Chukchi Sea and off Siberia pass through the Chirikof Basin during migration. Information on the distribution of whales in Soviet waters is insufficient to determine what proportion of that population passes through the Chirikof Basin. Northward migrating whales appear to congregate near St. Lawrence Island before dispersing to their summering areas. Thus most of these whales must pass through the Chirikof Basin. An assumption will be made that all of the Soviet-summering animals and all animals that summer in the American Chukchi Sea (see below) do SO. Mean traveling speed of migrating whales through the Bering Sea appears to be about 2 km/h and the distance across the Chirikof Basin is approximately 270 km. This journey would require six days and is performed twice. Following these assumptions, utilization of the Chirikof Basin by migrating whales would be on the order of 100,000 whale-days.

Resident Population

The total population of gray whales is estimated to be 17,600 (Reilly et al. 1983; Rugh in press). Most of these whales appear to summer in the Bering Sea and areas to the north (Rugh in press). Zimushko and Ivashin (1980) estimated that 7700 to 7800 gray whales summered off the coast of Siberia between Mys Olutorskiy and Wrangel Island. In July 1982, Ljungblad et al. (1983) found mean densities of 0.006 to 0.430 whales/n.mi.^{2} in their six survey areas in American Chukchi Sea in 1982. This represents an uncorrected total of 2550 whales. Application of our correction factor for whales below the surface (Würsig et al. and Miller, this report) yields a corrected estimate of 9109 whales.

Miller (this report) estimated that 1929 gray whales were found in the Chirikof Basin in July of 1982. Ljungblad et al.'s (1983) raw estimates for a larger area, including the west coast of St. Lawrence Island, for the period June to August 1981 and July 1982 were 743 and 666 whales, respectively. Application of Miller's (this report) correction for whales below the surface yields estimates of 2805 whales in 1981 and 2379 in 1982.

The estimates listed above for numbers of gray whales near St. Lawrence Island and in regions to the north in 1982 total 19,338, greater than the total number of whales that enter the Bering Sea. In July 1982, gray whales had apparently not yet completed their migration to Russian waters. Something on the order of 14% of the entire population of gray whales summered in the American Chirikof Basin and vicinity of St. Lawrence Island in 1982.

Whales arrive at St. Lawrence Island in May and June and depart in October and' November (Pike 1962; Rugh and Braham 1979; Braham in press). If we assume that the Chirikof Basin fraction of the population is in residence from 1 June to 30 October and if we use the maximum population estimate of 2479 whales for June, July and August and the estimate of 701 whales for September and October (includes 100 whales in vicinity of St. Lawrence Island) (Miller this report), then utilization by these whales would be on the order of 265, 170 whale-days. Total utilization of the Chirikof Basin would be on the order of 365,170 whale-days, 27% of which is by migrating whales.

Würsig et al. (this report) have estimated that gray whales made 198 feeding dives per day in July and 164 feeding dives per day in September. If we apply these estimates to the number of whale-days in the Chirikof Basin for summer residents, we obtain a total of 51.1 x 10^6 feeding dives for the entire resident population. We shall conservatively assume that whales en route to waters to the west and north make 164 feeding dives/day, the number of feeding dives recorded for whales in September by Würsig et al. (this report). Total number of feeding dives for whales migrating through the Chirikof Basin would be 16.4 x 106.

Total number of feeding dives made by gray whales in the Chirikof Basin during the tour se of a year would thus be on the order of 67.5 x 10^6. Mean area cleared during a feeding dive was estimated to be 15.5 m^2. Total area cleared would be 1046 x 10^6 m2 (1046 km^2).

The total area of the American Chirikof Basin used as foraging grounds by gray whales is approximately 20,000 to 27,000 km^2. The area cleared by whales represents about 4.4% of their feeding habitat in the Chirikof Basin. The side scan records made during this study indicate that mean area of bottom disturbed in the areas of the Chirikof Basin used by whales was 3.9% in July and 6.1% in September. Johnson et al. (1983), based on many side-scan sonar records collected in 1980, have estimated that 1200 km^2

of seabed (5.6%) within the above mentioned foraging grounds were disturbed by the whales during that summer. Oliver et al. (1984) have shown through field experiments off Vancouver Island that feeding features made in an ampliscid mat by grey whales do not persist more than one year. The above estimate of bottom disturbance, therefore, represents annual feeding pressure.

Food Consumption by Gray Whales

Estimate from Behavior and Observations of Feeding Features

Most previous estimates of feeding intensity and food consumption by baleen whales have been made on the basis of assumed energy requirements (Brodie 1975, 1981; Gaskin 1982). The discussion that follows represents an attempt to estimate food consumption by a baleen whale in its natural habitat through observations of behavior and mode of feeding.

Gray whales made a mean 198 feeding dives per day in July and 164 feeding dives per day in September (Würsig et al., this report). Feeding dives lasted 3.7 ± s.d. 1.0 min in July and 3.5 ± 1.4 min in September (Wursig et al. this report). Two varieties of features made by feeding whales were noted on the sea floor. Furrows were a mean of 47 m long and encompassed a mean area of 18 m^2, and feeding events composed of pits made on one dive encompassed a mean area of 13 m^2.

Unfortunately, we were unable to determine directly whether gray whales create one or more than one bottom feature composed of several pits or furrows per dive. Oliver et al. (1984) have observed a small gray whale making five pits 0.72 m2 in area on one dive of 3 to 4 min duration. It appears likely that gray whales can clear only one feeding feature per dive. They would have less than 4 min in which to clear over 800 kg of sediment from an area of 15.5 m^2. A great deal of water must be taken into the mouth while sucking mud off the bottom and this must also be processed through the baleen. In fact a large amount of water may be necessary to dilute the mud and keep it from consolidating on the baleen when expelling contents of the mouth, Most of the food consumed consists of benthic amphipods, based on comparison of benthic animals found inside and outside of feeding features and the examination of literature on stomach contents of summering gray whales. Airlift sampling has shown that most of these amphipods are found in the upper few centimetres of the substrate. Some of these amphipods are too small to be retained by the baleen. However, as shown above, these small amphipods account for less than 5% of the total biomass of benthic amphipods over most of the feeding range. A food retention efficiency of 95% is assumed in the following calculations.

Assuming that the whales consume only amphipods and do so with a 95% retention efficiency, clear a mean area of 15.5 m^2 per dive, and feed on mean concentrations of amphipods (133 g/m^2), then the average whale in the Chirikof Basin will consume 388 kg/day in July and 321 kg/day in September or a mean of 361 kg/day over the 150 days in the Chirikof Basin.

As previously discussed, gray whales probably feed selectively in areas with a high biomass of amphipods. Twenty-five percent of samples contained a biomass of amphipods greater than 200 g/m^2 and 10% contained greater than 250 g/m^2. Table 17 gives estimates of daily food consumption (averaged over the summer) by a gray whale selectively feeding in areas with an amphipod biomass higher than the mean of 133 g/m^2.

Table 17. Estimated daily gray whale food consumption at three assumed above-mean levels of amphipod biomass.

Assumed mean biomass of amphipods at feeding locations (g/m^2)	200	250	300
Food consumption (kg/d)	542	678	813

Estimate from Energetic Requirements

Daily food intake of gray whales was estimated using data on daily requirements of an active whale provided by Rice and Wolman (1971) and Sumich (1983). These values were compared to standard metabolism calculated according to Brodie's (1975) method.

Computations were made for an adult male gray whale 12.5 m in length and weighing 23 metric tons. The average whale taken by Russian whalers in the northern areas weighs 23 metric tons (calculated from data provided by Zimushko and Ivashin 1980 and Blokhin and Vladimirov 1983). A male was used to avoid the problem of accounting for pregnancy and lactation. A male of this weight is approximately 12.5 m long (Rice and Wolman 1971).

Separate calculations were made assuming that (1) whales feed sufficiently during migration to offset energetic requirements during that time, (2) feeding during migration accounts for only 50% of energetic requirements at that time, the remainder coming from reserves stored during shiner, and (3) feeding during migration provides a negligible proportion of a migrating whale's energetic requirements.

Standard Metabolism.—Standard metabolism of a cetacean includes basal metabolism and the energetic costs of buoyancy. This estimate of energetic requirements was calculated according to Brodie's (1975) method. Surface heat production was calculated from the following equation

$$H = k \frac{(36-Te)}{d}$$

Where H is the surface heat produced in $Kcal/m^2$ of surface area, k is conductivity of blubber (Brodie's 1975 figure of 21.18 $Kcal/m^2/h$ per degree difference for 1 cm thickness was used), Te is the temperature of the environment, d the depth of blubber in cm (taken as 13 cm from Rice and Wolman 1971), and 36 is the body core temperature in ‘C.

Mean temperature at the bottom of the Chirikof Basin in July was 2.5° ± s.d. 1.4°C (n = 9) and temperature at the surface was 5.3 * s.d. 2.7°C (n = 9)* In July, gray whales made 198 feeding dives/day lasting an average of 3.68 min per dive (Würsig et al., this report), or 12 h of feeding dives. If the remaining 12 h were spent at or near the surface then the average temperature of the whales' environment was 3.9°C. Surface heat production was, therefore, calculated to be 52.2 $Kcal/m^2/h$.

Sumich (1983) estimates the metabolically active surface area of a gray whale at 0.33 x (length in m)^2 or in this case 51.5 m^2. Thus, total heat loss from the surface was estimated at 64.5 x 10^3 Kcal/d.

Heat is also lost through respiration and warming of food. Volume per breath of 644 liters was calculated from mean lung capacity 2.65% of body weight (in kg; see below) and a tidal volume of 80% of capacity (Rice and Wolman 1971). During the summer the whales breathe once a minute (Würsig et al., this report). Mean air temperature in the Chirikof Basin in July was 7*C. Warming this air to 36°C at a rate of 0.2 Kcal/°C/L (Brodie 1975) involves a heat loss of 5.1 x 10^3 Kcal/day. This figure must be doubled to account for heat loss through humidification of the air (Brodie 1975). A further 30 x 10^3 Kcal/day is lost through warming food that is ingested (Brodie 1981).

Considering surface heat loss, respiration and warming of food, total heat loss in July would be on the order of 1.0 x 10^5 Kcal/day. Basal metabolism may also be calculated from the formula (Lockyer 1981)

$$(Q = 70.5 W^{0.7325})$$

where Q = basal metabolism in Kcal/d and W is the body weight in kg. For the 23 Mt gray whale under consideration basal metabolism would be 1.1 X10^5 Kcal/day. These figures represents standard and basal metabolism, If migrating and food gathering activities require energy expenditure above that allowed for by standard metabolism, then the additional energy expenditure must be added to these estimates (Brodie 1975).

Active Metabolism

Sumich (1983) estimated active metabolism of a gray whale through observations of the breathing rate of migrating animals. However, his estimate may be too high. He extrapolated tidal volume of a 6.2 Mt young gray whale with a total lung volume of 7% of body weight and a vital capacity of 50% of total lung capacity to an adult animal. The total lung capacity in large whales appears to be between 2.5 and 2.8% of body weight (Lockyer

1981). Vital capacity may be about 80% of total capacity, but appears to vary with activity levels. Lockyer, therefore, cautions about calculating metabolic rate from blow rate and swimming speed.

However, it is constructive to estimate metabolic rate from respiration rate using Sumich's (1983) method and different assumptions for comparison with other estimates. Breathing rates for gray whales are shown in Table 18. The following estimates for active metabolism assume a breathing rate of 1.1 blows/rein while on the feeding grounds, and 0.72 blows/rein while migrating and while on the winter grounds. Total annual energy expenditure and the food required to meet this expenditure for a 23 Mt gray whale are shown in Table 19.

Table 18. Breathing rates for gray whales in various locations and under various activity levels. Values are average for that activity.

Location/Activity	Speed (m/s)	Blow/min	source
Winter Grounds			
Resting		0.5	Sumich (1983)
Resting		0.5	Harvey and Mate (in press)
Swimming	1.1	1.0	Harvey and Mate (in press)
California			
Migrating	1	0.52	Sumich (1983)
	2	0.69	Sumich (1983)
	3	1.14	Sumich (1983)
Average	1.97	0.72	Sumich (1983)
Feeding Grounds			
All activity, July		0.997	Würsig et al. (this report)
All activity, September "		1.122	Würsig et al. (this report)
Shallow water feeding <20 m, July		0.794	Würsig et al. (this report)
Deep water feeding 20-40 m, July		1.043	Würsig et al. (this report)
60-80 m, July		1.193	Würsig et al. (this report)
Shallow water feeding <20 m, September		1.085	Würsig et al. (this report)
Deep water feeding 20-40 m, September		1.116	Würsig et al. (this report)

Table 19. Annual food requirements of a 23 Mt male gray whale calculated from the breathing rate using Sumich's 1983 method.

Area/ Activity	Days	Breathing rate (blows/rein)	Oxygen Consumption[a] (litres x 10^6)	Energy Expended[b] (Kcal x 10^6)	Food Required[c] (kg)
Winter	62	0.72	3.13	15.12	25,511
Migration	153	0.72	7.73	37.32	62,956
Chirikof Basin	150	1.10	11.59	55.90	94,297
				108.34	182,765

[a] Assumes total lung volume of 2.65% body weight and that tidal volume is 80% of total (Lockyer 1981).

[b] Assumes that 1 litre of oxygen metabolizes 4.825 Kcal (Lockyer 1981).

c Assumes dry weight is 15% of wet weight, caloric value of amphipods is 5.2 Kcal/g dry weight, assimilation efficiency is 80%, and baleen retention efficiency is 95% (Stoker 1978; Lockyer 1981).

Daily ration calculated by the respiration method and averaged over the year would be 501 kg per day. Assuming no net gain or loss in energy stores during migration, a summering whale would have to collect 629 kg/d to meet its daily requirements while on the feeding grounds plus 170 kg/d to store energy for the 62 days it spends off the Baja. If the whales consume half their daily energetic requirements through" feeding during the 152 days of migration, then a further 210 kg/d must be collected during summer to account for the other half of the energy needed for migration (i.e. a total of 1009 kg/d). If no feeding at all occurs during migration then whales feeding on the summer grounds must consume 1218 kg/d.

Averaged over the year, metabolic requirements calculated by this method would be almost 3.0 x 10^5 Kcal/d or about three times basal metabolism, and food consumption necessary to meet these requirements would be about 501 kg/d or about 2.2% of body weight per day (8 times body weight per year). In comparison, Hinga (1979) has collected data on the feeding rates of captive cetacea ranging in weight from 100 to 6000 kg and found energy usage between 1.5 and three times the basal rate. However, Gaskin (1982) cautions against using metabolic data from captive animals because many tend to be overfed and become obese.

Through an exhaustive study of food, feeding habits, feeding rates and energetic computations that allowed for growth, Lockyer (1981) concluded that blue and fin whales consume approximately five times their body weight in one year. Applying this value to the 23 Mt gray whale yields an average daily ration of 315 kg of amphipods. In order to store enough energy for the time spent on wintering grounds, the whale would have to consume a total of 445 kg/d while on the feeding grounds, according to this method of calculation. If energy must be stored for half the migration, then food consumption must be on the order of 604 kg/d for the 150 d spent on the summering grounds.

Comparison of Estimates

The eleven estimates of food consumption (Table 20) determined by four different methods represent a wide range of feeding rates. The greatest unknown in the calculations is the amount of feeding that occurs during migration. There is little evidence of benthic feeding while on the winter grounds (Oliver et al. 1983) but there is fairly strong evidence of pelagic feeding (Norris et al. 1983).

Available knowledge about gray whale behavior during migration makes it unrealistic to accept either that whales feed throughout the migration or not at all. Food consumption during migration was estimated as follows. South of Vancouver Island, mean traveling speed is over 4 km/h during both the northward and southward migrations and feeding is negligible (see Migration). North of the Aleutians, traveling speed is 2 km/h and feeding activity is extensive in the whole area. Therefore, we shall assume that on those portions of the route that involve traveling at 2 km/h, whales feed sufficiently to offset the energetic *cost* of migration. This would occur over all of the route north of Vancouver Island for northbound whales (70 days) and north of the Aleutians for southbound whales (22 days, see Migration). Sixty-one days are spent feeding only sporadically along the migration route and 62 days are spent *on* the winter grounds.

Energetic requirements based on our calculations from respiration rate data required the whale to consume 799 to 1218 kg/day while on their summer foraging grounds (Table 20). This is greater than the range of values

Table 20. Daily food intake of gray whales while on their summer feeding grounds calculated by four different methods. Also shown is the standing crop of amphipods necessary to meet these requirements assuming 198 feeding dives/day in June, July and August and 164/d in September and October, 15.5 m^2 cleared per dive, a retention efficiency of 95% and an assimilation efficiency of 80%.

Methods and Assumptions	Daily Food Intake kg (wet weight)	Biomass of Amphipods[1] (g/m^2)
1. Behavior, analysis of furrows		
(a) feeding on mean amphipod density	361	133
(b) feeding on 200 g/m^2 of amphipods	542	200
(c) feeding on 250 g/m^2 of amphipods	678	250
(d) feeding on 300 g/m^2 of amphipods	813	300
2. Energetic, daily ration + storage for winter		
Respiration		
(a) no storage for migration	799	280
(b) storage for 1/2 migration	1009	356
(c) storage for all migration	1218	427
Using Lockyer's assumptions		
(a) no storage for migration	445	164
(b) storage for 1/2 migration	604	223
(c) storage for all migration	763	281
3. **Analysis of stomach contents[2]**	1200	443

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[1] Biomass of amphipods that whales must feed on to meet the daily intake shown.

[2] Zimushko and Lenskaya (1970).

derived from examination of behavior and food removal. A feeding rate of 1009 kg/day determined by the respiration method allows for storage of energy required for one half of the migration and requires a standing stock of 356 g of amphipods/m^2. Only a few of our samples contained a biomass of amphipods greater than 350 g/m^2.

Based on Lockyer's (1981) assumptions, a feeding rate of 604 kg/d would store energy for about half the migration and for winter. Based on our data concerning behavior and size of feeding events, this feeding rate would require feeding on concentrations of amphipods of about 223 g/m^2. This value represents the mean biomass in the 35% of our samples that contained the highest biomass.

The estimate of energy intake based on . observations of whale behavior and furrow characteristics may be 678 kg/whale/day (estimate 1c in Table 20). As previously mentioned, gray whales preferentially feed in areas with a higher than average standing crop of amphipods and this feeding rate requires.. whales to seek. out areas with a mean amphipod biomass of 250 g/m^2. Using Sumich's (1983) method based on respiration, feeding at a rate of 678 kg/d would not allow sufficient energy storage to meet the requirements of migration or the 62 days spent wintering off Baja California. In order to balance the annual energy budget using Sumich's method, the whale would have to feed at an average daily rate of 678 kg/d for the entire 150 days spent on the northern feeding grounds and during the 92 days of migration when whales travel at speeds of 2 km/h; furthermore, the whales would have to meet 40% of the daily requirements (271 kg wet weight of food/d) on the remainder of the migration route and while on their wintering grounds off Baja. In contrast, the 678 kg/d estimate from food removal and behavior does meet energetic requirements as computed using Lockyer’s (1981) assumptions, provided that some feeding occurs during migration (Table 20).

A comparison of five estimates of gray whale energetic is presented in Table 21. The estimates based on food removal and energetic using Lockyer's assumptions and our calculations of respiration all fall within the envelope of acceptable values developed for feeding rates of captive cetaceans by Hinga (1979) which, as previously mentioned, may be too high. The active metabolic rate for a gray whale calculated by Sumich (1983) may also be too high. It is 3.8 times basal metabolism and as such is higher than Hinga's 1979 envelope of values. It is also worth noting that the metabolic rate computed from observations of behavior and furrows would fall below this envelope if whales fed on mean concentrations of amphipods.

Our best estimate of the feeding rate while on the summer grounds would be between 600 and 700 kg/d (650 kg/d will be used in following computations). Using Lockyer’s assumptions this would allow for storage for all the

Table 21. Comparison of estimates of energetic requirements of gray whales.

Method	Weight (kg)	Daily Energy Expenditure		Food Required to Meet Requirements		
		Kcal/d	as a multiple of basal metabolism	kg/d[1]	% Body wt per day	as a multiple of body wt/yr
Theoretical/EMR	23,000	1.1 X105		186	0.8	3.0
Respiration	23,000	3.0 x 10^5	2*7	501	2.2	7.9
Food removal[3]	23,000	2.5 X 10^5	2.3	420	1.8	6.7
Energetics[4]	23,000	1.9 x 10^5	1.7	315	1.4	5.0
Respiration[5] Weight Loss	23,000	4.2 X 10^5	3.8	708	3.0	11.2

[1] Averaged over the year.

[2] Calculated using Sumich's (1983) method and Lockyer's data on lung volume and vital capacity.

[3] Assumes feeding at 678 kg/d for 1/2 the migration period and all of the time on the summer grounds. See text.

[4] Using Lockyer's assumptions.

[5] AS presented by Sumich (1983) converted to 23,000 kg whale.

time spent off Baja California and for 1/2 the migration period. This would necessitate that the whales feed on a mean biomass of about 220 to 260 g/m². Based on the total number of whale days in the Chirikof Basin as determined above (365, 000), total food removed by the whales would be about 10 g/m² for the 23,500 km² of the Chirikof Basin used by gray whales.

Mean biomass of amphipods in the area of the Chirikof Basin utilized by gray whales is 133 g/m². The productivity to biomass ratio for amphipods in the area was 1.9 (Thomson, this report) . The above value for food removed represents about 7.5% of standing stock and 4% of productivity of the amphipods.

Trophic Interactions Between Gray Whales and Benthic Animals

In the following discussion, we attempt to trace the flow of energy through the benthic food web of that portion of the Chirikof Basin utilized by feeding gray whales. This type of exercise is useful in that it identifies major energy pathways and key components in the food web. In this case, the purpose is to compare the food removal by gray whales with food availability and removal by other components in the benthic food web.

Animals taken in grab and airlift samples were assigned to feeding guilds according to the nomenclature and definitions of Fauchald and Jumars (1979). Information on the trophic position of each species was taken from Fauchald and Jumars (1979), Stoker (1978) and Thomson (this report).

Filter feeders include bivalves of the genera Liocyma, Serripes, Astarte, Hiatella, sabellid polychaetes, tunicates, and some phoxocephalid and haustoriid amphipods. These animals filter the water, extracting phytoplankton, small zooplankton and detritus.

Surface deposit feeders feed at the water/substrate interface and include ampeliscid amphipods, cumaceans, and bivalves of the genera Macoma and Yoldia.

Deposit feeders often burrow through the mud and ingest it to extract nutritive value. This group included many polychaetes and some holothurians. Carnivores and scavengers included polychaetes of the genus Nephtys, lysianassid amphipods, starfish, and some isopods.

Surface deposit feeders, mainly amphipods, comprised 63 to 75% of standing crop within those portions of the study area utilized by gray whales (Table 22). Filter feeders were next in order of importance, comprising 5 to 19% of standing crop. Carnivores and scavengers comprised between 9 and 19% of standing crop. The guild whose abundance differed most between areas that were and were not used as foraging grounds by gray whales was the surface deposit feeding guild (Table 22).

In the central Chirikof Basin, grab samples contained a mean of 6.05 liters of substrate with a carbon content of 2.9 g/kg. Assuming a water content of 10% and a specific gravity of 2.7, the mud associated with the animals taken in the grab contained a mean of 252.9 g C/m^2. Some of this carbon was in the form of bacteria, meiofauna and nutritive detritus directly utilizable by animals. Some of it was refractory and of little nutritive value. The low carbon to nitrogen ratio found in this region (7.0 ± s.d 1.0,

Table 22. - biomass (g %?) and percent of total 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 - was accomplished using data provided by Stoker (1978).

Area	No. samples	Surface deposit feeders		Deposit feeders		Filter feeders		Carnivores, scavengers		Not classified	Total
		g C/m^2	%	g C/m^2	%	g C/m^2	%	g C/m^2	%	%	g C/m^2
Chirikof Basin											
Ares not used by ties	38	2.2	33	0.8	12	1.2	18	1.0	15	22	6.7
Area used by whales	37	11.3	75	0.5	3	O*7	5	1.5	10	7	15.0
St. Lawrence Island											
West mast	11	11.5	63	1.0	10	2.7	15	1.6	9	4	18.4
South coast	15	10.2	64	0.4	3	3.0	19	1.6	10	4	15.9
Southeast cape (offshore)	10	13.2	71	0.7	4	1.9	10	1.5	8	6	18.5
(nearshore)	55	10.1	64	0.9	6	1.0	6	3.0	19	6	15.9

n = 8) indicates that much of this organic matter may have been of direct use to the animals.

To estimate total productivity of ‘the benthos, we multiplied measured biomass by assumed production to biomass ratios. Most of the surface deposit feeders were amphipods. Thomson (this report) determined a productivity to biomass ratio of 1.9 for the dominant amphipods in this region. Polychaetes in west Greenland have a productivity-to-biomass ratio approaching unity (Curtis 1977) and this value was used to approximate productivity of polychaetes. Stoker (1978) found a productivity-to-biomass ratio of 0.32 for Macoma calcarea. Stoker claimed, however, that this estimate is too low. In the following computations we have conservatively estimated a productivity to biomass ratio of one for bivalves. A productivity to biomass ratio of one was also applied to all other groups. A gross production to consumption efficiency of 0.15 was assumed for all groups. Values for productivity of zooplankton in the area north of St. Lawrence Island were taken from Ikeda and Motoda (1979).

Consumption by whales was calculated as follows. The previously derived estimate of 650 kg per whale per day was assumed for the previously determined 365,000 whale-days in the 23,500 km^2 of the Chirikof Basin utilized by gray whales. Wet weight was converted to carbon using data provided by Stoker (1978). Total consumption by whales in the Chirikof Basin would be on the order of 237 x 10^6 kg/yr or 10 g/m^2 wet weight (0.7 g C/m^2).

Figure 18 summarizes these estimates of standing crop, productivity and energy flow between the various components of the benthic ecosystem of the central Chirikof Basin. Benthic deposit feeders consume more than one half of the available carbon in sediments. Filter feeders, on the other hand, appear to consume only a small fraction of primary productivity. Productivity of the benthic filter and deposit feeders as a whole may approach 23 g C/m^2/yr and as such appears larger than the estimated productivity of zooplankton. Infaunal benthic carnivores consume approximately one half of the productivity of filter and deposit feeders. Gray whales, on the other hand, consume about 5% of total benthic standing crop and 3% of

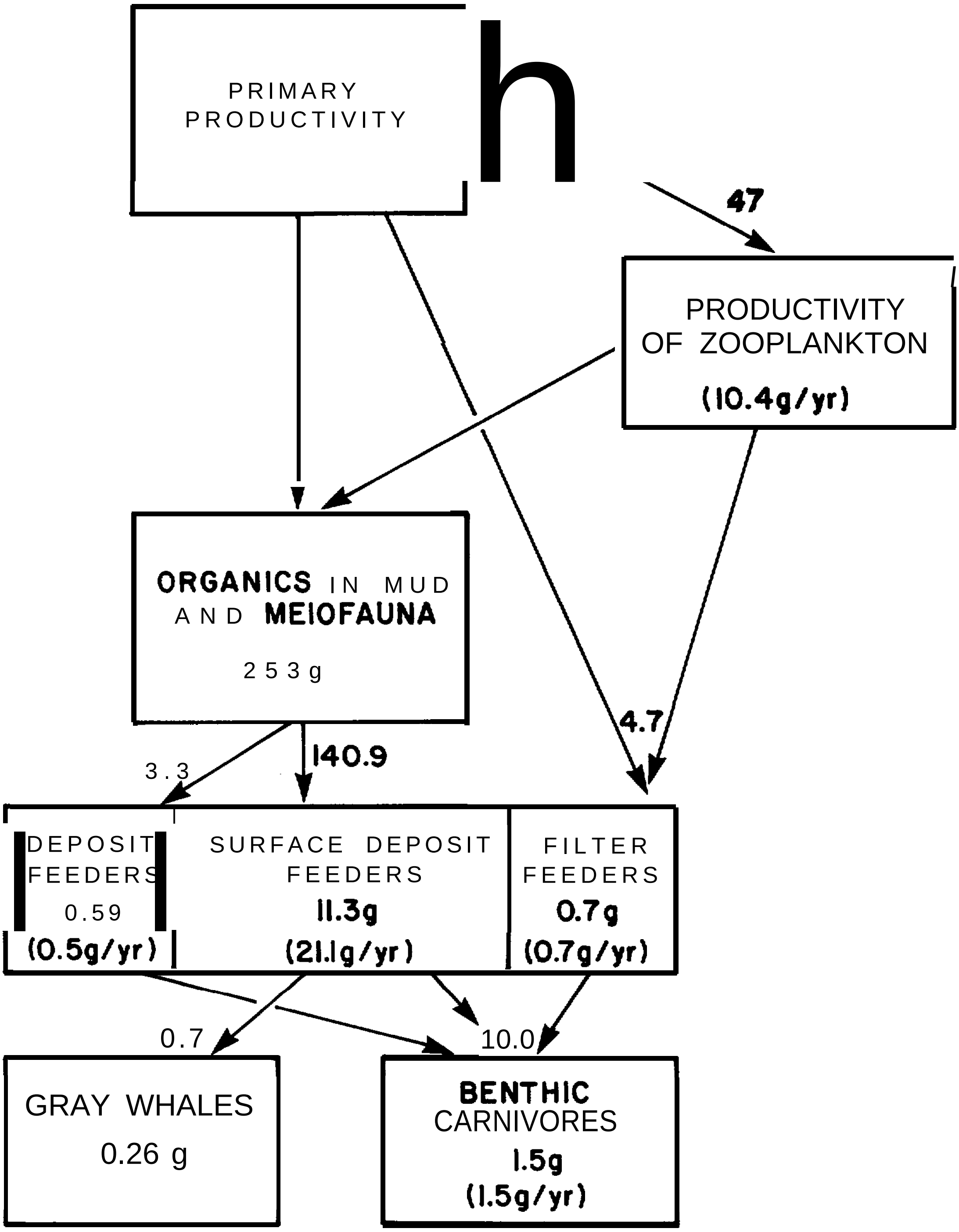

FIGURE 18. Energy flow through the benthos of that part of the Chirikof Basin utilized by feeding gray whales. All values are expressed as g Carbon/m^2. Transfer of energy (g C/m^2/yr) is noted beside arrows. Standing crop and productivity (in parentheses) are shown within the blocks.

productivity. They consume approximately 7.5% of the standing crop of amphipods, their primary food source, and approximately 4% of amphipod productivity. The remaining 23 g C/m^2 annual benthic productivity is available to walrus, bearded seal, ringed seal, fish and large epibenthic animals.

Overall, gray whale food requirements do not appear to be as close to the carrying capacity of their environment- as are the food requirements of some other consumers. The Pacific walrus is believed to be near the carrying capacity of its environment in that its annual consumption of the bivalves that form its major food resource approaches the annual productivity (Fay et al. 1977). In the North Sea, demersal fish consume approximately 60% of the annual productivity of the benthos (Crisp 1975). In *contrast,* gray whales *in* the Chirikof Basin consume approximately 4% of the productivity of the benthic amphipods. However, as previously mentioned, gray whales appear to selectively feed in areas with a higher than average standing crop of benthic animals and energetic computations show that they may, in fact, have to do so in order to survive. The areal extent of areas with a sufficient standing crop of amphipods usable as a food resource for the gray whales within 23,500 km^2 identified as suitable feeding habitat is unknown. About 30% of our samples contained a mean biomass of amphipods sufficient to meet the needs of the whales.

IMPLICATIONS FOR DEVELOPMENT

The Chirikof Basin appears to be a major migration corridor for gray whales and is the foraging grounds for at least 14% of the population over the summer. Feeding pressure by migrating and resident whales appears to be low when compared to the overall food resource in the area. However, gray whales appear to feed selectively in areas with a high biomass of amphipods. As shown by the uneven distributions of feeding features and of whales, some areas are heavily utilized and some are not.

Darling (in press) has theorized on the basis of his own work and information presented in the Russian literature that gray whales occupy 'pockets' of suitable habitat and move quickly between these. In order to meet the requirements of food storage for migration and the stay off the Baja, it appears that gray whales may have to feed in areas with an extremely high biomass of amphipods. These prime areas may represent only a small fraction of apparently suitable habitat in the Chirikof Basin. Several heavily utilized areas are evident in. Figure 15. Our survey of the Chirikof Basin was by no means comprehensive and we cannot identify all of the areas that are more important than others within the 23,500 km^2 of suitable habitat defined by us, Johnson et al. (1983), Nerini (in press), and Ljungblad et al. (1982).

The primary concern with regard to potential development would be disruption or denial to the whales of 'pockets' of prime feeding habitat. This might have an effect on the whales out of proportion to the area affected.

LIMITATIONS, DATA GAPS AND RECOMMENDED STUDIES

Our estimates of food consumption and utilization of the American Chirikof Basin by gray whales are based on several major kinds of data of varying precision. In the following section, we identify those data in which we lack a reasonable degree of confidence and outline the kinds of studies needed to strengthen the estimates.

1. Migration: A great deal is known about migration routes and timing for gray whales in the vicinity of Unimak Pass and south of Vancouver Island. However, the nature and extent of use of the Chirikof Basin by whales en route to and from Siberia and the Chukchi Sea are poorly known. Systematic surveys would have to be conducted at monthly or shorter intervals from May through November to determine numbers, movements and frequency of feeding for gray whales in the Chirikof Basin. Some of the requisite data have been collected by Ljungblad et al. (1982, pers. comm.) but not yet reported in detail. The amount of feeding that occurs along the migration route is also unknown. This information is required for more precise energetic computations.

2. Behavior: Our estimates of feeding dive duration, blow rates and surface times are based on large data sets from July and September of one year. Our estimates of the percentage of time that a whale spends feeding are rough and should be refined by prolonged observations of individual whales. It is possible that some whales travel between 'pockets' of concentrated food. These whales should be distinguished from whales feeding in 'pockets'. The apparent tenacity of individual gray whales with respect to particular feeding locations requires further study, as does the possibility that specific feeding territories may exist.

Movements and behavior of whales resident in the study area should be studied along the lines of the work performed by Darling (in press) off Vancouver Island. Shore-based work at St. Lawrence Island could provide much additional information on the behavior of summering gray whales.

3. Food removal: Our estimate of the amount of food removed during an average dive is weak, mainly because we obtained no direct underwater observations of feeding whales. Single bottom features made by one whale during one dive should be isolated by divers, the area determined, and the standing crop of potential prey organisms immediately adjacent to the feature determined. This sampling should be conducted over the season to determine changes (if any) in mode of feeding. A large number of features would have to be sampled to determine the extent of small scale selectivity of feeding sites by the whales.

4. Studies of the gray whale may offer the only opportunity to obtain detailed and precise data concerning the energy budget of *a* large cetacean. The gray whale's mode of feeding lends itself to the determination of food consumption in nature. An energy budget incorporating accurate estimates of food consumption in nature would provide valuable insight into the energetic requirements of large cetaceans that migrate and store food for a period of relative food scarcity.

   The present procedure for estimating energetic requirements is based on assumed lung capacity, assumed oxygen utilization, and estimated weight loss during winter. Estimates of weight loss while in Baja are useful but must be used with caution. It is uncertain whether all of the weight loss by non-pregnant females in winter is due to metabolic requirements. Whales may be overinsulated for tropical waters (Gaskin 1982) and some weight loss may ***represent*** adaptation to warm water.

   High technology telemetric techniques may offer an opportunity to refine some of the data used in energetic computations. Measurements of CO_2 content of expelled air and temperature at various depths in the blubber of active animals would be helpful. Positional and movement data obtainable via telemetry (especially satellite telemetry) would also assist in characterizing behavior during the parts of the migrations that have not been studied in detail.

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