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ORIGINAL PAPER

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The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard

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Abstract We studied the influence of the distribution of prey and hydrographic fronts on the spatial distribution of foraging Brünnich's guillemots (*Uria lomvia*) in Storfjorden, southeastern Svalbard in late July 1992. Two large breeding colonies, comprising a total of 540,000 individuals, were located adjacent to the study area, and large numbers of Brünnich's guillemots from these colonies foraged within the area, as well as to the south, outside of Storfjorden. Within the study area, most guillemots foraged on the west side of the fjord, coincident with a weak subsurface front between warm Atlantic water, which penetrated Storfjorden from the south, and cold Arctic water. Food samples from the guillemots collected in the study area contained primarily crustaceans (*Parathemisto* spp. and *Thysanoessa inermis*) and polar cod *Boreogadus saida*. Acoustic observations of prey were differentiated into two classes of signals, which we interpreted as originating from aggregated and dispersed organisms. The numbers of foraging guillemots were strongly correlated with the strength of echoes of the aggregated type, whereas correlations with dispersed echoes were consistently weaker. The distribution of foraging guillemots showed no significant correlations with either horizontal or vertical gradients of physical properties of the water column. Our finding that guillemots respond differently to aggregated and dispersed prey has important implications both for the interpretation of past work on the

foraging ecology of marine birds, and for the management of fisheries.

Introduction

The Brünnich's guillemot (*Uria lomvia*) constitutes a major component of the seabird community in waters surrounding the high-arctic archipelago of Svalbard, where about 1.3 million individuals occupy breeding colonies (Mehlum and Bakken 1994). The largest breeding colonies are located in the southeastern part of the archipelago, and nearly half of the breeding population is located in the Storfjorden area (Figs. 1, 2). The two main seabird colonies in Storfjorden are Stellingfjellet (77°06'N, 17°20'E) and the adjacent Kovalskifjellet (77°03'N, 17°17'E) (Fig. 2), where the numbers of Brünnich's guillemots have been estimated recently at 450,000 and 90,000 individuals, respectively (Mehlum and Bakken 1994). During the breeding season, the guillemots in these colonies show a great demand for food, both for feeding themselves and for provisioning their chicks (Mehlum and Gabrielsen 1993). Brünnich's guillemots provision their nestlings almost exclusively with fish, whereas the adults may also consume a large proportion of crustaceans (Bradstreet and Brown 1985; Decker et al. 1995).

Little information is available on the foraging ecology of Brünnich's guillemots at sea during their breeding season. Kinder et al. (1983) and Decker (1995) demonstrated that Brünnich's guillemots were concentrated at tidal fronts around the Pribilof Islands during summer. They hypothesized that these concentrations were related to an enhanced availability of prey. Schneider et al. (1990) showed that such aggregations occurred where currents interacted with bathymetry to force the pycnocline to the surface, and Coyle et al. (1992) found that guillemots foraged where tidally forced upwelling opposed the downward swimming of euphausiid prey.

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Fig. 1 Svalbard Archipelago and the northern Barents Sea; the study area in Storfjorden is indicated by a box. The 100-m, 200-m, and 500-m depth contours are given

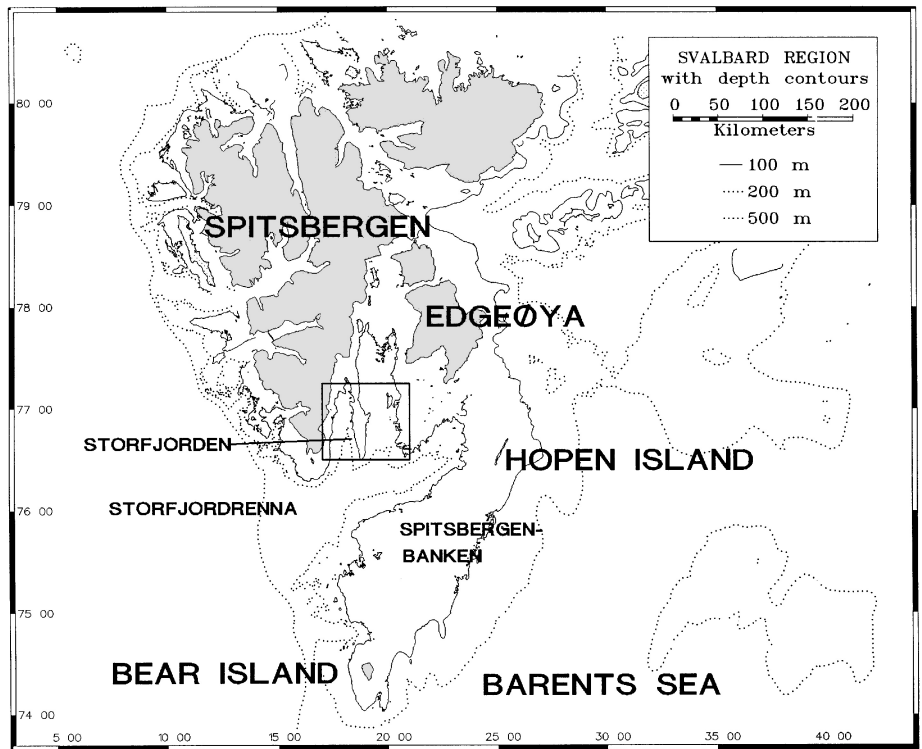
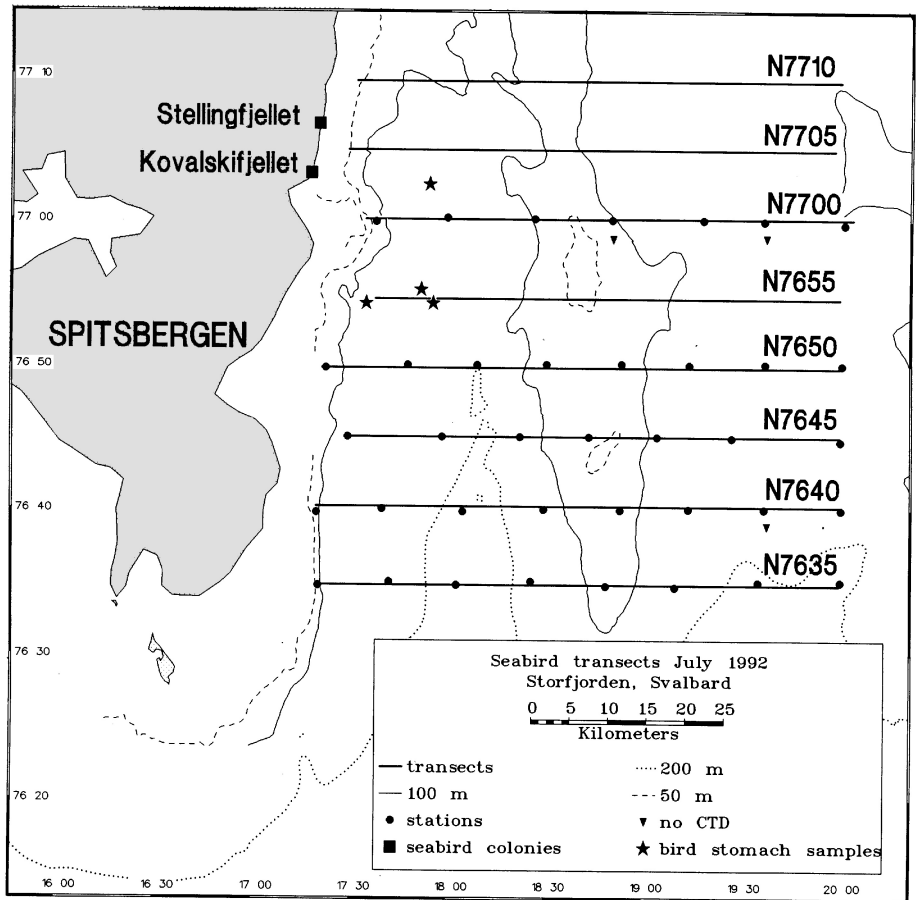


Fig. 2 Eight east-west seabird transects and sampling stations included in the study. Hydroacoustic data were obtained along the same five transects as those with stations. Each transect is named according to its latitude. The 50-m, 100-m and 200-m bathymetry contours are shown



During the chick-rearing season, the foraging radius of seabirds is constrained by the delivery rate of prey to chicks. Seabirds, however, often travel considerable distances to forage (reviewed by Bradstreet and Brown 1985). The mechanisms used by seabirds for selecting their foraging area, the types of cues used to locate prey, and the extent to which foraging information is transferred between individuals are not known.

In this paper, at a scale of ~ 10 km we analyzed the distribution and abundance of foraging Brünnich's guillemots in relation to physical oceanography and acoustically determined biomass in Storfjorden. We also sought evidence for physical processes or features in the ocean that might enhance the concentration or availability of prey to guillemots.

Materials and methods

Study area

Storfjorden is a shallow fjord with depths < 180 m (Fig. 1). A north-south oriented submarine ridge is located in the western part of the fjord. A deeper canyon, Storfjordrenna, is located south of the mouth of Storfjorden through which warm Atlantic water penetrates from the west. Further south is a shallow bank, Spitsbergenbanken (or Svalbardbanken). Anderson et al. (1988) and Quadfasel et al. (1988) found three different layers of water in Storfjorden during the summer: (1) relatively warm and low salinity near-surface water, which is influenced by summer warming and melting of ice; (2) warm Atlantic water (at 50–70 m depth); and (3) cold bottom water. The area is usually completely ice-covered during winter. At the start of our study (20 July) there was no sea-ice present in the portion of Storfjorden at which the study took place.

Survey design

We studied a major foraging area of Brünnich's guillemots exploited by the two large breeding colonies of Stellingfjellet and Kovalskifjellet. We selected a grid of latitudinal transects (59–68 km in length) from shallow waters near the eastern coast of Spitsbergen and eastward to $20^{\circ}00'E$, at $5'$ intervals (9 km) north-south from $76^{\circ}35'N$ to $77^{\circ}10'N$ (Fig. 2). Studies from previous years (F. Mehlum, unpublished work) had indicated that few Brünnich's guillemots from the two colonies fly in northern or northeastern directions for foraging; thus, most of our transect lines were selected to the east and south of the colonies. The previous studies also indicated that few guillemots foraged east of $20^{\circ}E$. All latitudinal transects (8) were surveyed once during the period 20–31 July 1992. We also conducted a transect northward from $76^{\circ}45'N$, $17^{\circ}34'E$ to $78^{\circ}16'N$, $20^{\circ}17'E$ to confirm that few guillemots foraged to the north or northeast of the colonies. Seabirds were registered on all transects; the locations of CTD casts are shown in Fig. 2. Hydroacoustic data were obtained along five of the transects. On transects where hydroacoustic work was done, the ship's speed was reduced from a normal cruising speed of 10–11 knots to 5.0–5.5 knots.

Data collection

Birds

The abundance of Brünnich's guillemots observed sitting on the sea surface was recorded from the research vessel *Lance* using standard-

ized transect methods (Tasker et al. 1984). A 300-m standard transect width was used and the presence of all birds observed within the transect was registered directly using a computer. Individuals spaced less than 10 m from each other were treated as a group. The computer's clock was synchronized with the ship's clock. The ship's geographical position (GPS system) was entered into the field computer every 30 min–1 h during periods with steady course and speed, and otherwise when any changes in speed or direction occurred.

Foraging birds were collected using a shotgun from a small boat. Only 1 of 18 birds examined did not have a brood patch, which indicates that these samples were mainly from breeding individuals. Stomach and esophagus contents were stored in alcohol within 1 h after collection. The food items were identified to the lowest taxon possible. Fish otoliths were measured to the nearest 0.5 mm. Two otoliths that differed less than 0.5 mm in length were considered to be from the same fish. We assumed that unidentified partly digested fish belonged to the same species as otoliths found in the same bird, if the fish's length was similar to that estimated from otolith length. We used the equation provided by Frost and Lowry (1981) for conversion from otolith length to fish length for polar cod *Boreogadus saida*.

We used the *frequency of occurrence* and the *numerical abundance* of different prey taxa in the analysis of the diet (Duffy and Jackson 1986). *Frequency of occurrence* was determined as the percentage of sampled birds in which the prey type occurred. *Numerical abundance* was defined as the percentage in numbers of a prey type compared to the total number of identified prey items.

Oceanography

The distance between oceanographic stations was 8–11 km, but in some cases single stations were omitted because of technical problems. Profiles of temperature and salinity as a function of depth were obtained by using an ME-CTD probe (Meerestechnik Electronics). For calibration of the conductivity cell, water samples were collected using a Niskin bottle attached to the wire above the CTD. All water samples were collected at the bottom of each station. The ME-CTD was equipped with a bottom alarm and a ca. 290-m wire. At stations shallower than 290 m, data were collected down to about 5 m above the bottom, and at the deeper stations to the end of the wire.

Acoustics

Acoustic data were obtained using a single beam/single frequency echo sounder (LAZ 4700 ELAC) operating at 30 kHz. The transducer with a full beam angle of 16° was mounted inside a V-fin body towed at a depth of 2–3.5 m. The source level and sensitivity of the acoustical system were measured before and after the cruise using a hydrophone (B&K 8100) and a copper calibration sphere. The time interval of ping repetition was 0.56 s and ping duration was usually 0.6 ms. The echo envelope voltages for each ping were converted to digital form at the rate of 3 (or 4) kHz, using 12-bit resolution in real time, and were stored on a hard disk in blocks of 128 pings. Because of imperfections in the hardware TVG (Time-Variied-Gain) function, corrections were made during post-processing for the attenuation and spreading losses of sound in the seawater, as well as for nonlinearity of the system. Because we do not know the target strength of the organisms detected by the echo sounder, echo signals are represented as volts^2 only. Estimates of biomass are not essential in this study because we are interested in relative differences in acoustically detected biomass between different parts of transects. During most of the transects the sea was calm (0–1 Beaufort scale), and therefore unwanted noise and excess attenuation of acoustical signals from bubbles were low.

Post-processing of echo signals included: filtering out the ship's echo sounder signals, echo type recognition, integration of echo

intensity in layers and along the transects, and examination of the statistical properties of signals and space-depth distribution. The sampling window for the quantitative analysis was in the interval 10–50 m depth. The acoustic signals were classified into two groups, dense concentrations of targets (echo type A – aggregated), and dispersed targets (echo type D – dispersed). A simple algorithm for discriminating between the two different type of echoes was developed, based on the dimension and the strength of the echoes. The methods used for removing echoes from the ship’s depth sounder, and the algorithm for discriminating between the two types of targets are presented in Appendix 1.

Data analyses

The abundance of Brünnich’s guillemots was represented as the number of birds recorded per kilometer transect length between neighboring CTD stations. We tested the hypothesis that there were no relationships between the abundance of birds along transects and echo return or physical oceanographic gradients.

Spearman Rank correlation coefficients were computed for bird abundance vs echo returns in 10–15, 15–20, 20–25, 25–50, and 10–50 m depth intervals for total echo return, and for type A and type D echoes, separately. In each depth interval, the acoustic data were averaged over the transect interval between two neighboring stations. Bin sizes equalled the distance between neighboring stations (8–11 km). The significance levels of the correlations were set at $P < 0.05$.

We also computed Spearman Rank correlation coefficients for both horizontal and vertical gradient strength of temperature and salinity at four depth intervals versus bird abundance, echo type A and echo type D. Horizontal gradients are given as the gradient strength per kilometer distance between neighboring CTD stations along transects at the four depth intervals (10–15, 15–20, 20–25 and 25–50 m). For each depth interval, the gradients were computed by first calculating a regression line through each meter depth value at the actual depth interval for each of two neighboring stations (1 and 2). From these two regression lines, average values of temperature T_{i1} and T_{i2} or salinity S_{i1} and S_{i2} for the depth interval at each of the two stations were estimated. Horizontal temperature and salinity gradients were calculated using the formulae:

$$\Delta TH_i = \frac{|T_{i1} - T_{i2}|}{d} \quad \text{and} \quad \Delta SH_i = \frac{|S_{i1} - S_{i2}|}{d}$$

where i = depth interval, and d = distance in km.

Vertical gradients between neighboring CTD stations (1 and 2) at depth interval i are given as the gradient per meter depth using the formula:

$$\Delta TV_i = 0.5 \cdot \frac{(T_{1a} + T_{1b}) - (T_{2a} + T_{2b})}{b - a}$$

where a = upper and b = lower range of the depth interval, respectively. A corresponding formula was used to calculate salinity gradients where salinity values were substituted for temperatures.

Results

Bird transects

The highest average densities of Brünnich’s guillemots were recorded on the transects just south of the large breeding colonies Stellingfjellet and Kovalskifjellet (Table 1, Fig. 3). Brünnich’s guillemots were mainly concentrated on the water in the western portion of the transects. However, we observed a few birds close to the colonies, and peak abundances were found over areas of deep water (100–200 m) between the coast of Spitsbergen and the north-south submarine ridge in central Storfjorden. On the 77°00’N transect, high numbers of birds were also recorded in the eastern part of the transect. The abundance of birds observed on a transect decreased as one moved to the southern part of the study area. From 76°45’N and southward, peaks in bird numbers were less pronounced (Table 1, Fig. 3). The numbers of guillemots to the north of the 77°10’N transect were low (Fig. 3). The average density of Brünnich’s guillemots observed during our east-west transects was 13.8 birds per km². In addition to the birds on the water, considerable numbers of guillemots were observed on the western portion of the transects flying southward, out of the study area.

Group sizes of birds on the water

The distribution of group sizes of guillemots varied among the transects (Table 1). Most groups were small, and single birds composed from 14.0% (76°55’N) to 52.3% (76°40’N) of all birds along transects, corresponding to 41.9–74.3% of all groups. The largest median group sizes were recorded on transects close to the colonies (77°05’N, 77°00’N, and 76°55’N) (Table 1).

Table 1 Numbers of Brünnich’s guillemots on the water and the distribution of group sizes of birds along the transects

| Transect/ latitude | Transect length (km) | Total no. of birds | Average density of birds (per km ²) | Total no. of groups | Median group size | Range in group sizes | Percent of single individuals | Percent of birds in groups > 5 |
|-----------------------|----------------------------|-----------------------|--|------------------------|-------------------------|----------------------------|-------------------------------------|--------------------------------------|
| 77°10’N | 61 | 248 | 13.6 | 109 | 1 | 1–40 | 21.9 | 37.7 |
| 77°05’N | 61 | 380 | 20.8 | 255 | 2 | 1–20 | 47.8 | 9.2 |
| 77°00’N | 59 | 479 | 27.1 | 229 | 2 | 1–30 | 21.9 | 18.3 |
| 76°55’N | 59 | 371 | 21.0 | 124 | 2 | 1–37 | 14.0 | 45.8 |
| 76°50’N | 67 | 175 | 8.7 | 98 | 1 | 1–17 | 35.8 | 18.2 |
| 76°45’N | 64 | 183 | 9.5 | 120 | 1 | 1–4 | 38.2 | 0 |
| 76°40’N | 68 | 149 | 7.3 | 105 | 1 | 1–5 | 52.3 | 0 |
| 76°35’N | 68 | 146 | 7.2 | 107 | 1 | 1–3 | 51.0 | 0 |

Fig. 3 Densities of Brünnich's guillemots observed on the water along transects in Storfjorden. Transects covering areas to the north of the main study area are also included. The data are grouped in a grid with units $1/4^\circ$ longitude and $1/12^\circ$ latitude

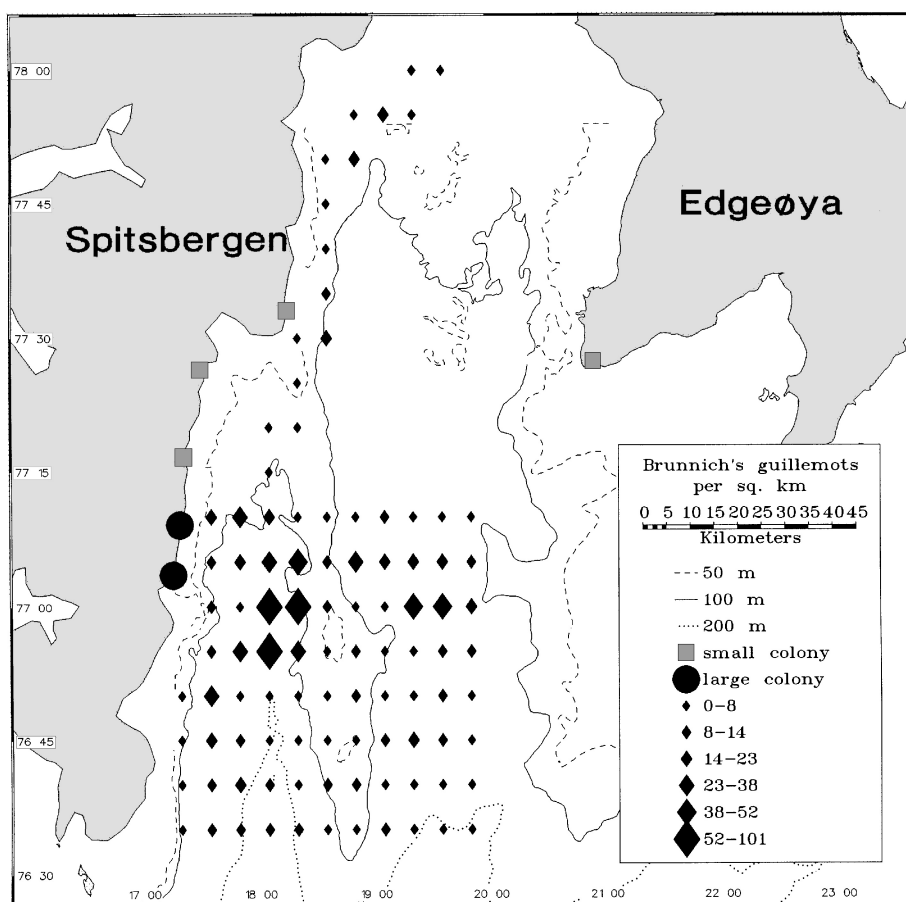


Table 2 Numerical abundance and frequency of occurrence of prey taxa in Brünnich's guillemots collected in Storfjorden, 1992 ($n = 23$)

| Taxon | No. of items | % Numerical abundance | % Frequency of occurrence |
|--------------------------------|--------------|-----------------------|---------------------------|
| <i>Boreogadus saida</i> | 34 | 12.1 | 56.5 |
| <i>Mallotus villosus</i> | 2 | 0.7 | 8.7 |
| <i>Liparis</i> sp. | 2 | 0.7 | 4.3 |
| <i>Myoxocephalus scorpicus</i> | 2 | 0.7 | 4.3 |
| <i>Sebastes mentella</i> | 1 | 0.4 | 4.3 |
| <i>Thysanoessa inermis</i> | 22 | 7.8 | 26.1 |
| <i>Parathemisto libellula</i> | 85 | 30.2 | 69.6 |
| <i>P. abyssorum</i> | 115 | 40.9 | 30.4 |
| <i>Hyperia galba</i> | 2 | 0.7 | 8.7 |
| <i>Onisimus</i> sp. | 3 | 1.1 | 4.3 |
| <i>Gammarus wilkitzkii</i> | 11 | 3.9 | 30.4 |
| <i>Eualus gaimmardi</i> | 1 | 0.4 | 4.3 |
| <i>Sclerocrangon borealis</i> | 1 | 0.4 | 4.3 |
| Total | 281 | 100.0 | — |

These transects also held the highest densities of guillemots. Group sizes of more than five birds were not recorded on the three southernmost transects. The percentages of birds occurring in groups > 5 individuals were highest on the $76^\circ 55'N$ and $77^\circ 10'N$ transects (Table 1).

Diet of Brünnich's guillemots

Crustaceans and fish dominated, both in numerical abundance and frequency of occurrence, in the diet of guillemots collected in Storfjorden (Table 2). Two species of pelagic amphipods, *Parathemisto abyssorum* and

P. libellula, together with the euphausiid *Thysanoessa inermis*, accounted for 79% of all identified prey items. The amphipod *Gammarus wilkitzkii* occurred in 30% of the birds, but was not taken in large numbers. Polar cod was the only important species of fish, occurring in 57% of the birds examined. The estimated lengths of the polar cod ranged from 7 to 19 cm (mean 11.7 cm).

Distribution of biomass detected by acoustic surveys

The total acoustically detected biomass was highest on the 77° 00'N transect (Fig. 4). This transect also had the highest bird densities of the five acoustic transects. Echo type D predominated on all transects (Fig. 4), but showed little obvious spatial pattern at the scale used in this study (ca. 10-km bin size). Type A echoes on all transects were most often encountered in the western part of the transect (Fig. 4). Additionally, on transect 77°00'N there was a second peak in type A echoes in the eastern part. Echo type A (Fig. 4) constituted a larger proportion of the total echo return on transects 76°50'N and 76°35'N (36.8 and 34.6%, respectively) than on the other transects (range 14.0–21.3%). Echoes of type A were strongest in the 10- to 15-m depth interval and decreased with depth. The depth intervals 10–15, 15–20, 20–25 and 25–50 m accounted for 61.0, 25.6, 10.9 and 2.5%, respectively, of the type A echo return integrated over the 10- to 50-m water column.

Correlations between acoustically detected biomass and bird abundance

For the five acoustic transects combined, we obtained a significant positive correlation between bird numbers and total acoustic returns within each of the three most shallow depth intervals (10–15, 15–20 and 20–25 m) and for the total water column (10–50 m) (Table 3). One acoustic transect included (77°00'N) had high bird densities (27 birds/km²), whereas the other acoustic transects had relatively low densities (7–10 birds/km²) (Table 1).

Correlations between bird abundance and echo returns from aggregated targets (type A) were stronger than those between birds and the more dispersed targets (type D) (Table 3). The correlations for type A echoes were highly significant for all depth intervals, whereas the corresponding values for type D echoes were lower. In the latter case, only the correlations for the uppermost depth intervals and the total 10- to 50-m water column were significant.

To test if the parts of transects with peak bird densities also were characterized by high prey biomass, we compared bird density and prey biomass of the 10% of the sections with the highest bird density (≥ 8 birds/km) with the remainder of the sections. The transects with high bird density had significantly higher

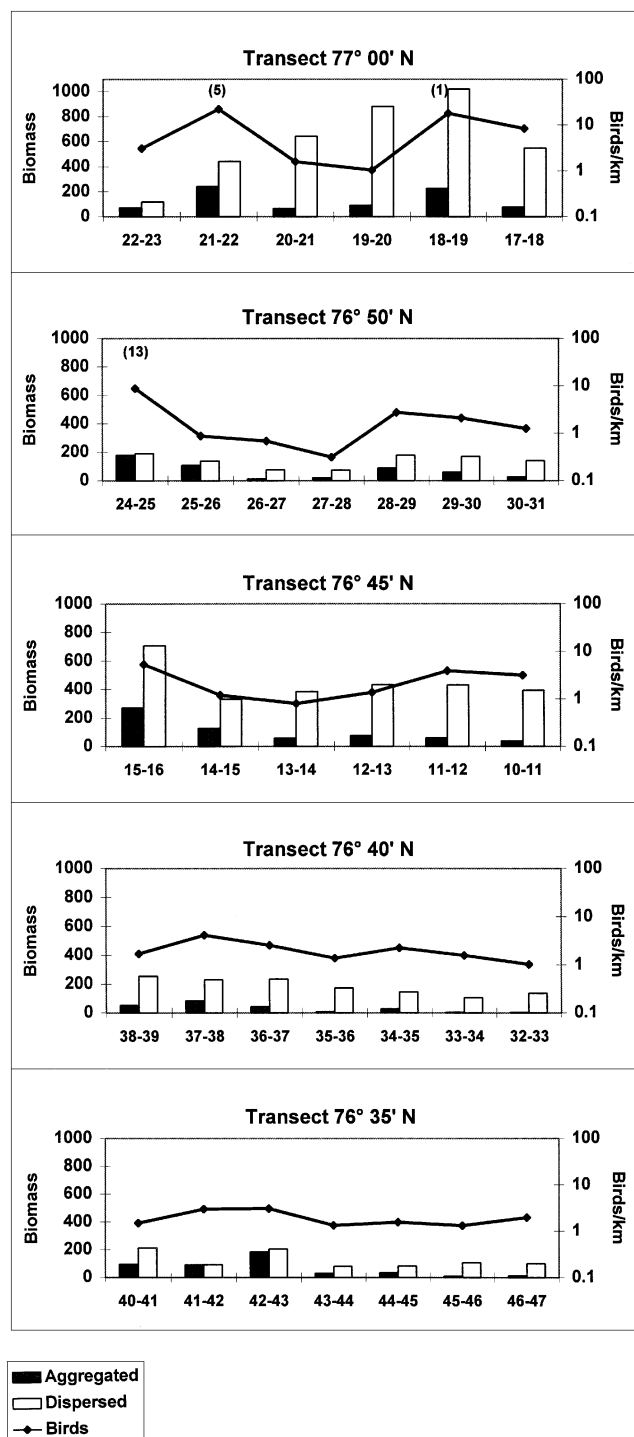


Fig. 4 Brünnich's guillemot abundance (birds per kilometer transect length) and acoustic return (volt² per minute) of echo types A (aggregated), and D (dispersed), integrated between each station for the 10- to 50-m depth interval. Numbers in parentheses are number of bird groups > 5 in different between-station intervals

type A echo values than the sections with lower bird abundance for all depth intervals, as well as for the total water column (10–50 m) (Table 4). When looking at group sizes of birds along the transects, we also

Table 3 Spearman rank correlation between guillemot number and echo return for all 33 transect intervals. Correlations were computed for aggregated (echo type A), dispersed (echo type D), and total echoes (A + D)

| Depth interval (m) | Type A | Type D | Types A + D |
|--------------------|---------|--------|-------------|
| 10–15 | 0.48** | 0.41* | 0.47** |
| 15–20 | 0.47** | 0.31 | 0.39* |
| 20–25 | 0.50** | 0.26 | 0.37* |
| 25–50 | 0.55*** | 0.11 | 0.27 |
| 10–50 | 0.51** | 0.44* | 0.49** |

* $P < 0.5$; ** $P < 0.01$; *** $P < 0.001$

Table 4 Mann-Whitney U -test for values of different echo types and high (≥ 8 birds/km) versus low (< 8 birds/km) densities of guillemots, computed for aggregated (echo type A), dispersed (echo type D) and total echoes (A + D)

| Depth interval (m) | Type A (U) | Type D (U) | Types A + D (U) |
|--------------------|----------------|----------------|---------------------|
| 10–15 | 19* | 20* | 22* |
| 15–20 | 13* | 25 | 16* |
| 20–25 | 5** | 21* | 12* |
| 25–50 | 10** | 32 | 23 |
| 10–50 | 13* | 19* | 15* |

* $P < 0.05$; ** $P < 0.01$

found that all groups > 5 on the five transects where acoustics measurements were performed were located on sections with high biomass of type A echoes (Fig. 4).

A similar analysis for echo type D showed significant differences in echo values between transect segments with high bird numbers versus segments with low numbers only at depths of 10–15, 20–25 and 10–50 m, but with lower significance values than in the echo type A analysis (Table 4). When the sum of echo types A and D was used, we obtained significant differences for the depths 10–15, 15–20 and 20–25 m, as well as for 10–50 m (Table 4). We conclude from these tests that sections of transects with high densities and large group sizes of birds correspond with high acoustically detected biomass, especially of type A echoes.

Physical gradients, acoustic biomass and bird numbers

Temperature and salinity sections at $77^{\circ}00'$, $76^{\circ}50'$, $76^{\circ}45'$, and $76^{\circ}40'N$ are presented in Fig. 5. Three main water masses were identified that correspond to those described by Anderson et al. (1988) and Quadfasel et al. (1988): a relatively warm and low salinity surface layer of melt water, warm Atlantic water, and cold and saline deep water. Additionally, we found cold and low salinity Arctic water. Two cores of Atlantic water were found penetrating from the Storfjordrenna canyon northward on each side of the north-south submarine ridge in Storfjorden. Frontal zones between Atlantic

water and the Arctic water were located in the region between the eastern coast of Spitsbergen and the central ridge in Storfjorden. These frontal zones were expressed as areas with high horizontal gradients in temperature and salinity (Fig. 5).

We found no correlation between bird abundance and the strength of either horizontal or vertical temperature and salinity gradients at any depth interval (Table 5). However, strong correlations were obtained between echo returns and the strength of physical gradients. Both echo types A and D were significantly positively correlated with horizontal gradient in temperature and salinity (Table 5) in the lowest depth interval (25–50 m). For vertical gradients the pattern is less consistent, showing both negative and positive correlation with echo return.

Discussion

Southern Storfjorden is an important foraging area for Brünnich's guillemots that nest in the two largest colonies in Svalbard, Stellingfjellet and Kovalskifjellet. Other important foraging areas lie to the south of Storfjorden.

Within Storfjorden, foraging Brünnich's guillemots were mostly concentrated on the west side of the fjord and in the vicinity of the colonies. On transects with high bird densities, the guillemots were observed more often aggregated in groups than on the other transects. Few guillemots were recorded on the transect conducted to the north of the east-west transects. This result is in agreement with information from previous years (F. Mehlum, unpublished work). Most of the birds encountered north of $77^{\circ}10'N$ are likely to have originated from smaller colonies to the north of Stellingfjellet and Kovalskifjellet (Fig. 3). Guillemots did not forage commonly in the inshore coastal water, but flew across it. In the Bering Sea, alcids have also been shown to forage preferentially in offshore waters (Hunt and Harrison 1990; Hunt et al. 1990a). At the Pribilof Islands, Decker (1995) has shown that Brünnich's guillemots forage preferentially at tidal fronts associated with the 70-m isobath around the islands, 5–31 km from shore. At Bear Island in the central Barents Sea ($74^{\circ}30'N$, $18^{\circ}50'E$), aggregations of foraging Brünnich's guillemots are associated with a frontal zone between the well-mixed and cold water inside the 100-m isobath surrounding the island and the stratified warm Atlantic water further offshore (F. Mehlum, N. Nordlund and K. Isaksen, unpublished work). In Storfjorden, we do not know why guillemots avoided foraging in the near-coastal waters, but we assume that it was because suitable prey were less abundant there.

Oceanic fronts are locations where the interactions between physical forcing mechanisms and the behavior of marine organisms result in the accumulation of biomass (Franks 1992). Predators, including fish,

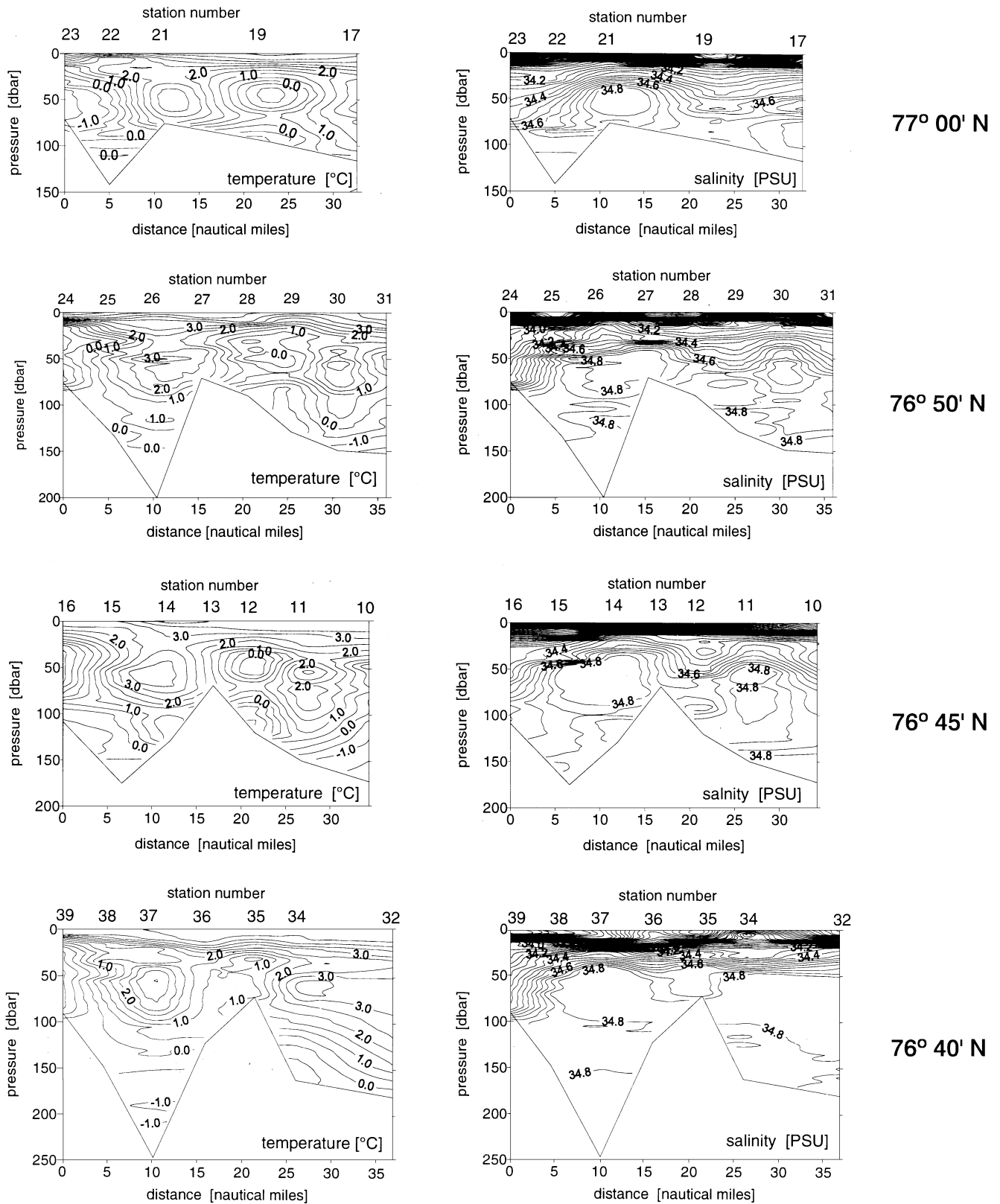


Fig. 5 Contour plots of temperature (°C) and salinity (‰) along four east-west transects. The *left end* of the graphs represents the western end of the transects. The values on the *vertical axis* (pressure in dbar) equal depths in meters. The *lower line* in each plot illustrates the bottom profile and shows the location of the subsurface ridge

Table 5 Spearman Rank correlation coefficients between horizontal and vertical temperature and salinity gradients at different depth intervals, and bird abundance (*B*), echo type *A* and echo type

D ($n = 27$ between-station intervals). The acoustic data are integrated over the 10- to 50-m depth interval

| Depth (m) | Temp. horizontal | | | Temp. vertical | | | Salinity horizontal | | | Salinity vertical | | |
|-----------|------------------|---------|--------|----------------|---------|--------|---------------------|-------|--------|-------------------|-------|--------|
| | B | A | D | B | A | D | B | A | D | B | A | D |
| 10–15 | 0.02 | 0.09 | –0.12 | 0.21 | 0.07 | –0.14 | –0.15 | –0.17 | –0.03 | 0.29 | 0.28 | 0.41* |
| 15–20 | –0.17 | –0.01 | –0.18 | –0.21 | –0.51** | –0.47* | –0.36 | –0.16 | –0.05 | 0.02 | –0.31 | 0.18 |
| 20–25 | –0.27 | –0.08 | –0.25 | –0.07 | –0.06 | –0.47* | –0.12 | 0.20 | 0.19 | 0.20 | –0.08 | 0.41* |
| 25–50 | 0.23 | 0.62*** | 0.56** | 0.17 | 0.08 | –0.14 | 0.19 | 0.40* | 0.59** | 0.20 | 0.08 | 0.50** |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

marine mammals and seabirds, take advantage of these concentrations when they include suitable prey (Haney 1986; Fiedler and Bernard 1987; Wishner et al. 1988; Hunt and Harrison 1990; Schneider et al. 1990; Podestá et al. 1993; Decker 1995). In the present study, the major concentrations of foraging guillemots were in the vicinity of a weak subsurface front where Atlantic water abutted Arctic water. However, correlations between the numbers of foraging guillemots and frontal areas in the study area were not strong. Schneider et al. (1987) have shown that strong fronts are more likely to be attended by marine birds than are weak fronts. Likewise, Elphick and Hunt (1993) found that responses by seabirds to clearly differentiated water masses in the northern Bering Sea were strong when compared to the relatively weak responses of the Antarctic seabird community to weakly differentiated water masses in the Bransfield Strait (Hunt et al. 1990b). In the present study, the subsurface frontal systems were deep and weak. Nevertheless, acoustic biomass was positively correlated with the strength of subsurface horizontal temperature gradients. Over 95% of the aggregated acoustic biomass in the 10- to 50-m depth interval was found between 10 and 25 m. Prey may also have been accumulated in the 0- to 10-m depth interval, but we do not have acoustic biomass data from this interval. Our analyses of bird abundance in relation to horizontal and vertical gradients in temperature and salinity failed to show significant correlations. However, large aggregations of foraging birds occurred in the western parts of the transects over deep water where strong sub-surface fronts were evident. It seems possible that birds observed foraging in the vicinity of these subsurface fronts were attracted to prey that had aggregated at these features.

Food samples obtained from foraging guillemots collected in the Storfjorden study area contained primarily crustaceans and polar cod, whereas capelin (*Mallotus villosus*) and other fishes were of less importance. Data from 1989 and 1992 on foods brought to the chicks at the colonies indicate that fish, particularly polar cod, predominate, whereas crustaceans were absent (Mehlum and Gabrielsen 1993; V. Bakken, personal communication). Interestingly, no capelin were identified among the prey items recorded in 1989 and 1992.

Although many guillemots were observed flying south through the study area to forage in an area where capelin schools were common (F. Mehlum, unpublished work), we have no data showing a significant use of capelin for feeding guillemot chicks at the two largest colonies in Storfjorden. We are unable to explain why, apparently, a large proportion of the guillemots nesting at the colonies flew south out of the fjord when there were suitable prey nearer to the colonies that were exploitable.

In the acoustic records, we were able to differentiate two classes of signals. One class consisted of groups of strong echoes, and we interpreted these as being from schools of fish or dense aggregations of large zooplankters such as *Parathemisto* spp. and *Thysanoessa inermis*. The second class of signals consisted of single, relatively weak, echoes, and we interpreted these as representing a diffuse or scattered distribution of organisms. If our interpretations are correct, these targets were probably small fish, because single small zooplankters would have been too small to reflect a 30-kHz signal.

Foraging guillemots reacted differently to the sources of the two classes of echoes. The numbers of foraging guillemots were strongly correlated with the strength of echoes believed to be from aggregated prey, whereas correlations between guillemot numbers and the strength of echoes from diffuse distributions of acoustic biomass were consistently weaker. This result is the first suggestion that avian predators react differently to aggregated and dispersed prey. When foraging at patches, the correlations between guillemots and acoustically detected biomass suggest that foraging guillemots adjust their numbers in accordance with the predictions of the ideal free distribution (Fretwell and Lucas 1970; Milinski and Parker 1991). When foraging on dispersed prey, the guillemots are apparently relatively insensitive to variations in the biomass present in the water.

Previous studies of distributions of marine avian predators with respect to their prey have employed techniques that integrated prey biomass over transect segments varying in length from 0.1 to 10 km (for a recent compilation of these studies, see Hunt et al. 1992). In the present study, recording of echoes ping by

ping allowed classification of echo types. Our analysis showed that the inclusion of echoes from scattered targets with those from aggregated targets significantly reduced the strengths of correlations between the predators and their prey. In most of the studies reviewed by Hunt et al. (1992), correlations between seabirds and their prey were weaker than those found between guillemots and aggregated targets in this study, and are roughly similar to those found between the guillemots and total prey echoes. It may be essential to remove the estimated biomass attributed to scattered prey if we are to fully appreciate the extent to which marine birds are able to adjust their foraging effort with respect to prey distribution and abundance.

The majority of guillemots observed foraging in the study area were associated with patches of aggregated prey rather than with scattered prey. This preference for aggregated prey may have consequences for the conservation of Brünnich's guillemots and the management of fisheries in the vicinity of guillemot colonies. If fishery practices remove or disperse schooling prey, these birds may experience difficulty in meeting their nutritional requirements.

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Appendix 1

To identify and remove the signals of the ship's depth sounder, we used the fact that bottom echoes from the ship's depth sounder were not present in adjacent pings at the same depth. Therefore we considered an echo (u_{ij}) (where i is ping number, j is sample number in the ping, u is echo return expressed in voltage, that could be transformed to acoustic pressure) to originate from the ship's echo sounder if the following three conditions were simultaneously fulfilled: (1) the value of u_{ij} was larger than some threshold level $pg1$, typical for the transect's acoustical background (noise + dispersed targets); (2) and if a minimum of five successive samples (to distinguish single fish echoes from those shorter echoes from the ship's echo sounder) in the i -th ping including the j -th sample are above the $pg1$ value; (3) and if, in comparing samples in the two adjacent pings ($i-1$ and $i+1$) in the depth indices interval ($j-1..j+1$) with the second threshold level $pg2_j$, we could not find a minimum of two samples from the pings $i-1$ and $i+1$ that were above $pg2_j$ (i.e. we did not have a biomass patch).

The value of $pg2_j$ for i -th ping was defined as $pg2_j = u_{ij}/4$ (sometimes, depending on the rate of ship's echo sounder to our echo sounder signals $pg2_j = u_{ij}/6$). The ship's echo sounder signals were removed and substituted with the mean from two adjacent ping sample values from the same depth.

Threshold levels were established on the basis of many experimental trials. The values of $pg1$ were calculated as averages of maxima from locations with dispersed targets. The $pg2_j$ values de-

pended on depth and were different in each block of data. They were defined as the value of an average block (of 128 pings) profile multiplied by 1.41. The selected echoes were those with intensities higher than the 2-dimensional moving averages, i.e. both vertical and horizontal. This means that dense aggregations of targets were defined as patches with echo intensities higher than the local background level. For the purpose of the present paper the acoustic data were reprocessed into a 1-min bin size (corresponding to a distance of 150–160 m) and averaged between neighboring stations. These averaged acoustic returns are given in volts² per minute. Precise locations of echo signals were obtained using the ship's GPS system and time of registration. The echo intensity was integrated for the depth layers 10–15, 15–20, 20–25 and 25–50 m. Depths shallower than 10 m were omitted from the analyses to avoid the dead zone of the echo sounder and interference from bubbles and sea surface reflections.

For discriminating between dense concentrations of targets (echo type A – aggregated) and the second, dispersed targets (echo type D – dispersed) we applied the following procedure:

At the first stage the value s_{ij} was calculated as:

$$s_{ij} = \frac{1}{9} \sum_{k=-1}^{k=1} (pf1_{i+k} + pf2_{i+k} + pf3_{i+k})$$

where s_{ij} is a 2-dimensional (3×3) moving average of voltages of echo signals around the point with i, j indices, $pf1$ = value of previous echo profile, $pf2$ = value of present echo profile, and $pf3$ = value of next profile.

Echoes were classified as aggregated if the following conditions were fulfilled: the s_{ij} values were larger than the thresholds $pg1$ and $pg2$; the minimum number of samples surrounding the u_{ij} sample (among 8 surrounding samples) higher than $pg2$ equalled 5.

Otherwise, the echoes were classified as dispersed. The first condition used the fact that the level of echo from an aggregated patch was usually higher than the echoes from dispersed targets; the second and third conditions used the fact that a patch of aggregated targets could be immersed in a layer of dispersed targets.

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