Statistical relationships between the distributions of groundfish and crabs in the eastern Bering Sea and processed returns from a single-beam echosounder

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Groundfish and benthic invertebrates are not randomly distributed over the continental shelf of the eastern Bering Sea (EBS). Annual trawl surveys reveal distributional patterns that vary according to species, and substantial interannual variation in these patterns suggests some degree of environmental control. Quantitative habitat models are developed to explain the distribution and abundance of species in the EBS. Simple models based on readily available data (temperature and depth) are somewhat informative, but offer limited practical value. Earlier research in the EBS indicated that surficial sediments affect the distribution and abundance of groundfish. However, traditional sampling with grabs and cores is impractical over large areas, and an efficient sampling strategy is needed. Echosounders allow surveys of large areas, but it is unknown if they measure the relevant properties of sediments. Seabed echoes from a calibrated, single-beam echosounder were recorded over 17 000 km of trackline covering the EBS shelf. Generalized additive models were used to fit acoustic and other variables to abundance data for ten species. The final models explained 28–77% of the variability in abundances, including a marginal contribution of 2–13% by the acoustic predictors.

Keywords: Bering Sea, generalized additive models, marine-fish habitats, single-beam echosounder.

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Introduction

The habitat of a marine species is generally described as a geographic area within which various biotic and abiotic factors influence the survival, growth, and reproduction of the individuals. These fundamental rates vary within the range of tolerable conditions, such that some areas are more productive than others, indicating functional differences in habitat quality. For this reason, effective conservation and management of marine resources require specific knowledge of habitat requirements. Consequently, various national and international programmes have emerged to characterize fish habitats and map their locations on the seabed (e.g. Integrated Mapping for the Sustainable Development of Ireland's Marine Resources, INFOMAR). These programmes are intended to improve our understanding of significant ecological dependencies and ultimately to identify critical areas for protection from fishing and other potentially harmful disturbances (Newell *et al.*, 1998; McConnaughey *et al.*, 2000). An underlying premise is that habitat quality varies in space and time according to the specific requirements of species during their various life-stages. Furthermore, it is commonly assumed that animal densities reflect different levels of habitat utilization, and the degree to which a habitat is utilized is indicative of habitat quality (Fretwell and Lucas, 1970; MacCall, 1990; McConnaughey, 1995; Laurel *et al.*, 2007). As such, broad-scale efforts to characterize and map fish habitats generally include systematic sampling of biological populations and the associated habitat characteristics. The habitat requirements of a species during a particular life-history stage are subsequently defined with correlative analyses, using either qualitative or quantitative methods as determined by programme objectives and the characteristics of available data. Often, the habitat data are summarized according to predefined hierarchical schemes that are based on a selection of habitat variables (Greene *et al.*, 1999; Davies *et al.*, 2004; Madden *et al.*, 2005). A species' habitat can then be defined as the combination of categorical attributes that describes the area it occupies (e.g. *Sebastes ruberrimus* in Greene *et al.*, 1999). Alternatively, quantitative relationships with quantifiable uncertainty can be developed between the habitat variables and calculated fish densities, permitting more continuous definitions of habitat and habitat quality. In this case, it is the actual values of the independent variables that define habitat for a specific level of abundance.

Progress in associating marine fish with specific habitats has been elusive, in part because of an overreliance on easily measured and readily available habitat variables (Anderson *et al.*, 2007). Although mechanistic relationships with factors such as depth and temperature are easily demonstrated, explanatory and predictive models based on these variables alone are generally of limited practical value. This presents a need for more relevant and independent habitat variables (Anderson *et al.*, 2007). To this end, associations between marine-fish abundance and seabed sediments have been investigated for a variety of species. In the eastern Bering Sea (EBS), for example, strong associations between pleuronectid flatfish and sediment texture have been demonstrated using grab- and core-sample data (McConnaughey and Smith, 2000). The strength of this association varied among the species according to the degree of dependence on benthic prey, suggesting an indirect relationship with sediments. That is, primarily benthic-feeding species were closely associated with the sediment textures preferred by their prey, whereas piscivorous species were apparently indifferent to sediment texture while feeding in the water column. Unfortunately, direct sampling of sediments is impractical over large geographic areas, and the overall availability of high-quality synoptic data is correspondingly low (cf. Smith and McConnaughey, 1999).

Acoustic returns from the seabed include considerable information about the physical properties of the seabed and could substitute sediment data in fish–habitat models. Theoretical and empirical models indicate that refraction and scattering of sound are influenced by as many as 80 different seabed properties, although most of the acoustic response may be explained by 6–12 independent physical descriptors, including the physical properties of sediments (Holliday, 2007). Backscatter amplitude and character are also affected by acoustic-system parameters, such as frequency, beam width, pulse duration, and power. Despite some recent progress (Fonseca and Mayer, 2007), a general-purpose relationship with seabed composition does not exist, meaning that sediment type cannot be unambiguously determined with acoustic sensing (the "inverse problem"; Holliday, 2007; Kloser, 2007). Nevertheless, acoustic systems represent a promising tool for broad-scale mapping of fish habitats, because data can be collected efficiently over large areas and include information about an important habitat component. Currently, however, higher-frequency acoustic-backscatter data are generally unproven for characterizing groundfish habitats.

This study is part of a continuing research programme in Alaska to address essential fish habitat (EFH) mandates in the primary laws regulating marine-fishery management in the United States. Included among these mandates is a requirement to define, in environmental terms, the EFH of all federally managed species. The specific objective of this paper is to evaluate the utility of backscatter from a vertically projecting, single-beam echosounder (SBES) in basin-scale, quantitative models that characterize the habitats of commercially important species. The investigation is limited to an evaluation of outputs from commercially available QTC View software (reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA), without an assessment of the tool's processing methods, and we do not seek to establish the mechanism of association between the acoustic data and observed species distributions, as was possible for McConnaughey and Smith (2000).

Methods

Study area

The EBS is a broad and generally shallow basin that is one of the world's most productive and biologically diverse marine ecosystems (National Research Council, 1996; PICES, 2004). It is a semi-enclosed extension of the North Pacific, connected through the Aleutian archipelago and joined to the Arctic Ocean by the relatively shallow Bering Strait. Average water depth over the continental shelf is 60 m. The vertical relief is low, and there is a relatively uniform, cross-shelf slope averaging <0.0003. The properties and dynamics of surficial sediments in the study area were reviewed by Smith and McConnaughey (1999). In general, surface strata on the shelf are 1.5–6.0 m thick deposits of contemporary sediments that originate from erosion, surface run-off, and volcanism on the Alaskan mainland. The average grain size in the deposits decreases with increasing depth and distance from shore, with some irregularities related to the height and intensity of storm waves, and to intermittent scouring by alongshore currents. Estimated average depositional rates in the study area are 8–70 cm per millennium or 0.2–1.6 cm during the 23-year period considered here.

Fish-abundance data

The Alaska Fisheries Science Center (AFSC), US National Marine Fisheries Service, NOAA, conducts an annual, bottom-trawl survey of the EBS continental shelf using standard gear and methods (Acuna and Lauth, 2007). These surveys provide data for stock assessment and the management of the fisheries resources. Each June–August, the AFSC systematically surveys $\sim$490 800 km^2 of the shelf with AFSC 83–112 eastern otter trawls. The trawls are deployed from chartered fishing vessels at 356 standard stations in a sampling grid with 37 × 37 km (20 × 20 nautical miles) cells. Each trawl sample is targeted at the centre of a grid cell and consists of a 30-min tow at 3 knots (Figure 1); the average area swept is $\sim$45 000 m^2. A mechanical tilt sensor attached to the footrope is used to determine when the trawl is in contact with the seabed (Somerton and Weinberg, 2001). The catch is processed to estimate total biomass and numbers by species and sex. Acoustic net-mensuration data and GPS fixes for the vessel are used to standardize catches according to the area swept by the trawl, measured as catch per unit effort (cpue; kg ha^{-1}). A recording micro-bathythermograph attached to the headrope of the trawl provides depth and the surface- and bottom-water temperatures for each tow.

Trawl-survey data from 1982 to 2004 were used, totalling 5108 successful tows in the acoustic-survey area (Table 1). Catch data for eight representative species of fish and two species of crab were investigated: Alaska plaice (*Pleuronectes quadrituberculatus*), arrowtooth flounder (*Atheresthes stomias*; ATF), flathead sole (FHS), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), rock sole (*Lepidopsetta* spp., Orr and Matarese, 2000), yellowfin sole (*Pleuronectes asper*), walleye pollock (*Theragra chalcogramma*), snow crab (*Chionoecetes opilio*), and Tanner crab (*Chionoecetes bairdi*). In keeping with standard survey practice, ATF combines ATF and Kamchatka flounder (*Atheresthes evermanni*), whereas FHS includes both FHS and Bering flounder (*Hippoglossus robustus*). Overall, there was considerable interannual and spatial variation in abundance within species, as is typical for the area (McConnaughey, 1995; National Research Council, 1996).

Echosounder data

The AFSC also conducts a midwater assessment of walleye pollock stocks on the EBS shelf (Honkalehto *et al.*, 2002). Echosounders and midwater trawls are used to develop distribution and abundance time-series for fishery-management purposes. The biennial surveys proceed from east to west along parallel north–south transects spaced at 37 km intervals, beginning at longitude 160°20′W and ending at longitude 178°55′W. The transects intersect the

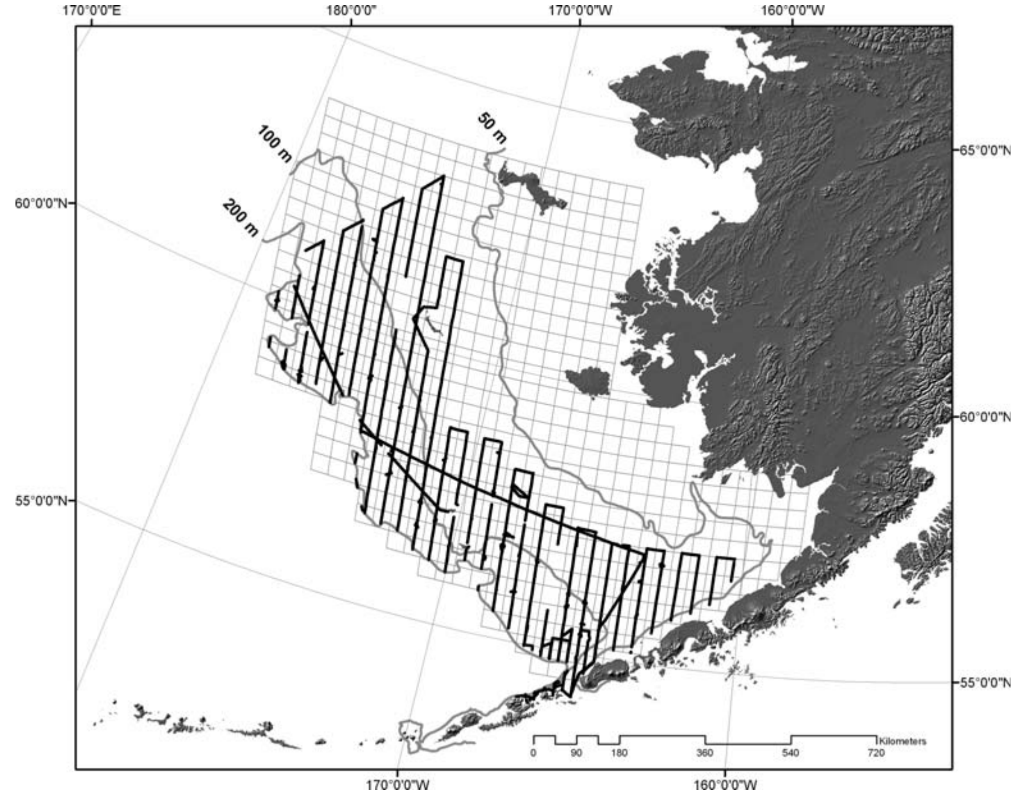

Figure 1. Sampling plan for the 1982–2004 bottom-trawl surveys of the EBS continental shelf. The overlaid solid line indicates the north–south transects of the 1999 acoustic survey by NOAA ship "Miller Freeman" covering >17 000 km of seabed.

Table 1. Descriptive statistics for dependent and independent variables used in the GAM analysis of habitat associations in the EBS.

Model variable	Count	Median	Mean	s.d.	CV%	Minimum	Maximum
Cpue							
Alaska plaice	3 987	1.9	10.7	27.4	255	0.0	723.2
ATF	4 485	3.1	11.0	21.1	192	0.0	397.9
FHS	4 835	6.9	14.6	30.6	210	0.0	1 019.9
Pacific cod	4 835	10.5	18.3	35.3	193	0.0	1 594.8
Pacific halibut	4 835	0.5	2.3	4.7	199	0.0	76.8
Rock sole	4 835	4.1	21.5	51.6	240	0.0	1 455.5
Walleye pollock	4 835	47.1	134.3	265.2	197	0.0	5 301.2
Yellowfin sole	4 030	2.5	31.7	64.8	205	0.0	1 380.2
Snow crab	4 835	1.8	10.2	21.6	211	0.0	417.7
Tanner crab	4 577	0.4	2.1	6.8	327	0.0	154.3
Standard							
Depth (m)	5 108	94.0	97.4	29.1	–	33.0	230.0
Surface temperature (°C)	4 980	7.6	7.4	1.7	–	−0.1	11.3
Bottom temperature (°C)	4 835	2.5	2.3	1.6	–	−2.1	6.9
Acoustic							
Q_1	43 897	−0.80	−0.81	0.30	–	−1.56	0.26
Q_2	43 897	2.14	2.19	0.19	–	1.74	2.96
Q_3	43 897	0.43	0.44	0.08	–	0.23	0.91

The cpue statistics are based on the 5108 survey tows, less tows with missing water temperature values and, by species, tows with observations deemed to be structural zeros (see text). The statistics for the Q-values are based on the QTC View observations in the 236 bottom-trawl survey grid cells used in the analysis.

centres of selected bottom-trawl survey grid cells to coincide with the target locations for bottom-trawl samples (Figure 1). The acoustic data were collected aboard the NOAA ship "Miller Freeman" using a calibrated, centreboard-mounted, Simrad EK500 echosounder system emitting 1 ping s^{-1} at 38 kHz, with 500 W transmit power per quadrant, a 1-ms pulse duration and a beam width of 7° fore-aft and athwartship (von Szalay and McConnaughey, 2002). The standard surveying speed for the AFSC survey is 11 knots which, under standard conditions, yields ~6500 pings per trawl-survey grid cell.

During the June–August 1999 acoustic survey, ~4 million seabed echoes were recorded for comparison with bottom-trawl survey catches, the objective of the study. Personnel from the Quester Tangent Corporation (Sidney, BC, Canada; QTC) attached a multichannel, full-waveform recorder (Integrated System for Automated Hydrography-Seabed, ISAH-S) to the output stream of the EK500 echosounder. The ISAH-S digitized the analogue signal from the transducer at a 20-kHz sampling rate and a 12-bit dynamic range. Time-series of individual echoes were passed from the ISAH-S to a QTC View Series 4 where the carrier was removed and the echo envelopes were formed, time-tagged, and geo-referenced.

A 30-dB inductive attenuator was placed between the transducer and the QTC View amplifier circuitry to compensate for the transmit power of the EK500 and prevent signal saturation ("clipping"). After normalizing the data to a reference depth of 90 m to account for depth-related sound attenuation at survey depths of 40–155 m, QTC View software was used to identify the instant in the echo recording when the sound wave first hit the bottom (the bottom pick), average (stack) 50 individual echoes to reduce noise, and further process the data to create a full-feature vector (FFV) of seabed attributes (Quester Tangent Corporation, 2004). The FFV is a 166-element numerical vector derived from a decomposition of the summed echotracings. These vectors serve as input to a principal components analysis. The software calculates the first three principal components, designated as *Q*-values (Q_1, Q_2, and Q_3); these are the QTC's continuous-valued assessment of the bottom type at the given location. In their standard analysis, the *Q*-values are used as input to a modified K-means clustering algorithm to divide the observations into discrete seabed categories. In this analysis, however, the continuous *Q*-values were used.

In all, 236 trawl-survey grid cells were traversed during the 1999 acoustic survey (Figure 1). Across these cells, 43 897 sets of *Q*-values were generated, with data from some pings rejected by quality assessment of the echosounder data. Each set of *Q*-values included the latitude and longitude for the location of the observation, plus the depth at that location. Overall, the *Q*-values represented considerable acoustic diversity (*sensu* Holliday, 2007) over the surveyed area (Table 1; Figure 2).

Merging the fish-abundance and acoustic datasets

The acoustic and trawl-survey data were not collected simultaneously and therefore are not naturally co-registered. The bottom-trawl sampling did not occur precisely at the targeted centres of the grid cell; the actual locations varied from year to year. Moreover, the representative point locations of the (stacked) sets of *Q*-values were most often roughly 300 m apart, and only rarely was a set of *Q*-values located in a measured trawl path. Hence, it became necessary to estimate a set of *Q*-values for the annual location of each trawl sample. This was achieved by calculating a weighted mean set of *Q*-values for each bottom trawl, based on all the sets of *Q*-values within the specific grid cell, and the distance between the trawl path and the *Q*-value locations. Weights were based on exponential semi-variograms fitted to the *Q*-values, using S-Plus statistical software (Insightful Corporation, Seattle, WA, USA). The distances between the *Q*-value locations when fitting the semi-variograms and the distances between the *Q*-value locations and the tows were calculated as Euclidian distances, using an Alaska Albers projection to project the latitude and longitude values onto a Cartesian plane. Stationarity and isotropy were assumed in the models, i.e. the variance structure among observations was constant across the survey area, and the variance was the same in all directions.

Data analysis

A statistical analysis was used to investigate the extent to which the *Q*-values added to the ability to predict species density, as measured by cpue, over and above the current ability based on available environmental variables. Generalized additive models (GAM) in R (Wood, 2006) were used on a species-by-species basis to assess the marginal contribution of the *Q*-values when fitting the model covariates to the cpue values. GAM models allow fitting of non-parametric curved but smooth models to the data; there is no need for an underlying assumption regarding the functional form of the model as required for generalized linear models. Because there was no *a priori* sense of how the cpue values might relate to the *Q*-values, this trait was particularly desirable.

The cpue data included some zero values with differing numbers for each species. For this analysis, the zero catches were examined carefully. A zero was considered an observational zero if the species had been observed in the area where the tow was conducted, but none was caught in a given tow. Alternatively, a zero was considered a structural zero when the tow location was outside the observed range of the species. For a given species, if the cpue was zero for all tows in a given grid cell (i.e. across all years in which trawl performance was acceptable) and the adjoining grid cells also had all zero cpue values, the observations in that grid cell were viewed as structural zeros and were omitted from the GAM analyses for that species. Moreover, the distribution of the cpue data was highly skewed positive for each species. To meet our GAM-model assumption of a Gaussian error structure more closely, a fourth-root transformation of the cpue data was selected, based on a goodness-of-fit analysis.

The GAM model can be expressed as

$$E(Y_{it}|X_{1t}, \ldots, X_{kt}) = \gamma_{it} + \sum_{j=1}^{k} s_{ij}(X_{jt}),$$

where Y_{it} is the fourth root of the cpue in year t for species i, $t = 1982, \ldots, 2004$, $i = 1, \ldots, 10$; X_{jt} the continuous covariate j in year t, $j = 1, \ldots, k$, with k the number of covariates in the model (covariates included depth, surface- and bottom-water temperatures, and three estimated *Q*-values, Q_1, Q_2, and Q_3); γ_{it} the discrete intercept in year t for species i; and $s_{ij}()$ a cubic-spline smooth function that fits the covariates X_{jt} to the observations Y_{it}.

Initially, year, as a discrete factor accounting for annual variation in abundance, and the covariates depth, and surface- and bottom-water temperature were fitted to the transformed cpue values. (Hereafter, references to modelling cpue data imply use of the transformed data, $\sqrt[4]{\text{cpue}}$.) Then, the *Q*-values, each fitted with its own smooth function, were added to the model individually, in pairs, and all three together. The measure used for model selection (i.e. to identify which variables to include in the model) was the deviance-based, generalized cross-validation (GCV) score with assumed Gaussian errors. The GCV is a measure of model goodness-of-fit penalized by the number of parameters in the model (Wood, 2006); when a variable is added to a

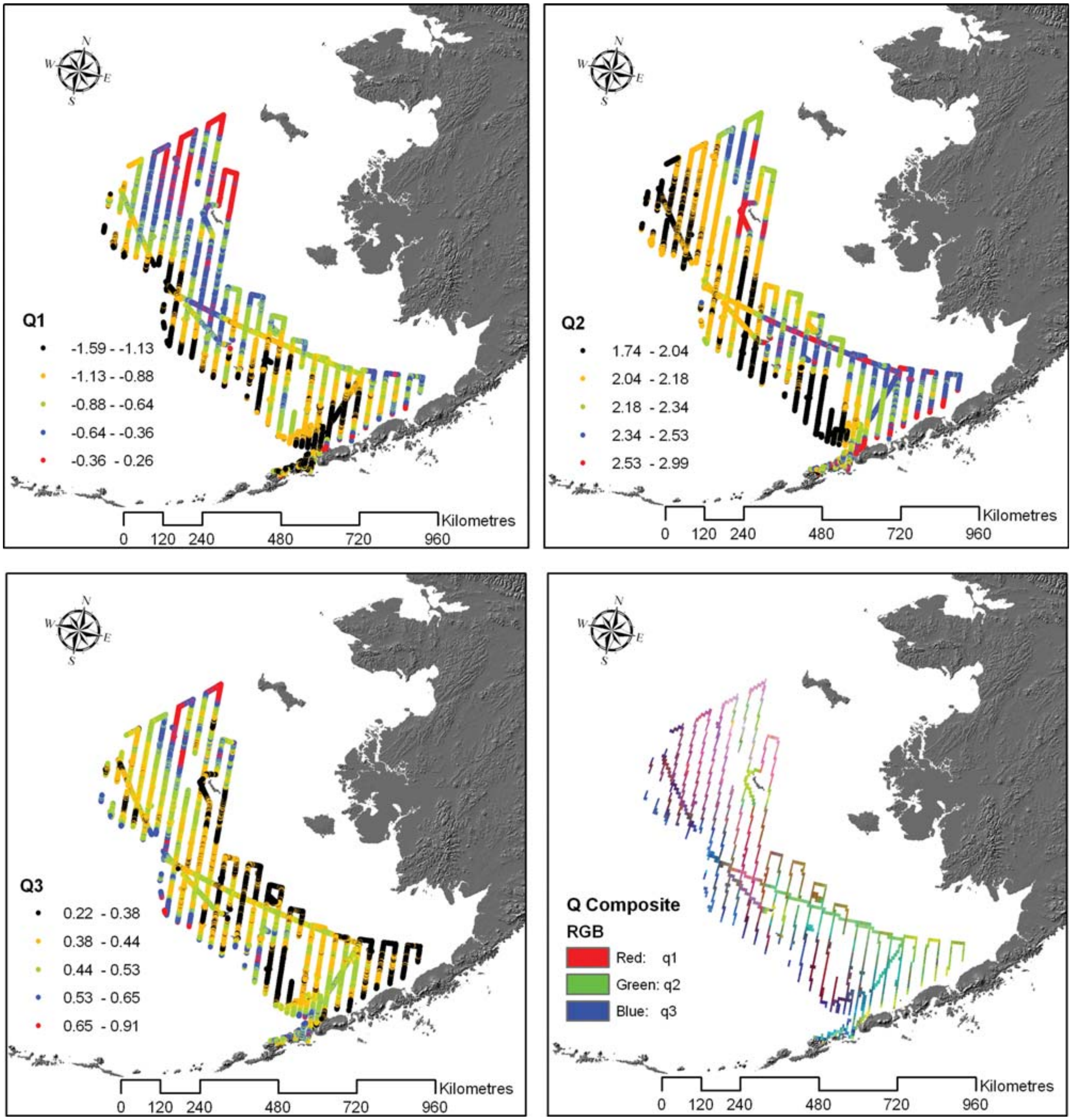

Figure 2. *Q*-values obtained by processing Simrad EK500 single-beam echo returns with QTC View software. In the composite representation, the values of Q_1, Q_2, and Q_3 are plotted in individual colour bands such that colours that are more similar indicate more similarity in the acoustic properties of the seabed (see Figure 1 for geographic coordinates).

model, a resulting smaller GCV supports inclusion of the variable in the model. Specifically, the GCV was used to assess whether adding the *Q*-values to a model yielded a statistical improvement in the model fit. As a measure of how much the addition of the *Q*-values to the models improved the fit, R^2 values were calculated for the various models as $R^2 = 1 - \text{SSR}/\text{SST}$, where SSR is the residual sum of squares and SST the total sum of squares corrected for the mean. Unlike the GCV value, which reflects not only the improvement in fit that results from adding covariates, but also compensates for the increased degrees of freedom that result from adding covariates, R^2 will always increase as covariates are added to a model.

Results

The bottom-temperature variable usually fitted the cpue data better (smaller GCV) than did either depth or surface temperature alone. However, for all ten species, a combination of depth and bottom temperature as covariates in the GAM yielded a smaller GCV than did any model with a single environmental covariate, or the model with both depth and surface temperature

Table 2. GCV values from GAM models used to fit the environmental variables and three acoustic Q-values to the fourth root of the cpue observations.

Taxon	Year + s(depth)	Year + s(surface temperature)	Year + s(depth) + s(surface temperature)	Year + s(bottom temperature)	Year + s(depth) + s(bottom temperature)	Year + s(depth) + s(bottom temperature) + $s(Q_1)$ + $s(Q_2)$ + $s(Q_3)$
Alaska plaice	0.542	0.730	0.539	0.768	0.479	0.398
Arrowtooth flounder	0.498	0.692	0.487	0.395	0.239	0.211
Flathead sole	0.338	0.369	0.329	0.324	0.301	0.273
Pacific cod	0.405	0.409	0.401	0.334	0.332	0.312
Pacific halibut	0.434	0.437	0.418	0.334	0.324	0.317
Rock sole	0.583	0.778	0.568	0.830	0.447	0.374
Walleye pollock	1.433	1.528	1.419	1.360	1.242	1.191
Yellowfin sole	0.604	1.086	0.555	1.515	0.459	0.381
Snow crab	0.519	0.562	0.481	0.445	0.394	0.336
Tanner crab	0.283	0.269	0.262	0.225	0.213	0.173

A smaller GCV indicates a statistically better fit, such that the model with the lowest GCV is considered best for that species.

(Table 2). Further, for all ten species considered, the model-selection criterion supported inclusion of the acoustic *Q*-values in the model. A smaller GCV value resulted every time only one or two of the *Q*-values was added to the model. Adding all three *Q*-values [i.e. cpue $\sim$ year + s(depth) + s(bottom temperature) + $s(Q_1) + s(Q_2) + s(Q_3)$] yielded for each species the smallest GCV value (Table 2). Therefore, this model-selection criterion supported inclusion of all three *Q*-values in the final model for each species. Because of structural zeros, the number of observations per species ranged from 3987 to 4835. With all five splines in the ten final models, the effective degrees of freedom (e.d.f.) for individual splines ranged from 5.7 to 9.0, except for two splines that were straight lines, each with 1.0 e.d.f., and totalled 29.0–40.9 overall. The e.d.f. numbers, the sample sizes, and the inspection of GAM plots did not indicate overfit models. Using AIC scores rather than GCV scores for model selection, there were slight variations in the order that variables came into the models, but the results were the same.

The best models, containing all predictors, explained 27.9–77.0% of the variability in cpue ($R^2 \times 100\%$). The component of this variability explained by the three *Q*-values, however, was small (Table 3). The improvements ranged from 1.9% for Pacific halibut to 13.2% for Tanner crab, with a mean increase in R^2 of 0.068 or 6.8%.

Discussion

Our GAM analysis, including cpue data collected over a 23-year period, indicates processed backscatter from a 38-kHz SBES improves our ability to explain the patterns of distribution for ten marine species in a 323 800-km^2 area of the EBS continental shelf (Table 2). The full models, which also included year, depth, and bottom temperature as independent predictors, explained 28–77% of the variability in abundance; the marginal contribution of the acoustic predictors was 2–13% (Table 3). Although the contributions from the basin-scale SBES data are relatively small, these findings are consistent with those from a similar study in the Bristol Bay region of the EBS (Yeung and McConnaughey, 2008). In the Bristol Bay study, environmental data and processed backscatter data from a sidescan sonar (Klein model 5410) were fitted to the estimates of abundance from the 2002 and 2003 AFSC bottom-trawl surveys. Despite a considerably smaller survey area (1375 km trackline, 26 trawl-survey stations) and correspondingly less environmental variability, the acoustic data explained a significant, though variable, portion of the variance in the cpue of four fish taxa (9–16%) and two invertebrate taxa (19–54%) after accounting for environmental variables that are routinely collected during the trawl surveys. Considered individually, these studies demonstrate that processed acoustic data can be used with varying success to improve broad-scale quantitative models characterizing the habitats of commercially valuable species. Taken together, they suggest that the relationship is reasonably robust because substantially different areas of the EBS were studied using distinctly different classes of sonar and backscatter processing, and both parametric and non-parametric methods were used to analyse the data. The most likely explanation for these observed associations between acoustic data and fish abundances is the physical relationships between the sediment properties and the acoustic echo from the seabed (Holliday, 2007), combined with the sediment preferences and substratum-mediated food habits of the species examined (McConnaughey and Smith, 2000). Although this indirect connection between

Table 3. R^2 values from GAM models illustrating the percentage of the variability in cpue, by species, accounted for by year, depth, bottom temperature, and the Q-values.

Taxon	Year + s(depth)	Year + s(depth) + s(bottom temperature)	Year + s(depth) + s(bottom temperature) + $s(Q_1)$ + $s(Q_2)$ + $s(Q_3)$	Increase in R^2 because of $s(Q_1)$ + $s(Q_2)$ + $s(Q_3)$
Alaska plaice	0.359	0.436	0.536	0.100
Arrowtooth flounder	0.414	0.720	0.755	0.035
Flathead sole	0.133	0.231	0.310	0.079
Pacific cod	0.056	0.229	0.279	0.050
Pacific halibut	0.065	0.304	0.323	0.019
Rock sole	0.397	0.540	0.618	0.078
Walleye pollock	0.122	0.241	0.280	0.039
Yellowfin sole	0.630	0.720	0.770	0.050
Snow crab	0.179	0.378	0.475	0.097
Tanner crab	0.086	0.316	0.448	0.132

acoustics and prey distributions is not examined here, the utility of acoustic data in habitat models is nonetheless supported for the EBS continental shelf.

An improved understanding of fish–habitat relationships would promote more effective conservation and management of fisheries resources. To date, progress in habitat management has been hindered by inadequate data, both in terms of spatial extent and variety, as well as an insufficient understanding of the functional relationships between fish and their environment. For the latter, at least some of the difficulty stems from an overreliance on descriptive methods that are better suited for general ecological summaries. For example, purely geophysical characterizations of habitat are overly simplistic and may ignore significant factors, such as temperature, that affect species distributions. Similarly, standardized habitat-classification schemes are too restrictive, in that they do not adequately account for the continuous nature of environmental variability or the associated biological responses. It is commonly observed that these standard habitats do not support unique biota and, conversely, that biota generally occupy multiple habitat types as defined by these schemes (Hewitt *et al*., 2004; Eastwood *et al*., 2006). Alternatively, continuous descriptions of fish habitat are possible and should be more realistic when acoustic (and other environmental) data are incorporated into quantitative habitat models. Progress, however, has been limited by the small number of variables that are both relevant and can be measured efficiently over large areas.

Continuous-valued acoustic data are particularly suited to quantitative habitat models for marine-fishery management. These data are both readily acquired and processed using commercially available hardware and software and can satisfy an implicit requirement of national- and international-scale habitat programmes for habitat metrics. In our case, a basin-scale survey of the seabed was accomplished while operating in the background of a dedicated midwater, acoustic stock-assessment survey. A group of international acoustic specialists considering future directions for acoustic seabed-classification science recently identified the need for "relevant habitat variables that are independent of each other" (Anderson *et al*., 2007). Note again, the acoustic parameters derived from the EK500 SBES echograms, and the previously considered Klein 5410 data, satisfy these essential requirements. Relevance and utility of the data are clearly demonstrated by improved model fits in the current study (Table 2) and statistically significant contributions to the best habitat models for each species in the previous study (Yeung and McConnaughey, 2008). Furthermore, the fact that these marginal contributions were measured after inclusion of the other environmental variables (e.g. depth, which commonly displays strong correlations with seabed composition and complexity; Anderson *et al*., 2007) indicates that unique information affecting the abundance of fish is involved. Notwithstanding, there are a number of technical and operational challenges to be considered before proceeding with costly, shelf-scale acoustic surveys of fish habitat (von Szalay and McConnaughey, 2002; reviewed by Kloser, 2007).

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