

MAPPING OF MARINE SOFT-SEDIMENT COMMUNITIES: INTEGRATED SAMPLING FOR ECOLOGICAL INTERPRETATION

J. E. HEWITT,^{1,3} S. F. THRUSH,¹ P. LEGENDRE,² G. A. FUNNELL,¹ J. ELLIS,¹ AND M. MORRISON¹

¹National Institute of Water and Atmospheric Research, P.O. Box 11-115, Hamilton, New Zealand

²Département de sciences biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

Abstract. Increasingly, knowledge of broad-scale distribution patterns of populations, communities, and habitats of the seafloor is needed for impact assessment, conservation, and studies of ecological patterns and processes. There are substantial problems in directly transferring remote sensing approaches from terrestrial systems to the subtidal marine environment because of differences in sampling technologies and interpretation. At present, seafloor remote assessments tend to produce habitats predominantly based on sediment type and textural characteristics, with benthic communities often showing a high level of variability relative to these habitat types. Yet an integration of information on both the physical features of the seafloor and its ecology would be appropriate in many applications. In this study, data collected from a multi-resolution nested survey of side-scan, single-beam sonar and video are used to investigate a bottom-up approach for integrating acoustic data with quantitative assessments of subtidal soft-sediment epibenthic communities. This approach successfully identified aspects of the acoustic data, together with environmental variables, that represented habitats with distinctly different epibenthic communities. The approach can be used, regardless of differences in data resolution, to determine location- and device-specific relationships with the benthos. When such relationships can be successfully determined, marine ecologists have a tool for extrapolating from the more traditional small-scale sampling to the scales more appropriate for broad-scale impact assessment, management, and conservation.

Key words: *acoustic-derived habitats; broad-scale surveys; epibenthic mapping; habitat fragmentation; side-scan sonar; video assessment.*

INTRODUCTION

Increasingly human activity has the potential to cause broad-scale changes in seafloor habitats and communities. Impacts associated with commercial fishing, terrestrial sediment run-off, and eutrophication clearly demonstrate the need for resource management to control broad-scale and long-term habitat change on the seafloor. In order to address management issues, such as developing adaptive, rotational fishing strategies, identifying and monitoring reserve areas, or determining environmental baselines, seafloor communities and habitats need to be surveyed over a range of scales relevant to both the process impacting the environment and to the ecology (Zajac et al. 2003). The ability to survey over large scales is also important for addressing more fundamental ecological questions because many processes structuring the natural world operate at large scales (e.g., variations in recruitment, productivity, or climate variation).

For many years, sampling logistics restricted the quantitative sampling efforts of ecologists to small scales or sampling designs based on a few sparsely

spaced samples collected from a very small proportion of the environment. Terrestrial ecologists were the first to be able to utilize remote sampling (aerial photography, satellite imagery) to map large areas and nest detailed information at smaller scales within the overlying landscape. Rules for the amount of sampling needed for ground truthing and techniques for assigning grid cells to vegetation classes have been developed and tested (e.g., Rosenfield et al. 1982, Curran and Williamson 1986, Congalton 1991, Hall et al. 1991). Continued development of these techniques has advanced the study of meta-populations and habitat utilization, as well as providing broad-scale information to resource managers concerned with conservation or impact assessment (e.g., Forman and Gordon 1986, Gilpin and Hanski 1991, Hall et al. 1991, Forsys and Humphrey 1999, Ferreras 2001). Unfortunately, in the marine environment, only intertidal areas and shallow subtidal areas with clear waters have been able to directly benefit from the use of this technology. The development of acoustic technology capable of surveying large areas of the seafloor has led to the expectation that detailed ecological information could be integrated with broad-scale physical habitat features, producing a cost-effective interface between traditional benthic ecological surveys and geo-physical mapping (Brown et al. 2002). However, simply transferring the rules and

Manuscript received 11 June 2003; revised 17 November 2003; accepted 4 December 2003. Corresponding Editor: P. K. Dayton.

³ E-mail: j.hewitt@niwa.cri.nz

analyses developed for terrestrial studies is often not possible due to differences in remote sensing technologies. For example, there is a strong link between water depth and survey resolution for many subtidal remote devices (Orlowski 1984, Bax et al. 1999, Kloser et al. 2001). Moreover, most acoustic data are not directly related to specific biological variables (cf. fluorescence and forest canopy cover) and may not be biologically related at all (Hamilton et al. 1999, Smith et al. 2001).

Quantitative benthic biological sampling has traditionally relied on collecting a relatively low number of small cores or grabs. Depending on the sampling design, samples were regularly or randomly dispersed either directly over the area of interest or within a stratified sampling regime. Dredges may also be dragged across the seafloor to collect larger organisms, although there is often debate about the quantitative nature of this type of sampling. For all of these traditional sampling devices, samples are assumed to be representative of a larger area and some uncertainty is expected. The development of underwater video systems allowed direct estimation of epibenthic floral and faunal densities, as well as identification of surface bioturbation, sediment microtopography, and sediment characteristics, over much larger scales (e.g., Grassle et al. 1975, Schneider et al. 1987, Auster et al. 1989, 1995, Parry et al. 2003). However, gathering high quality video data that enable quantification of these seafloor features requires that the video be moved slowly over the seafloor. Also individual video tracks are usually <1 m wide, except when water clarity is exceedingly high, further restricting the area sampled. Nevertheless, the combination of traditional sampling and video analysis has demonstrated that small-scale physical and biogenic features can be important in determining the structure and heterogeneity of benthic communities (Thrush et al. 2001, 2002, Hewitt et al. 2002).

Acoustic devices, although still not able to acquire data as rapidly as aerial and satellite imagery, can provide high resolution, continuous imagery of the seafloor. Devices are based on single or multiple transducers, sending acoustic pulses to the seafloor and measuring the energy of the reflected signal; this energy is affected by seafloor slope, hardness, roughness, and absorption. Initially acoustic devices were used only for mapping sedimentary features, due to the strong, demonstrated link between sediment characteristics of the seafloor and the returned acoustic signal. Now remote acoustic assessment is increasingly being used for benthic biological features (e.g., Magorrian et al. 1995, Doonan and Davies 1996, Schwinghamer et al. 1996), particularly epifauna and biogenic reefs, which can be expected to affect acoustic reflectance. New technology constantly sees new devices becoming available, and a major challenge facing ecologists is how to use the information provided by this technology to learn something about the distribution and abun-

dance of populations, communities, and habitats on the seafloor.

Recognizing the limitation in our ability to match acoustic habitats with particular benthic communities or the density of emergent flora and fauna is an important consideration in the development of broad-scale mapping techniques. When studying broad-scale distribution patterns of populations and communities or assessing impacts, habitat size, fragmentation, and connectivity are important, thus inconsistencies between habitats defined by different sampling techniques (e.g., different acoustic devices, video) can be a problem. Generally, acoustic data are analyzed to produce habitats, which are described in terms of depth and sediment characteristics (e.g., Hamilton et al. 1999, Bates and Byham 2001, Brown et al. 2002), although dense beds of large emergent bivalves, sponges, or seagrasses have occasionally been reported (Conway et al. 1991, Powell et al. 1995, Kaiser et al. 1998a, Smith et al. 2001). Studies investigating the benthic fauna of the acoustically derived habitats usually report a wide range of communities within a habitat (e.g., Zajac et al. 2000, 2003, Brown et al. 2002) or biological associations that occur in more than one habitat (e.g., Kostylev et al. 2001, Freitas et al. 2003), particularly for soft-sediment areas. These results are not surprising, as most benthic ecologists would anticipate variability of faunal communities both within and between sediment environments.

If we cannot develop techniques that integrate ecological information into acoustically generated maps and thus can only differentiate habitats with such distinctly different communities as would occur between rock vs. soft sediments or shallow vs. deep water, then the ability of these approaches to identify areas with high biodiversity values or detect ecological changes over time are severely limited. This is particularly true for soft sediments that dominate the seafloor because these areas are frequently of low relief with relatively homogenous sediment types covering large areas. On the other hand, if aspects of the data that do relate to benthic communities can be identified and used to interpolate between the spatially more restrictive, traditional forms of direct biological sampling, then this approach will be important for advancing our fundamental ecological understanding of seafloor ecosystems and facilitating sustainable management of its resources.

In this study, we investigate data collected by two different remote acoustic devices: side-scan sonar (henceforth referred to as side-scan) and a single-beam sonar coupled with the QTC VIEW data acquisition system (Collins et al. 1996) (henceforth referred to as single-beam) and compare it with information from a towed video camera. Information was collected from a variety of soft-sediment substrates with a similar amount of time spent collecting data using each system. First, we take a top-down approach and investigate the

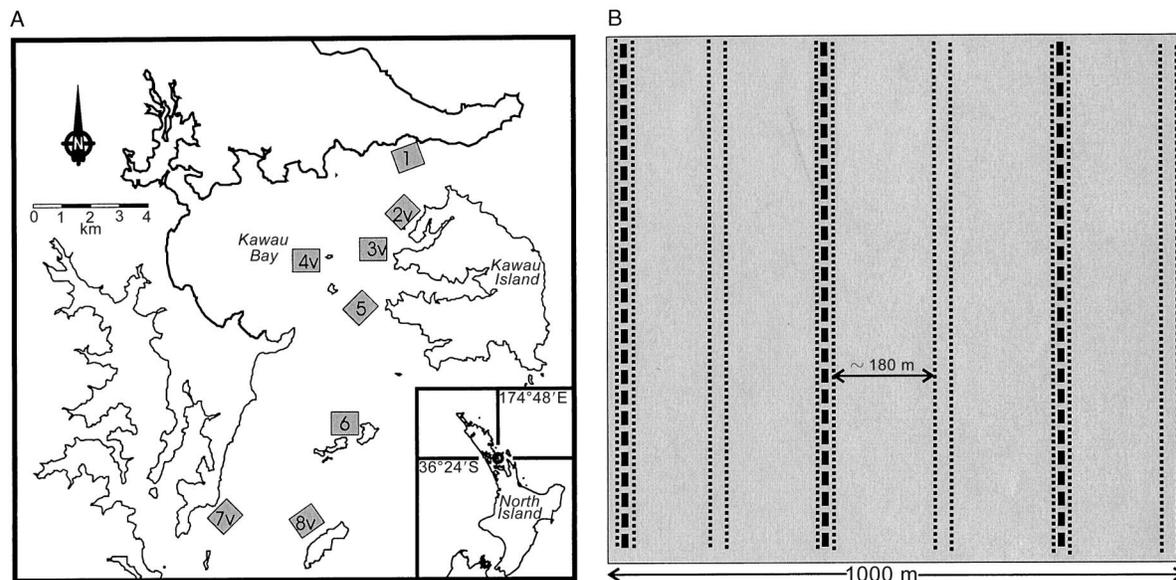


FIG. 1. (A) Location of sites 1–8 in Kawau Bay, New Zealand. Sites with video transects are marked with a “v.” (B) Schematic of survey design used in each 1-km² area. The entire area (shaded) was surveyed by side-scan sonar. Fine dashed lines are the single-beam transects, and the thick dashed lines are the video transects.

relationship between habitats derived from data collected by the two acoustic devices and those biological habitats identified from the video. Second, we use a bottom-up approach to determine whether there were relationships between epifaunal communities visible from the video and any of the data collected by single-beam and/or side-scan. We felt that if we could identify such relationships, even when acoustic habitats contained variable and overlapping communities, it was generally likely that the bottom-up approach would enable marine ecologists to use acoustic data to both interpolate between and extrapolate from more restricted video surveys.

METHODS

Study design

The study was conducted in the summer of 1999 in Kawau Bay, a large embayment on the northeast coast of North Island, New Zealand (Fig. 1A). Kawau Bay is composed mainly of soft-sediment habitats in the 10–20 m depth range; sediment characteristics and biogenic structure are variable. As it was not possible to survey the whole area, eight sites were chosen that reflected a range of biological habitats and geographic locations around the bay. Each site was comprised of soft sediment, with no rocky patches. There were no strong sedimentary patterns driven by differences in wave climate or currents, and there were reasonably dense but patchy epibenthic (mainly faunal) communities. Each 1-km² site was completely surveyed by side-scan sonar. Six pairs of 1 km long transects (20-m spacing between the members of a pair, ~180 m between pairs) were sampled with single-beam sonar

(Fig. 1B). At each site, the single-beam transects ran down depth gradients. Three of the eight sites could not be videoed due to the presence of sub-sea cables. However, at the other five sites, three 1 km long video transects were run in approximately the same position as three of the single-beam transects (Fig. 1B). Video was used rather than dredging, despite the higher time per unit area surveyed, as dredging is at best semi-quantitative and does not allow any identification of seafloor characteristics.

Data collection

All navigation was done using the software package HYDRO (Trimble 2001) and a Trimble DSM212 dGPS (Trimble, Sunnyvale, California, USA) to ensure an overall spatial positioning accuracy of less than 5 m (but see the Appendix). For both the side-scan and video, spatial positioning was adjusted for layback of the towed device relative to the dGPS, using tow length and angle to the boat. This was sufficient as low current speeds resulted in little lateral movement, the angle of which was easily incorporated into the layback.

Side-scan.—A Klein 595 sonar (Klein, Salem, New Hampshire, USA) operating at 500 kHz, towed at 1–1.2 m/s (2–2.5 knots), was used in this study. The system was capable of imaging targets as small as 1 cm diameter and resolving targets 0.5 m apart. The range was 75 m either side of the tow fish, altitude was maintained at 5–10 m above the seafloor, and transects were run with 150-m line spacing. To reduce variability associated with distance from the transducer across the image, an automatic time-varying gain was applied to amplify the returned signals by an amount dependent

TABLE 1. Classes of video data used while videoing the seafloor at Kawau Bay, New Zealand.

Class no.	Class description
1	dead <i>Atrina</i> bed
2	bare, sparse dead <i>Atrina</i> , bioturbation
3	patchy live <i>Atrina</i> bed
4	live <i>Atrina</i> bed with sponges
5	patchy live <i>Atrina</i> with dense sponges
6	patchy <i>Atrina</i> and tubeworms
7	bare with tubeworms
8	patchy sponges
9	patchy sponges and tubeworms
10	dense sponges
11	sponges and bioturbation
12	bare, sparse sponges

on the time since transmission. Fix marks and a ship track plot were used to align side-scan transects with each other across each box.

Single-beam.—A Simrad EA501P hydrographic sounder (Simrad, Horten, Norway), attached to the boat, was operated at 200 kHz, 250-W transmit power, with a ping rate of 5 pings/s and a fixed beam width of 7°. This was connected to a QTC VIEW series 4 (Collins et al. 1996) data acquisition system. Settings for the QTC VIEW system were a reference depth of 14 m and a base gain of 15 dB. Resolution varied from 0.37 to 3.0 m², depending on depth, although more generally the range was from 1.22 to 2.44 m². As QTC VIEW uses a stack of five consecutive pings for each record, at our speed of 2.6 m/s (~5 knots), a ping stack (generally covering between 6 and 12 m) was processed approximately every 8 m.

Video.—Video records of the seafloor were collected using two high-resolution color CCD video cameras (BENTHOS, North Falmouth, Massachusetts, USA), with independent light sources and scaling lasers, mounted on a sled. The scaling lasers consisted of three parallel lasers at 15-cm distances and one angled laser. Depth, heading, position, and time were continually recorded on the videotapes. The sled was towed at 0.26–0.41 m/s (0.5–0.8 knots) with cameras positioned 0.5 m above the seafloor. One camera was directed vertically downwards, and the other was forward-facing at an angle of approximately 45°. The record from each site was viewed during collection, and areas were assigned to classes based on obvious biological and

physical features on the seafloor (Table 1). Counts were made along 10 640-cm² (40 cm wide × 16 m long) strips on each transect of features passing between the lower scaling lasers (Table 2). The starting positions along each 1-km video transect for each strip were randomly selected, taking care that the position was fully within a single class and that each class observed on a transect was sampled. Seafloor microtopographical features sized greater than 10 mm (both physical and biological) and other sediment characteristics (Table 2) were noted in terms of relative abundance (0 = absent, 1 = present but not dominant, 2 = dominant [$>50\%$ of area]).

Classification of acoustic and video information

The first step for the top-down approach was to classify data collected by each of the devices (Fig. 2). We use the following terminology for the results: for the two acoustic devices, data were classified into groups; for the video data (flora, fauna, and seafloor microtopographical features and other sediment characteristics), data were classified into habitats.

Side-scan.—Side-scan maps were integrated with navigation information and corrected for directional changes. Although the sonograph produced by our side-scan sonar can be analyzed digitally, for this study the analysis was done visually as this was the easiest way of integrating areas with “dirty” data generated by rough seas during surveying. The process was confirmed by image analysis (Optimas 6.2; Optimas 1996) of the gray scales on a clean strip from each site/group. Three side-scan groups were identified: a homogenous light-gray group; a heterogeneous group with a large gray-scale range; and a relatively homogenous dark-gray group (Fig. 3).

Single-beam.—Data from all sites were processed together, initially using the proprietary procedure available in the program QTC IMPACT (QTC 2000). In this procedure, cluster splits were made in the first three axes in principal component data cloud until further splits failed to appreciably reduce the overall variance. Splitting decisions were made as detailed in Morrison et al. (2001) using inflexion points of the total scores and the “cluster performance index.” The classification based on the QTC proprietary software defined seven groups. However, 53% of the data points from

TABLE 2. Features recorded along video transects.

Character	Feature
Fauna†	bivalves (<i>Pecten</i> , <i>Atrina</i>), hydroids, sponges (four types), chaetopterids, tubeworms (sabellids and probably maldanids), ascidians, bryozoans, ophiuroids, star fish (<i>Patriella</i> , <i>Asterionella</i> , <i>Coscinasterias</i> , <i>Luidia</i>), hermit crabs (<i>Paguristes</i> and <i>Plyopagurus</i>), holothurians, crabs, gastropods
Flora†	kelp, diatom mats, coralline algae
Seafloor microtopography‡	burrows, holes, physical mixing, tracks, pits, mounds, ripples
Sediment characteristics‡	coarse particles (larger than sand), shell hash (whole or broken), sand, mud, mud-sand

† These features were counted.

‡ These features were ranked according to relative abundance on a scale of 0–2.

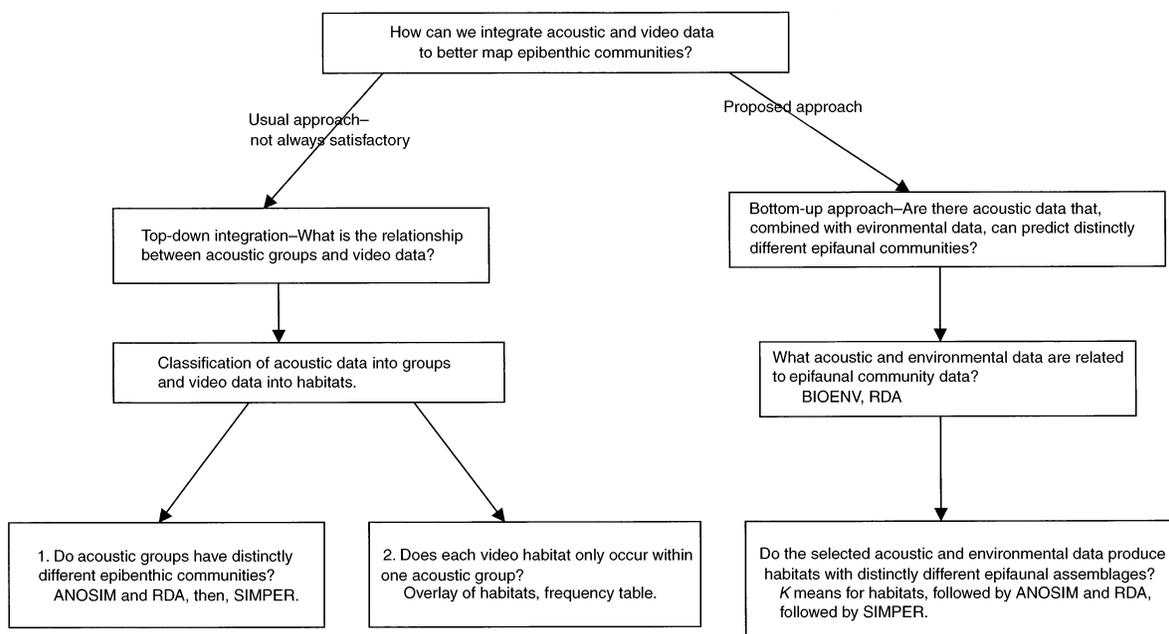


FIG. 2. Schematic of the top-down and bottom-up approaches and the analyses performed on the data. See *Methods: Integration of data collected acoustically with that collected by video* for descriptions of integration methods.

the single beam could be allocated correctly to these seven groups using depth alone (based on discriminant analysis), possibly due to the strong correlation between the first principal component axis and depth (Spearman's $\rho = -0.91$). As strong depth gradients in the distribution of epifaunal communities and sediment types were not apparent in the video data, we tried a second data-processing procedure.

For the second procedure, we determined the number of principal components (five) required to explain 95% of the variability in the 166 variables produced by the QTC VIEW system. The ping scores along those axes were used in the *K*-means partitioning procedure of The Q Package freeware, described by Legendre et al. (2002). The Calinski-Harabasz statistic was used as a stopping criterion to determine the best number of groups, in the least squares sense. This procedure resulted in a classification into six groups and reduced the number of points that could be allocated by depth alone to 34%. This is much closer to the 21% correct allocation by depth of video data points to video habitats, so these single-beam groups derived by *K* means were used in the further analyses.

At present the relative merits of these two classification procedures are under discussion, along with a clarification of the exact nature of the QTC proprietary software procedures (Legendre et al. 2002, Legendre 2003, Preston and Kirlin 2003).

Video.—Analysis of the video data was complicated by our desire to include, not just the count data of flora and fauna, but also signs of biogenic and physical sed-

iment reworking and indications of the dominant surficial sediment type. In order to achieve this, the following procedure was followed. The video data from all sites were split into four data sets: flora, fauna, seafloor microtopography, and sediment characteristics. Principal component analysis was carried out on each data set separately, as proposed by Lebart et al. (1979). The flora and fauna data sets were transformed, using a Hellinger transformation, so that principal component analysis based on Euclidean distances was appropriate (Legendre and Gallagher 2001). For each data set, the principal components were standardized to total variance of 1. The standardized principal components from the four principal component analyses were then assembled in a single data matrix (Lebart et al. 1979), in order that *K*-means partitioning could be carried out on the data as a whole.

Weighted *K*-means partitioning was applied to the combined data matrix of principal component axes. After preliminary trials determined that the resultant classifications were not particularly sensitive to changes of 10%, the weights for both the microtopography and sediment characteristics data sets were set to 10%. The residual percentage ($100 - 10 - 10 = 80$) was split into a proportion reflecting the number of different groups in the fauna vs. flora (i.e., 70 and 10, respectively). *K* means were then run and the resultant habitat assignments were then compared to those assigned during data collection, to determine whether the groups suggested by viewing during collection were useful for defining areas for counting.

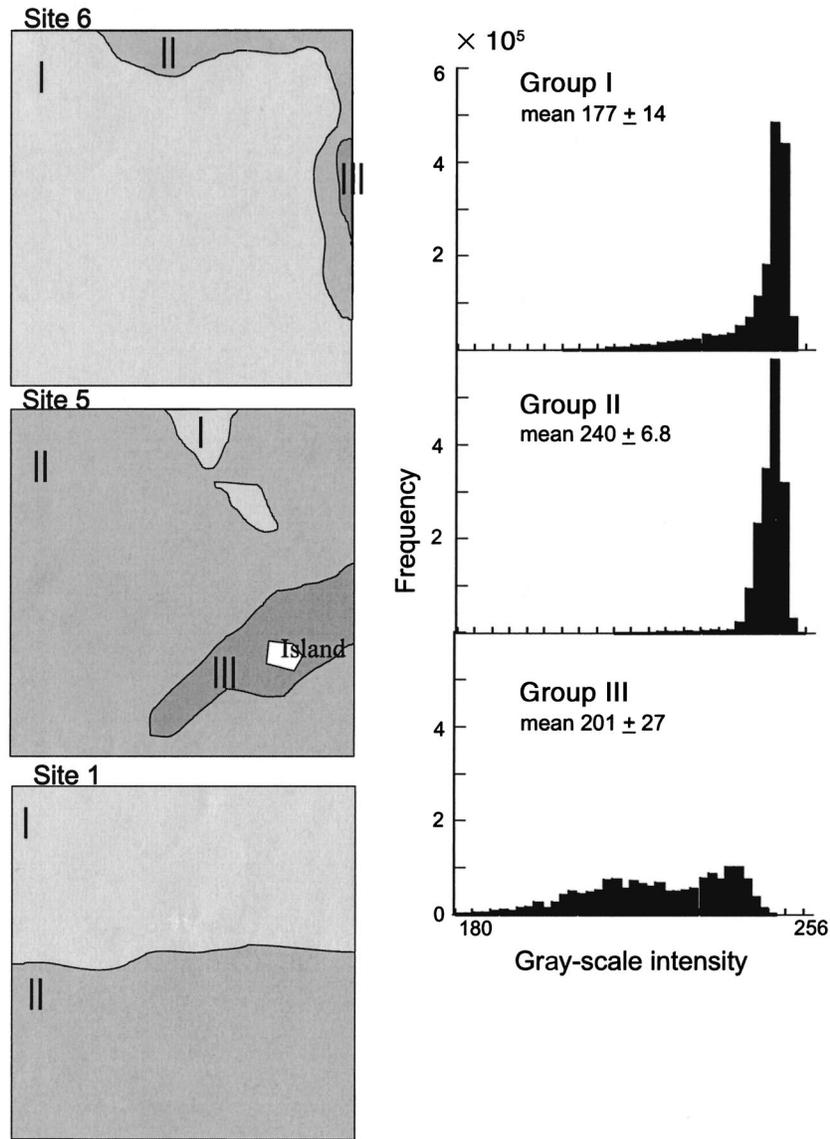


FIG. 3. Frequency histograms of the reflectance intensities found in the three side-scan groups (I, II, III), together with examples of their distribution within three 1-km² sites. Frequency is pixel frequency per 800 m²; gray-scale intensity is the intensity of reflectance linearly mapped onto gray shadings that range from 0 to 256. For each group, the mean (± 1 SE) intensity is given.

*Integration of data collected acoustically
with that collected by video*

Usually in mapping, integration is achieved by classifying the acoustic data into groups that are ground-truthed by biological data. However, while this may work for some of the larger epifauna and flora (particularly when they occur in dense patches), the acoustic groups may not relate well to smaller epibenthos (such as tube worms and gastropods) or even large epifauna that are diffuse spatially (e.g., low densities of sponges). So our first approach was to test for this top-down match and then address the problem from the bottom-up, that is, are there some acoustic data that

can explain the often low density seafloor communities in these soft-sediment environments?

Top-down integration: the relationship between acoustic groups and video data.—We tested whether the acoustic habitats were good representations of the epibenthos in two ways (Fig. 2).

First, we tested the hypothesis that, for each acoustic device, the acoustic groups did not contain distinct epibenthic communities, using a randomized permutation test (ANOSIM; Clarke 1993) on the Bray-Curtis similarity matrix derived from the epifaunal and floral data. To ensure that the results derived from the ANOSIM analysis were not a function of the power of the test,

we also used redundancy analysis (RDA) to test the same hypothesis (Legendre and Anderson 1999). We also determined the species that contributed the most to differentiating between the acoustic groups using an analytical classification procedure (SIMPER; Clarke 1993). ANOSIM and SIMPER are routines available in PRIMER (Clarke and Gorley 2001), while redundancy analysis was carried out using CANOCO (ter Braak and Smilauer 1998).

Second, the acoustic groups were compared to the video habitats, on a broad scale with a 50-m resolution, by using the maps of each site produced by data from the different devices (e.g., Fig. 4). For each site, the video habitats observed along the transects were overlain on both the side-scan and single-beam-derived maps with the video runlines identified using SURFER 7.0 (Keckler 1995). A 25-m no-count zone was set up on each side of the acoustic-group boundaries to minimize the effect of both geo-referencing errors and the differences in the way the classification procedures deal with points near the edges of clusters on the analysis (Appendix). The number of side-scan and single-beam groups in which each video habitat occurred was then determined over all sites. These maps also allowed us to determine geographic consistency of the acoustic groups and video habitats determined by the different sampling devices both across and along isobaths.

This second analysis clearly demonstrates the differences between mapping carried out by devices capable of collecting continuous data as opposed to those that merely sample a restricted area. To generate single-beam and video maps, the assumption has to be made that the data collected from a sample point or transect are representative of a larger area (with some uncertainty accepted) and that interpolation between transects is valid. Also, for the video, as the counts had not been made continuously along transects, the location of boundaries between groups were based on coordinates noted during the initial video viewing. For the single-beam, we needed to scale up from the detailed groups, produced for every 8 m, to groups that covered 50 m, to enable us to make comparisons between techniques at the same scale. To deal with areas where geoconsistency at the 8-m scale was low, i.e., 50-m windows covering more than one single-beam group, we used a procedure analogous to side-scan grouping procedures. That is, the frequency of occurrence of each single-beam group was calculated for each window, and a classification was run on this data to produce 50-m single-beam groups.

Bottom-up approach: identifying relationships for epibenthic communities, with acoustic data and environmental information (Fig. 2).—Environmental data used were: spatial coordinates (northings and eastings); depth; distance to the nearest rocky reef or island; mean distance to the two nearest rocky reefs or islands; and a sediment particle size classification determined from the video information. Distance to nearest rocky reefs

or islands (which was never less than 1 km) was included as a variable we could expect to be a structuring force in soft-sediment communities due to effects on currents, wave exposure, and predator foraging (Posey and Ambrose 1994). Acoustic data used were: the rank mean and variation in gray-scale intensity for each of the three side-scan groups and the scores along the first five PCA axes obtained from the QTC-VIEW data. The PCA axes rather than the 166 raw variables were used as many of the 166 variables were correlated. We used two statistical techniques to select variables useful in explaining epibenthic communities: redundancy analysis based on Hellinger transformed epibenthic count data and Spearman rank correlations between similarity matrices (BIOENV; Clarke and Gorley 2001). The variables selected as important were then classified by *K* means. The optimum groups obtained from this procedure were analyzed for similarities in their epibenthic communities using SIMPER.

RESULTS

Video data

K-means partitioning of the video data produced five video habitats corresponding to differing densities of live and dead *Atrina*, sponges, tubeworms, and gastropods, differing elements of seafloor microtopography (e.g., ripples and tracks), and general surficial sediment particle size characteristics (as given in Table 2). The five habitats were reasonably well defined in terms of characteristics (Table 3) and had significantly different epibenthic communities ($P < 0.01$) with a mean within-habitat similarity (based on Bray-Curtis distances of raw data) between 58% and 75%. Inter-habitat community dissimilarities ranged from 52% to 72%, with a mean dissimilarity of 64%. Two of the habitats (the gastropod/sponge/bioturbated habitat and the dead *Atrina*/muddy sand habitat) were limited in spatial distribution occurring at only a few sites (two and three, respectively) and at only a few places within each site. The other three habitats were more widely spread, although only the tubeworm/bare habitat occurred at all five sites.

Top-down integration: do the acoustic groups have distinctly different epibenthic communities?

The acoustic groups did not always have distinct epibenthic communities. No differences were found between the epibenthic communities in the side-scan groups by ANOSIM (global $r = -0.002$, $P = 0.519$), although redundancy analysis found differences between side-scan groups I and II ($P < 0.05$). Differences in communities were found between fewer than half of the single-beam groups by both ANOSIM and RDA ($P < 0.05$). While distinct communities represent the video habitats (e.g., dense gastropods with some sponges or dense live *Atrina*/tubeworms/sponges), it is more difficult to find distinct communities for the single-

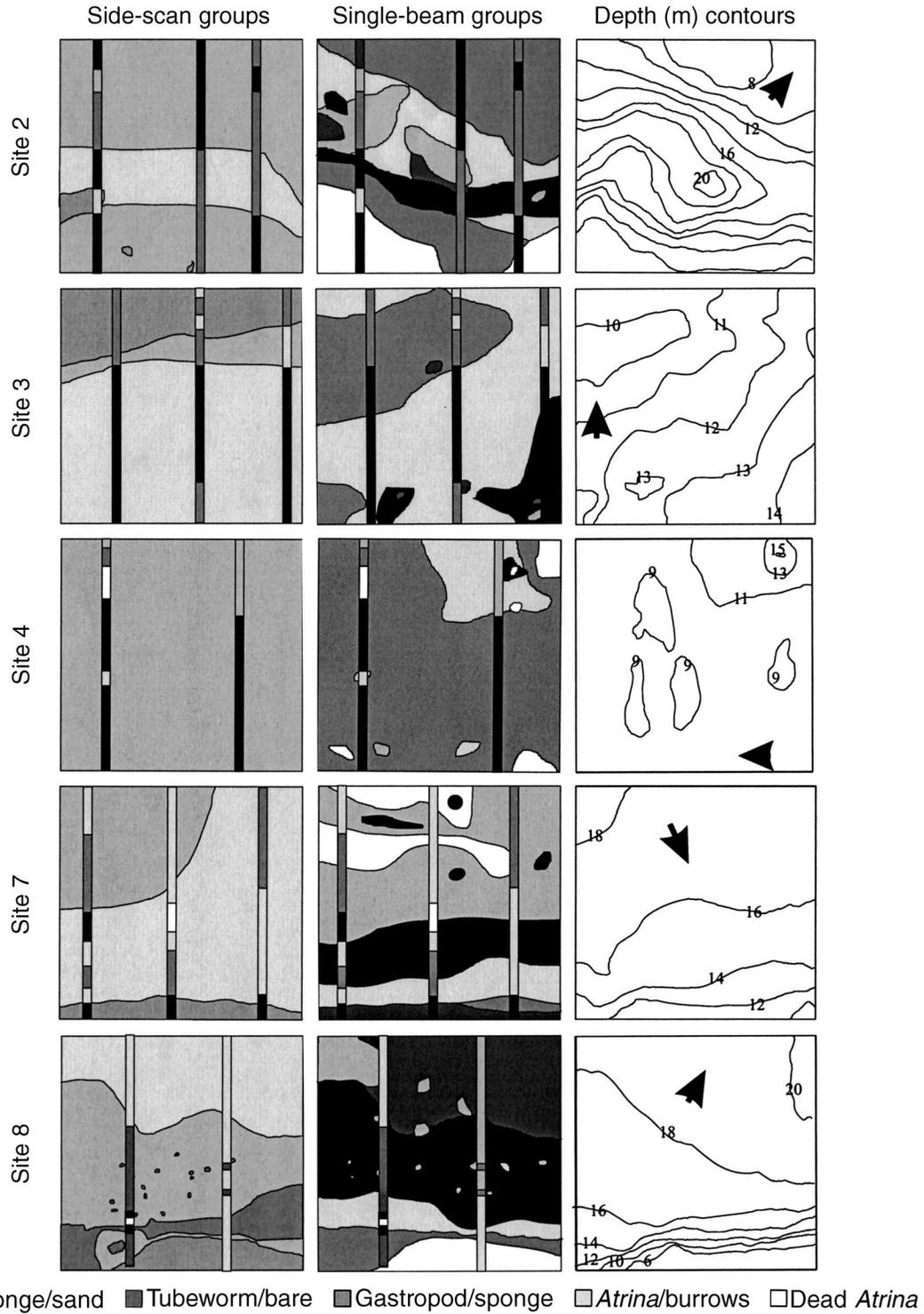


FIG. 4. Side-scan and single-beam maps for each of the 1-km² sites with video data and depth contour plots (arrows indicate north). For easy comparison between maps derived from video data and side-scan and single-beam maps, only some video map transects are shown, overlain. Note that Table 5 is not derived from these data, but from the actual video count locations.

TABLE 3. Video habitats classified by *K*-means partitioning of all sites with weights of 70:10:10:10 (fauna : flora : seafloor microtopography : sediment characteristics), compared to the initially assigned groups.

Habitat	Description	Initial class no.†	Similarity index (%)‡	No. sample locations	No. sites of habitat occurrence
Sponge/sand	sponges and tubeworms; coarse sand	5, 8, 9, 10	67	37	4
Tubeworm/bare	tubeworms or sparse sponges and scallops; mainly bare sediment with some coarse sand and shell hash	7, 12	58	46	5
Gastropod/sponge/ bioturbated	sponges and gastropods; sediment bioturbated	11	75	11	2
Live <i>Atrina</i> /burrows/mud	live <i>Atrina</i> , some tubeworms, sponges, and hermit crabs; tracks, burrows, and mud	3, 4, 6	61	26	4
Dead <i>Atrina</i> /muddy sand	dead <i>Atrina</i> and tubeworms, some live <i>Atrina</i> and chaetopterid tubes; tracks, mud, and fine sand	1, 2	67	7	12

† According to Table 1.

‡ The within-group Bray-Curtis similarity index of the epibenthic communities found within each video habitat.

beam and side-scan groups (Table 4). Even mean densities of individual taxa (for example the large emergent bivalve *Atrina*) do not show large variations among the single-beam or side-scan groups compared to the variations observed among the video habitats.

Top-down integration: in how many acoustic groups does each video habitat occur?

Table 5 demonstrates the absence of a simple hierarchical arrangement of physical drivers determining epibenthic communities. For the side-scan groups, video habitats were generally not confined to only one group. However, the video habitat dominated by gastropods and sponges with highly bioturbated sediment was only found in side-scan group II. No single video habitat was predominantly associated with any of the 50-m scale single-beam groups.

Bottom-up approach: identifying relationships for epibenthic communities, with acoustic data and environmental information

We investigated whether there were spatial, environmental, or acoustic data that would help us explain the epibenthic community data. Generally the two methods (redundancy analysis and BIOENV) gave similar results. Of the percentage of variation in community composition, 82.4% was explained by the redundancy analysis, and the variables selected (in order of entry to the model), with *P* values <0.05, were depth, distance to the nearest rocky area, mean gray-scale intensity from the side-scan groups, coarse sand content of the sediment, east coordinate, the fourth and third principal component axes derived from the single beam data, mean distance to the two nearest rocky areas, and

TABLE 4. The mean within-group similarity index and the taxa that most contribute to the within-group Bray-Curtis similarities based on faunal and floral counts.

Technique and Group	Similarity index (%)	Density (no./m ²)						
		Tubeworms	Sponges	Scallops	<i>Atrina</i> , live	<i>Atrina</i> , dead	Gastropods	Chaetopterids
Single-beam								
Group 1	47	50	4	1				
Group 2	47	40	4		2			
Group 3	47	40	4		2			
Group 4	54	50			4	1		
Group 5	46	40			3	4		3
Group 6	44	50	2		3			
Side-scan								
Group I	59	50	2		4			
Group II	43	40	3		2			
Group III	48	40	4		3			
Video								
Sponge/sand	67	40	7					
Tubeworm/bare	58	80	2	1				
Gastropod/sponge/ bioturbated	75		5			7		
Live <i>Atrina</i> /burrows/mud	61	20	2		6			1
Dead <i>Atrina</i> /muddy sand	67	20			1	7	2	

TABLE 5. Percentage of each video habitat found in each side-scan group.

Video habitats	Side-scan group		
	I	II	III
Sponge/sand	43	57	0
Tubeworm/bare	22	65	13
Gastropod/sponge/bioturbated	0	100	0
Live <i>Atrina</i> /burrows/mud	43	43	14
Dead <i>Atrina</i> /muddy sand	43	57	0

the mud content of the sediment. For BIOENV, the highest correlation (Spearman's $\rho = 0.91$) was achieved by depth, mean gray-scale intensity from the side-scan groups, depth, distance to the nearest rocky area, the fourth and fifth principal component axes, mud content of the sediment, and the northing coordinate.

K-means classification was carried out on the variables selected by either the BIOENV procedure or RDA as described above, and a further classification was conducted on the complete set of variables selected by either method (all selected variables). In each case, the classification suggested two groups were optimal; however, a secondary maximum was obtained for five groups (using either BIOENV-selected variables or all selected variables) and six groups (using RDA-selected variables). While the groups had distinctly different communities ($P < 0.05$ for all comparisons), regardless of which set of variables they were based on, both pairwise differences between groups and self-similarity within groups were greatest for the five groups derived from all selected variables ($P < 0.02$ for all comparisons). The communities found in these five environmental groups were markedly better than those observed for the side-scan or single-beam groups. In fact, communities in three of the groups were markedly similar to the communities observed in three of the video habitats, namely the sponge/sand, tubeworm/bare, and gastropod/sponge/bioturbation habitats (cf. Tables 4 and 6, groups I, II, and III). However, communities did not have such high within-group percentage of similarity. Inter-group community dissimilarities were also lower, ranging from 52% to 67%, with a mean dissimilarity of 59%. The groups were also more limited in spatial distribution. Three of the groups only occurred in a few places within three sites. The other two groups were more widely spread, although still only occurring at 3–4 sites.

DISCUSSION

The growing evidence for broad-scale disturbances in marine ecosystems means that many areas of marine ecology require definition of seafloor landscapes over large areas, e.g., whole embayments, gulfs, or continental shelves. The spatial distribution and size of habitats in a landscape play an important role in the functioning and structure of marine communities (Posey and Ambrose 1994, Irlandi et al. 1995, Peterson and

Estes 2000, Hewitt et al. 2002). Understanding broad-scale variation in seafloor features, which reflect environmental or ecological processes operating at multiple scales, is also important for assessing impacts and predicting recovery rates from large-scale disturbances. Furthermore, knowledge of how succession, larval dispersal, and rates of disturbance operate over a variety of scales in time and space, relative to scales of habitat variation, is essential for making predictions that are sensitive to the natural history of resident organisms. Sediments, currents, and wave environments as well as disturbances such as trawl marks and predator-feeding pits can often be discerned by remote acoustic sampling devices, providing an opportunity for ecologists to study large-scale processes.

In soft-sediment environments, however, the resident flora and fauna create much of the structure on the seafloor by affecting benthic boundary layer hydrodynamics, settlement surfaces, and refugia and can also modify sediment and biogeochemical fluxes (Thrush and Dayton 2002). Small resident organisms that have important effects on habitat structure and complexity present a challenge for broad-scale mapping because of the need for assessment at scales that focus on the organisms or surrogates for their activity (e.g., bioturbation measures). Studies to date suggest that acoustically derived habitat groupings may not always contain distinct communities, and discrete biological communities do not always show acoustic habitat group

TABLE 6. The mean within-group similarity index and the taxa that most contribute to the within-group Bray-Curtis similarities, based on faunal and floral counts, of the groups derived from the selected acoustic and environmental data.

Environmental group and taxa	No. sample points	No. occupied sites	Similarity index (%)	Density (no./m ²)
Group 1	5	3	59	
Sponges				6
Tubeworms				40
Live <i>Atrina</i>				3
Group 2	13	3	54	
Sponges				3
Tubeworms				4
Scallops				1
Group 3	20	3	53	
Sponges				3
Tubeworms				40
Gastropods				4
Starfish				1
Group 4	44	4	47	
Live <i>Atrina</i>				5
Tubeworms				50
Sponges				2
Hermit crabs				1
Group 5	45	3	55	
Tubeworms				30
Live <i>Atrina</i>				2
Chaetopterid				2
Crabs				0.5

fidelity, frequently occurring in more than one sedimentary environment (Zajac et al. 2000, Kostylev et al. 2001, Brown et al. 2002). Clearly, the appropriateness of habitat maps derived from different technologies will depend on the purpose to which they will be put, but we argue that in most instances this will require input of ecological information. For example, while Conway et al. (2001) reported success in detecting sponge reefs with side-scan sonar, living sponge distributions were more variable. The interpretation of acoustic maps for ecological purposes depends on a sophisticated understanding of biology. Using acoustic habitat groups to estimate habitat fragmentation and connectivity when groups contain multiple communities, or a community occurs in more than one habitat group, is likely to limit interpretation.

This implies that the data obtained from different survey scales and sampling/mapping devices must be well integrated. Integration between acoustic data and ecological information can be difficult for a number of reasons. First, differences in data resolution occur. Second, similarities between acoustic reflectance, sediment characteristics, and seafloor biology are probably location-dependent (e.g., see results for QTC from Sotheran et al. [1997], Kaiser et al. [1998*b*], Bax et al. [1999]), thus results cannot be translated from one study to another. Finally, the statistical procedures by which data are summarized into habitat types vary, yet differences in data partitioning have been observed between different statistical methods (Legendre and Legendre 1998, Legendre et al. 2002).

In this study we approached the problem of integration from both ends. The commonly applied top-down approach of classifying acoustic data into habitats and then comparing the benthic communities found within each habitat failed to reveal distinctly different epibenthic communities associated with specific habitats. However, we developed a bottom-up approach that integrated benthic community information with acoustic data that were site-specific, could be applied regardless of differences in data resolution, and did not rely on partitioning acoustic data into habitats. Using this approach, we successfully found relationships between epibenthos, determined from video transects, and a mix of aspects of acoustic data and environmental information that could be used to improve interpolation between restricted video survey points.

One solution, to the realization that communities of soft-sediment habitats vary considerably, is to use information on benthic communities collected by video, coring, etc., to assess the variability of community distributions within sedimentary habitats at multiple scales (e.g., Warwick and Uncles 1980, Zajac et al. 2000, 2003, Kostylev et al. 2001, Brown et al. 2002). This is an important approach in the study of ecological processes and the relationship between sedimentary habitats and the species utilizing them. It recognizes that spatial variability is not necessarily a problem, but

is ecologically important information. Transition zones that usually occur between one sedimentary habitat and another, and may cover significant proportions of the seafloor, have also been shown to be important (Zajac et al. 2003).

However, this approach, to some extent, imposes an hierarchical structure on benthic communities with local ecological relationships working within a broad-based framework of environmental variables (O'Neill et al. 1986). An increasing body of work is suggesting that local relationships can affect broader-scale processes. For example, benthic organisms can influence hydrodynamics and seabed stability (e.g., Frechette et al. 1989, Thrush et al. 1996, deDeckere et al. 2001). Our study developed a bottom-up approach that, while utilizing the concepts of relationships between a number of processes operating at different scales and the benthos, relates more to multi-scale theory (e.g., Wu et al. 2000) and allows us to take another step toward understanding and mapping the spatial distributions of communities.

The success of the bottom-up approach was not dependent on a specific statistical analysis and did not rely on partitioning acoustic data into habitats. It is true that the variables selected as important, and, indeed, the usefulness of the approach itself, are likely to be location-dependent. Also, the approach can only be used after biological data have already been collected. However, that the approach did work in an area where acoustic groups did not contain distinct epibenthic communities suggests that it may be generally useful. At the least, in locations where relationships can be obtained, broad-scale data (both acoustic and environmental) can be used to generate certainty on areas that have not been biologically sampled, for example by using them as covariables when interpolating by kriging (Legendre and Legendre 1998).

The results of this study also demonstrated problems in the use of limited biological data to solely ground-truth acoustic groups. Similarly, Freitas et al. (2003) noted that careful ground-truthing and examination of the relevance of habitats derived by classifying acoustic data to ecology was required. It is hard to determine from the literature how common ground-truth problems may be, as acoustic groups are generally ground-truthed by collecting benthic samples within particularly homogeneous areas of acoustic data (Smith et al. 2001). Such an approach may be naturally biased to supporting differences between the classifications and ignore the importance of variability within transition zones (Zajac et al. 2003). Also, statistical tests of the concordance between acoustic habitats and the ground-truth data are not always presented, and the number of ground-truthed sites (when reported) is generally low (Sotheran et al. 1997, Bates and Byham 2001, Smith et al. 2001).

The technologies available for assessments will influence the nature of the maps that can be produced. Often the newest and most sophisticated technologies

are not available, and many resource agencies that need broad-scale information cannot afford up-to-date technology. For example, the side-scan technology applied in this study is now considered outmoded. However, it is unlikely that the devices used in this study resulted in the lack of usefulness of the top-down approach we observed because, over a number of years, using a range of acoustic devices, many studies have observed that acoustic habitats do not necessarily contain unique communities (e.g., Zajac et al. 2000, Kostylev et al. 2001, Brown et al. 2002). Conversely, that the bottom-up approach provided useful results with outdated technology strengthens the potential usefulness of the approach, suggesting that even better results could be obtained with more sophisticated acoustic techniques. Also, characteristics of the area surveyed weighed against the usefulness of acoustic sensing. The area was all soft sediment, thus the extreme changes in reflectance due to differences between hard and soft surfaces were not seen. Moreover, there were no epifaunal reefs (such as those produced by serpulids, oysters, bryozoans, etc.) or large areas of macroalgae; the epifaunal and flora were patchy and generally not dense. However, these are characteristics of large areas of the seafloor and do not preclude the epibenthos from being important components of the ecosystem, affecting benthic-pelagic coupling (e.g., Dame 1993, Norkko et al. 2001), predation (e.g., Sebens and McCoy 1991), hydrodynamics (e.g., Frechette et al. 1989, Green et al. 1998), fisheries (e.g., Thrush et al. 2002), and infauna (e.g., Thrush et al. 2001).

Conclusions

Our results suggest that some acoustic data, augmented by environmental data, can be used to interpolate between restricted video information to produce maps of biological associations. To achieve this, the design of video surveys (the number of video samples and the level of matches between acoustic and video data) should be determined at least partially independently of sonar information, with emphasis placed on determining the likely heterogeneity of the benthos. The diversity of the information provided by the different techniques suggests that using more than one acoustic technique is useful.

Broad-scale assessments of marine benthic systems are not yet routine. We know very little about the spatial distribution of seafloor habitats, even those defined mainly by sediments, over scales relevant to addressing issues of habitat disturbance and fragmentation. Disturbances such as trawl marks, predator feeding pits, and sediment deposition can often be discerned by acoustic technology. Integrating information on the spatial and temporal scales of disturbance rates with observed changes in spatial arrangements of benthic communities will address important questions concerning broad-scale degradative change to the seafloor. Nevertheless, there are unresolved problems related to

scaling-up ecological data and the relationships inferred between benthic communities/habitats and data collected by indirect remote devices. Solving these problems will require data collection on a broad scale, in a number of marine ecosystems, and updating designs as new techniques become available. But in all this, it is important that ecologists focus on providing ecological information, at relevant scales and accuracy for the provision of meaningful broad-scale assessment and mapping.

ACKNOWLEDGMENTS

We thank Andy Hill, NIWA Wellington for collecting the side-scan sonar information and producing the side-scan groups. This research was supported by FRST (CO1X0212). We also thank Roman Zajac and two anonymous reviewers for improving the presentation.

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APPENDIX

MATCHING THE LOCATION OF DATA COLLECTED BY THE DIFFERENT DEVICES

Before comparisons could be made between the data collected by the different devices, we had to satisfy ourselves that the survey positions matched, at least within the 5-m error of the GPS. This was not a problem for the video–side-scan comparisons as the side-scan coverage was continuous and did not alter in resolution with depth. However, for the video–single-beam comparisons, we had two problems.

First, the single-beam data had a data point (ping stack made by adding 5 pings in an unknown manner) approximately every 8 m, with the data point covering 1.9–15 m, depending on depth. The video strip, however, covered 16 m, although at no time was the first half of the strip markedly different from the second half. Fortunately, in 94% of the video locations, the two ping stacks received identical group numbers from the single-beam grouping systems. For the remaining 6%, the group was randomly selected from the two possibilities.

Second, the video transects did not cover the same positions as the single-beam transects in the across-site (across depth) position. Obviously if the video data points were bracketed

by identical single-beam groups from the pair of single-beam run lines, it would not be difficult to convince ourselves (after all, this is the basis of mapping) that the group would also apply to the videoed area. However, there were many places where the single-beam group allotted to the line running down the depth gradient did not match that on the line running up the depth gradient 20 m away. This could be due to heterogeneity in seafloor characteristics at the 20-m or less scale, although three factors weigh against this. First, we did generally get down-gradient consistency between pairs of single-beam data points at 16 m. Second, more mismatches occurred in areas of faster depth changes. Third, at each site we had 2–3 transects perpendicular to the main transects (as the single-beam sonar was not switched off while the boat was travelling between transects), and these perpendicular transects exhibited high geographical consistency of groups. Together these points suggest that the mismatches may be due to differences in reflectance arising from opposite seafloor slopes (e.g., Kloser et al. 2001). To reduce this, only the single-beam lines running down the depth gradients were used for comparison with the video data.