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REVIEW

Underwater acoustics for ecosystem-based management: state of the science and proposals for ecosystem indicators

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ABSTRACT: Ecosystem-based management (EBM) requires more extensive information than single-species management. Active underwater acoustic methods provide a means of collecting a wealth of ecosystem information with high space–time resolution. Worldwide fisheries institutes and agencies are carrying out regular acoustic surveys covering many marine shelf ecosystems, but these data are underutilized. In addition, more and more acoustic data collected by vessels of opportunity are becoming available. To encourage their use for EBM, we provide a brief introduction to acoustic and complementary data collection methods in the water column, and review current and potential contributions to monitoring population abundance and biomass, spatial distributions, and predator–prey relationships. Further development of acoustics-derived indicators is needed. We review and propose indicators for assessing and monitoring zooplankton, population dynamics of fish and other nekton, and changes in diversity and food-web functioning. Acoustic methods have the potential to make a strong contribution to EBM. Evaluation of new indicators and suitable reference points in different ecosystems are the current challenges.

KEY WORDS: Active acoustics · Indicators · Ecosystem-based management

INTRODUCTION

Christensen et al. (1996) defined ecosystem-based management (EBM) as 'management driven by explicit goals, executed by policies, protocols, and practices, and made adaptable by monitoring and research based on our best understanding of the ecological interactions and processes necessary to sustain ecosystem structure and function'. Thus, transitioning from single-species fisheries management to EBM will require increased information regarding the state and functioning of biotic ecosystem components (here, a taxon or group of taxa). A central tenet of EBM is the need to understand the ecological mechanisms and processes according to which the ecosystem is organized and the factors that modify them. These range from natural production, mortality, and climate change to human-induced fishing and environmental impacts. Management is then responsible for developing and funding appropriate

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survey programs to monitor the relevant ecosystem indicators.

Both active and passive acoustic methods are increasingly employed for exploring the marine environment (Foote 2009, Southall & Nowacek 2009). As shown by Koslow (2009) in a recent review, underwater acoustics have provided a means of studying a wide range of ecological subjects, including benthic and pelagic habitats, predator–prey interactions, and fish recruitment. In parallel, for over 4 decades active acoustic methods have been used routinely for surveying the water column to derive single-species abundance indices (in numbers or weight) for direct input into stock assessments, as well as for fisheries research in general (Misund 1997, Fernandes et al. 2002, Simmonds & MacLennan 2005). Routine monitoring typically focuses on species and taxonomic groups such as the small pelagic species of anchovy, sardine (e.g. Muiño et al. 2003, Paramo et al. 2003, Giannoulaki et al. 2008), and herring (e.g. Misund et al. 1997), as well as juvenile and adult stages of a range of commercial fish stocks (Nakken 2008, Koslow 2009, Oeberst et al. 2009) and zooplankton (Brierley et al. 1997). The advantage of active acoustic methods over other means of sampling marine zooplankton and fish is their high space–time resolution over wide scales (Godø 2009), as well as their capacity to simultaneously sample across several trophic levels, such as walleye pollock and their euphausiid prey (Ressler et al. in press), or large pelagic predator fishes like tuna and their micronekton prey (Bertrand et al. 2003). Acoustic methods can also yield data simultaneously on organisms and habitat. For example, Mackinson et al. (2004) extracted information on both sandeels and seabed sediment classes from a single-beam echosounder. An overview of acoustic methods for carrying out benthic habitat classifications is provided in a report by ICES (2007a). Finally, acoustic methods are particularly advantageous for sampling abundant but patchily distributed organisms such as schooling fishes or micronekton, following small-scale oceanographic features (Bertrand et al. 2010).

Beyond single-species abundance indices, however, acoustic methods provide a means of collecting a wealth of other ecosystem information relevant to EBM. While indicators are regarded as the cornerstone of ecosystem-based fisheries management (Jennings 2007, Rochet & Trenkel 2009), the use of acoustics-derived indicators is in its infancy. In this paper we provide an overview of acoustic methods, complementary data collection (i.e. sampling of target composition and habitat properties using non-acoustic tools), and the relevant ecosystem quantities and processes which can be studied with them. We then review and develop the concept of acoustics-derived indicators and metrics for EBM. Examples of indicators are given, not as an exhaustive list, but to highlight cases where acoustics-based indicators can readily transition from current practice to EBM. We illustrate cases where acoustics-derived indicators and metrics can fill information gaps in EBM, and emphasize where further development would be fruitful.

ACOUSTIC DATA COLLECTION

Sampling coverage and resolution

Active acoustic methods and technologies are characterised by their capacity to sample over a very wide range of spatial scales and resolutions for each transmission (i.e. 'ping') compared to other underwater and surface sampling methods (Fig. 1). With the use of a sufficient range of acoustic frequencies, simultaneous sampling of organisms spanning body sizes from millimetres to metres is possible within seconds. Manned or unmanned surface and underwater vehicles can sample large areas in a relatively short time, while stationary deployments customarily monitor single locations over long periods. Active acoustic methods detect targets very well in the water column, but are less reliable in detecting targets on or near boundaries, such as the sea surface ('surface blind zone') or sea floor ('acoustic dead zone'; Ona & Mitson 1996, Scalabrin et al. 2009). This is because the boundary generates a very large echo that can dominate echoes from biota. Multibeam systems and directional sonars (e.g. Trenkel et al. 2008, Korneliussen et al. 2009) and transducers deployed on alternative platforms (as opposed to scientific research vessels) such as autonomous underwater vehicles (AUVs; Fernandes et al. 2003, Scalabrin et al. 2009), buoys, and landers (Totland et al. 2009) offer improved capabilities in these situations, but do not entirely resolve the difficulties.

Fig. 1 shows the sampling resolution of some of the most commonly used instruments, but there is no limit to the imagination of innovative developers (Holliday 2009). Acoustic instruments are the only sampling devices that, unlike the selection or aggregation over depth accomplished by trawls, nets, etc., permit quasi-continuous sampling of fish and plankton throughout the water column. The resolution of acoustic measurements is similar to the spatial and temporal scales at which physical oceanographic

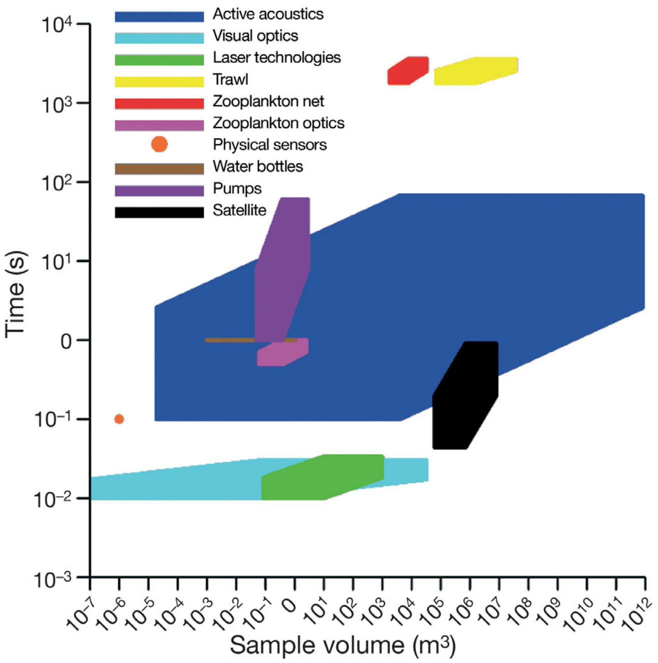

Fig. 1. Spatio-temporal scope of a single observation by various sampling devices and sensors. Resolution of the measurement is indicated by the lower-left side of the polygon and its range by the upper-right side. These represent the spatial extent of a single observation, not a time series (see description in Appendix 1)

data can be collected, a factor which has been exploited in spatially explicit analyses of acoustic data (e.g. Brandt et al. 1992, Holliday et al. 2009, Benoit-Bird et al. 2010, Moline et al. 2010).

Coupling acoustic data with other sampling techniques

Survey estimates are susceptible to biases introduced by fish and zooplankton behaviour. Examples of behaviours that alter the availability of fish to acoustic surveys include reaction of fish to sounds and survey vessels (Gerlotto & Fréon 1992, Misund & Aglen 1992, Popper et al. 2004, Handegard & Tjøstheim 2005, De Robertis et al. 2008, ICES 2010, De Robertis & Wilson 2011) and diel migrations (Lawson & Rose 1999). Coupling acoustic data with complementary data on size and species composition is often challenging, due to varying sampling selectivity and resolution among sampling methods, but it is necessary for proper interpretation of acoustic data, and comparisons among different complementary techniques can be insightful (McClatchie et al. 2000, Yule et al. 2007, Williams et al. 2010a).

The fundamental results of fisheries acoustics surveys and research are well-constrained solutions to the so-called 'inverse problem' for marine organisms (Holliday 1977a,b, Simmonds & MacLennan 2005), where the number, size, and type of acoustic targets (fish and plankton) are estimated from acoustic volume backscatter (S_v; dB re 1 m^{-1}) measurements (see MacLennan et al. 2002 for a review of acoustics terminology). The corresponding 'forward' problem involves computing the expected backscatter, given known numbers, sizes, and types of targets. A model that predicts the acoustic target strength (TS; dB re 1 m^2) is required in either case. Although inverse methods can in principle be used to estimate abundance, size, and composition of fish and zooplankton from S_v measurements at multiple, appropriately selected frequencies (Holliday 1977a,b, Costello et al. 1989, Holliday et al. 1989), the problem is generally underdetermined (i.e. the number of unmeasured, or unknown, variables is greater than the number of measured, or known, variables) and complementary data collection methods are required to establish the size and species composition of dominant acoustic targets as well as to parameterize the scattering models. Complementary biological data are often collected with trawls or cameras, and complementary physical oceanographic measurements are typically made with CTD profilers or satellite data.

The appropriate complementary methods for use in determining acoustic target composition depend on the ecosystem component being studied. For acoustic surveys of fish, trawl catches contribute information on species composition, size, and age structure, which are necessary to estimate abundance indices (ICES 2000, Simmonds & MacLennan 2005). They also contribute information on gender, maturity, reproductive potential, and diet. For zooplankton, acoustic information is often combined with species composition information from nets, pumps, and optical methods (Foote & Stanton 2000, Wiebe & Benfield 2003). Net sampling gear does not retain all sizes and species equally well (e.g. Clutter & Anraku 1968, Bethke et al. 1999, Williams et al. 2010a), a fact that affects the corresponding acoustic estimates of abundance and distribution (Godø et al. 1998).

Optical methods have been used in conjunction with acoustic measurements for estimating species composition, size, and packing density, and for observing behaviour (e.g. Gledhill et al. 1996, Thomas & Thorne 2003, Doray et al. 2007, Alvarez Colombo et al. 2009). While species identification is the most frequent use of optics in support of acoustic measurements, estimating fish size and behaviour with stereo-camera methods is also becoming more common (Long & Aoyama 1985, Osborn 1997, Harvey et al. 2003, Williams et al. 2010b,c). For zooplankton and ichthyoplankton, optical instruments (e.g. cameras, video plankton recorders, optical plankton counters) are commonly towed or lowered through the water column and used for species identification and enumeration (Herman 1992, 2001; Benfield et al. 2007, Cowen & Guigand 2008), although stationary instruments have also been used to observe behaviour (e.g. Jaffe et al. 1998). Since light energy is attenuated relatively rapidly in water, optical methods have a limited range compared to underwater acoustic methods, and when artificial light is required, avoidance and attraction by fish and zooplankton may significantly bias the observations (e.g. Sameoto et al. 1993, Benoit-Bird & Au 2003a, Trenkel et al. 2004, Stoner et al. 2008).

CONTRIBUTION OF ACOUSTICS TO ECOSYSTEM KNOWLEDGE AND EBM

Monitoring abundance and biomass

Acoustic methods have been routinely used for assessing and monitoring the abundance and biomass of many pelagic and some semi-demersal fish and zooplankton species of commercial importance (Fernandes et al. 2002, Simmonds & MacLennan 2005). Examples include Norwegian spring-spawning herring and herring in the Barents Sea (Toresen et al. 1998), anchovy in the Bay of Biscay (Massé 1996, Trenkel et al. 2009), sardine in the Spanish Mediterranean (Abad et al. 1998), walleye pollock in the Bering Sea (Karp & Walters 1994, Honkalehto et al. 2009), and Antarctic krill (Hewitt & Demer 2000, Kang et al. 2005). These long-standing acoustic surveys are the legacy of years of work in the field of fisheries acoustics and are fundamental to single-species stock assessment (e.g. ICES 2009, Cardinale et al. 2010), and they will continue to be important for EBM. However, biomass and abundance information for other ecosystem components which are not commercially important, but which may have a substantial influence on the food webs and ecosystems, are also needed.

Cost and logistical constraints prohibit the development of dedicated acoustic surveys for all taxa in an ecosystem. Fortunately, in many cases, indices can be derived from the same acoustic data collected for commercially important fish species. For example, De Robertis et al. (2010) demonstrated a classification method capable of distinguishing several acoustically important biological groups in the Bering Sea using data collected by acoustic and midwater trawl surveys of walleye pollock. Ressler et al. (in press) have applied this method to create an estimate of euphausiid biomass in the eastern Bering Sea using data collected during those same surveys. Euphausiids are a key component of the Bering Sea ecosystem as well as of many other ecosystems, comprising important prey for pollock and other groups of fish, birds, and marine mammals. The results of this index are being considered in the stock assessment process for pollock (Ianelli et al. 2010) and in a much broader assessment of the Bering Sea ecosystem (Zador & Gaichas 2010). Brierley et al. (2005) and Alvarez Colombo et al. (2009) have made target-strength measurements and have proposed acoustic survey techniques for large jellyfish medusae, a group of organisms important in many ecosystems (Purcell et al. 2007, Suchman et al. 2008), but not regularly monitored through surveys.

If no suitable survey data exist, it may be possible and even cost-effective to use acoustic data collected by vessels of opportunity (ships other than dedicated acoustic research vessels; ICES 2007b), data collected in cooperative projects with fishing vessels, or other opportunistic data as a means of increasing the number of species for which abundance and distribution data exist. O'Driscoll et al. (2009) have monitored mesopelagic micronekton off the coast of New Zealand since 2001 using opportunistic acoustic data from bottom trawl surveys. There is considerable uncertainty in interpretation of this backscatter as an index of abundance for this group of organisms due to the mixed composition of the assemblage, but the investigators have pursued midwater trawling and target-strength modelling in an attempt to refine and better understand their index. Honkalehto et al. (2011) used a relative index of acoustic backscatter collected by chartered fishing vessels conducting a bottom trawl survey to increase the frequency of abundance estimates for pelagic walleye pollock in the eastern Bering Sea. The fishing vessels were unable to sample detected pelagic fish aggregations and were not equipped with multifrequency echosounders to aid in classification. The aggregations were classified, however, using historical data on species distribution, echogram morphology, and, when possible, by comparing the index with the results of traditional acoustic-trawl surveys in the region. Ressler et al. (2009) argued that monitoring acoustic backscatter using commercial fishing vessels at a suite of known habitat sites instead of the whole stock range (e.g. sentinel sites), accompanied by underwater camera sampling and trawling to monitor the composition of detected fish schools, would be sufficient to provide a relative index of abundance for the widow rockfish *Sebastes entomelas*, a depleted stock for which no reliable survey existed previously. Acoustic data of opportunity may also be a source of information on other, previously unmonitored, ecosystem components. Kloser et al. (2009) used data from vessels of opportunity to measure backscatter from midwater micronekton in the Tasman Sea; the composition of this backscatter was initially established through historical data and dedicated scientific sampling. The observed patterns over several years are intriguing, but Kloser et al. (2009) also noted the large uncertainty in interpreting this index of midwater micronekton until the variability in target composition is understood. They proposed strategies for routine monitoring using acoustic and optical gear deployed on a trawl. Lehodey et al. (2010) showed a promising correlation between model-estimated mid-trophic biomass and backscatter time series from acoustic doppler current profiler moorings, although more work is needed to properly characterize the biological composition of these backscatter layers (Radenac et al. 2010).

Monitoring spatial distribution

Current stock assessment models are usually not spatially explicit, but it is likely that future stock assessments and EBM will more fully incorporate spatial considerations (Quinn 2003, Methot 2009). The same survey data used for biomass and abundance provide information on the spatial distribution of fish and zooplankton populations. Woillez et al. (2007) describe indices of spatial distribution derived from acoustic data that could be used to monitor changes in distribution over time. The relationship between stock abundance and spatial spread provides information on potential changes of catchability with stock size (Petitgas 1998, Barange et al. 2009). Honkalehto et al. (2011) demonstrated that large-scale spatial patterns in midwater pollock distribution, as well as abundance, could be described using both dedicated acoustic-trawl survey data and acoustic data of opportunity from chartered commercial fishing vessels. The spatial distribution of fish biomass (possibly by species or groups) may also be a useful indicator in the study of marine reserve effects, particularly if estimates extend to either side of reserve or zoning boundaries.

Predator–prey relationships and habitat requirements

Knowledge of predator–prey relationships is necessary for constructing ecosystem models and assessing food web integrity (Livingston et al. 2005). The high spatial resolution of biological acoustic surveys and physical and biological oceanographic data, and recent development of powerful statistical tools for multivariate and spatial data analysis, can enable in-depth analysis of predator–prey processes. A growing number of studies has elucidated the spatial relationship between fish and their zooplankton prey (e.g. Swartzman et al. 1999, Bertrand et al. 2002, Grémillet et al. 2008) and marine mammals and their prey (Benoit-Bird et al. 2003b, 2009, Hazen et al. 2009b, Certain et al. 2011). Prey distributions mapped by acoustics matched to the physical environment have been used in spatially explicit models to characterize the pelagic habitat in terms of potential growth (Brandt et al. 1992). Ressler et al. (in press) used an acoustic estimate of euphausiid biomass on the Bering Sea shelf to conclude that pollock predation may be an important control on standing stock, and suggested that changes in springtime spatial distribution of euphausiids and pollock inferred from acoustic data by De Robertis & Cokelet (in press) could mitigate the size of this predation impact.

An emerging number of habitat modelling studies has appeared in the last decade. These have combined acoustic with oceanographic data (e.g. Paramo & Roa 2003, Petitgas et al. 2006, Peltonen et al. 2007, Lebourges-Dhaussy et al. 2009, Zwolinski et al. 2010) or with satellite-based environmental data (Bellido et al. 2008, Giannoulaki et al. 2008, Tugores et al. 2010, Zwolinski et al. 2011). Habitat characteristics and fish densities have been mapped at comparable extents and resolutions in coral reef and other coastal ecosystems by integrating the output of several sonar systems on multibeam hydrographic survey vessels (Kracker et al. 2011). Signal-processing advancements have allowed simultaneous extraction of information on fish in the water and bottom habitat from acoustic backscatter (Mackinson et al. 2004, Cutter et al. 2010).

Finally, the spatial distribution of organisms detectable with acoustic methods can in turn describe habitat conditions. For example, Bertrand et al. (2010) demonstrated that the vertical distribution of epipelagic organisms marked the position of the oxycline (the beginning of the oxygen minimum zone). Acoustic methods have been used for decades to observe physical oceanographic features such as internal waves and thermoclines when the organisms are passive tracers of these features (e.g. Andreyeva & Makshtas 1977, Haury et al. 1979, Lavery et al. 2003).

Current uses of acoustic survey data in EBM

Abundance and biomass estimates from acoustic surveys can be used directly for stock assessment and management (e.g. Cotter et al. 2009), can be fed into stock assessment models (e.g. Quinn 2003, Methot 2009, Antonakakis et al. 2011) and ecosystem models such as Ecopath (Shannon et al. 2003, Coll et al. 2007, Tsagarakis et al. 2010), or can aid in the interpretation of model results. Potential indices of ecosystem processes and quantities, appropriate space and time scales, and the use of these indices in EBM are summarized in Table 1. Parameterisation of population and ecosystem models can be accomplished either by estimating model parameters singly from acoustic and other data or, jointly, by a model-fitting procedure. In either case the information must be on the appropriate space–time scale. Models used for assessment (i.e. for determination of state) require time series, while simulation models require only plausible parameter values or short time series for validation. Parameterised ecosystem models are increasingly used for scenario modelling, in particular for climate change and fishery management. Examples of these are Ecopath with Ecosim (Christensen et al. 2000, Pauly et al. 2000), Atlantis (Fulton et al. 2004, 2005), and Osmose (Shin & Cury 2001).

ACOUSTICS-DERIVED INDICATORS

Concepts and definitions

Literature on the definition, use, and critique of indicators is abundant (e.g. Rochet & Trenkel 2003, Rice & Rochet 2005, Jennings 2007). Rochet & Trenkel (2009) have proposed the following definitions:

'Indicator': a variable that quantifies how well an ecosystem (fishery in the original definition) is managed in relation to specified objectives.

'Metric': a variable that summarizes a process or pattern of interest in an exploited ecosystem.

The main difference between an indicator and a metric is that the former requires the definition of reference points, i.e. absolute reference values, to interpret measured indicator values, and the latter does not. One of the important challenges in the use of new indicators for EBM is the development of reference points. For most ecosystem indicators, apart from some population indicators, no reference points with a theoretical base are currently available (Rochet & Trenkel 2003). For this reason, empirically based values have been suggested (Link et al. 2002, Rice 2009). A second important challenge is to understand how indicators might change with environmental change or the application of different management strategies. In the case of fisheries management, some form of regulation of fishing pressure has typically been the only action available to resource managers, but EBM may require consideration of coordination with management actions for other regulated pressures on the ecosystem (e.g. nutrient input to coastal marine systems; Caddy 2000). Detecting and understanding changes in the

Table 1. Overview of types of quantities and processes for which information can be extracted from active acoustic data, and their actual or potential use for ecosystem-based management (EBM). MY: multi-year monitoring time series; E: experimental process study of limited duration. The space and time scales indicated are those relevant for EBM

Quantity or process of interest	Spatial scale	Time scale	Ecosystem components	EBM usage
Stock biomass or abundance index	Stock	MY	Fish, krill	Fish stock assessment; interpretation of single-species results; ecosystem models
Abundance index	Ecosystem	MY or E	Zooplankton, jellyfish, fish, species groups	Resource (prey) assessment; ecosystem models
Relationship between stock biomass and spatial spread	Stock	MY	Fish	Monitoring catchability
Predator–prey spatial relationships	Local or ecosystem	E	Fish–zooplankton interactions, marine mammal–zooplankton interactions	Identifying and monitoring food web structure; ecosystem models
Spatial distribution–physical habitat relationship	Ecosystem	E	Fish, zooplankton, hydrography/substrate	Ecosystem models; habitat mapping; climate change scenarios; spatial management

environment is challenging in itself, but understanding the resulting impact on a complex ecosystem and on associated ecosystem indicators may be even more difficult. In the absence of reference points, time trends in metrics have provided useful insights into ecosystem dynamics (Rochet et al. 2005, Rochet et al. 2010). However, this does not dispense with the need to have interpretable metrics in the first place.

Metrics and indicators

Up to now, as has been discussed, acoustics-derived indicators have primarily been used in the context of single-species management. Very little use has been made of acoustic data for deriving other indicators, despite the recognised potential for doing this. Indicators and metrics that can be calculated with traditional technology and for which time series already exist are used as a starting point in the following discussion. Future instrument developments will enlarge this list. For each indicator, the theoretical basis, possible reference points, and the expected direct effects of fishing and environmental change are considered (Table 2).

Status of commercial and other species

Acoustics-derived biomass and abundance indices have long been used in single-stock assessments and will remain important for EBM. Species classification issues determine the achievable accuracy and precision of these indices, where reliable estimates are achieved when species are in mono-specific aggregations, as described above, and accuracy decreases as species co-occur. For use as indicators to monitor management performance, reference points can be derived as relative values with respect to some period in the past, provided the time series covers a period of satisfactory stock status (Table 2). An increase in fishing will decrease biomass of the target species, while the expected effects of changing environmental conditions are difficult to determine.

Mean body length is an established indicator, and its expected change under fishing pressure is well understood (Table 2, Shin et al. 2005). However, natural fluctuations in length unrelated to fishing pressure, such as the temporal decrease in mean length with increasing recruitment, often reduce the utility of length as an indicator; this is largely the reason why no reference point for mean length is currently used. Acoustically, length can be derived from target-

Table 2. Indicators and metrics for assessing environmental status of exploited marine ecosystems, derivable from acoustic data, and expected direction of change due to fishing and environmental changes

Category	Indicator/ metric	Description	Theoretical basis	Effect of changes in environment	Effect of changes in fishing	Reference points
Species	*B/N*	Biomass/abundance index	Yes	Unknown	Decrease	Biomass or abundance relative to historical situation
	L_{bar}	Mean length	Yes	Decrease by favourable recruitment	Decrease	Unknown
	SA	Spreading area	Yes	Depends on species	Decrease	Relative to historical situation
	$B_{\text{zooplankton}}$	Timing of zooplankton peak biomass	Yes	Spatio-temporal shifts in peak biomass	None	Relative to prey abundance timing
Diversity	Acoustic diversity	Diversity of acoustic species	Empirical	Depends on definition of acoustic species	Depends on definition of acoustic species	Relative to historical situation
	Acoustic spectrum	Slope of acoustic energy spectrum	Empirical	Depends on definition of acoustic groups	Depends on definition of acoustic groups	Relative to historical situation
	Acoustic dominance	Acoustic energy by frequency	Empirical	Unknown	Unknown	Relative to historical situation
Food web	B_k	Biomass of key group	Empirical	Depends on trophic position	Depends on trophic position	Relative to historical situation
	GIC	Predator–prey global index of co-location	No	Unknown	Decrease	Relative to historical situation

strength measurements, or from using multiple frequencies and the inverse method (though the frequencies needed to accomplish this for fish with swim bladders are lower than those typically used in fisheries surveys). Similarly, weight can be empirically derived if both target-strength:length and length:biomass relations are known. In certain cases, mean length and weight in the population can be derived using trawl information or recently developed techniques for determining fish size from acoustics information alone (e.g. Chu et al. 2003). More research and analysis is needed to generate reference points for these potential length-based indicators.

The spatial range of a species and how it is distributed within that range has the potential to be a useful indicator. The 'spreading area' is a measure of the spatial occupancy of a population (Table 2, Woillez et al. 2007). Its meaning as an indicator comes from the existence of abundance-occupancy (A-O) relationships that describe how individuals maintain distance between each other in relation to the total number of individuals, and it can be seen as a reflection of intraspecific competition for a limited resource combined with social and reproductive behaviours (Gaston et al. 2000). A-O relationships for many fish species reach an asymptote (Frisk et al. 2011). Thus, apart from situations with very high stock abundance, the spreading area can provide an indication of population size. In addition, it may identify situations where a species has increased its catchability through spatial contraction. At this time, a theoretical reference point is not available. Further studies are required to examine how spreading area varies with population size, intraspecific competition and environmental conditions, and to ultimately provide an index for the status of the stock and its vulnerability to environmental conditions. Acoustic methods serve very well in making these kinds of measurements and can be used to examine the usefulness of spreading area or other measures of spatial occupancy.

Spatial and, in particular, temporal mismatch between juvenile predator stages and their zooplankton prey can lead to recruitment failure due to starvation (Cushing's 'mismatch hypothesis'), though absolute prey abundance is also important (Durant et al. 2005). Acoustics can provide estimates of zooplankton peak abundance, which can be related to production timing, and spatial coverage, which might then be used for forecasting recruitment strength. Reference points could be based on optimal spatio-temporal predator–prey overlap.

Biodiversity changes

Species diversity indices such as the Shannon index are used in combination with species richness to summarize the distribution of individuals among species (see discussion in Rochet & Trenkel 2003 regarding their suitability as EBM indicators). In the absence of species-specific information, surrogates for species, such as coarser taxonomic groupings, other species in the same genus, or other indirect proxies of species richness, have been used. Examples of non-taxonomic proxies are the remote-sensing-derived terrestrial surrogate species estimators used for terrestrial vegetation applications (see review in Rocchini et al. 2010) and the analysis of phytoplankton pigment ratios to rapidly index phytoplankton taxonomic composition (Mackey et al. 1996, Jeffrey et al. 1999). For terrestrial fauna, the relationship between species habitat preferences and species distribution are commonly used to derive indirect habitat-based biodiversity estimators (see review in Leyequien et al. 2007). Recently, Mellin et al. (2011) reviewed the literature for evaluating the effectiveness of taxonomic- and abiotic-based surrogates for predicting marine biodiversity indicators but did not find a single study for the pelagic domain.

As described above, acoustic data contain information on species or size groups (roughly corresponding to trophic levels) which can serve as surrogates for species in the computation of index values. Further refinement is possible when data are collected for several appropriately chosen echosounder frequencies due to the distinct frequency-response curve (i.e. backscattered energy depending on frequency) of organism groups such as zooplankton, fish with swim bladders, and fish without swim bladders. Godø (2009) suggested deriving ecosystem indicators from the multi-frequency backscattering spectrum, but this has not been done so far. A possible approach for deriving 'acoustic' diversity indices may be to derive information on surrogate species from multi-frequency acoustic backscatter data and then calculate a single acoustic diversity index by combining the surrogate species information (Table 2). Reference points, or maps in the case of spatial calculations, could then be derived from historical data sets. It might also be possible to develop acoustic species richness estimators which are indicative of actual species richness, similar to what is done for terrestrial remote sensing data. Finally, an alternative to single-valued diversity indices are dominance curves (Clarke 1990), which in this context might be a curve of the proportion of total energy per frequency (band) plotted versus the rank of that frequency (Table 2).

The use of backscattering spectra similar to size spectra may be possible. The slope of the size spectrum is a widely used community indicator (see overview in Shin et al. 2005). The size spectrum is defined as ln (abundance) linearly regressed against ln (size class). Abundance and biomass versions exist. There is theoretical and empirical evidence that the slope increases under the impact of fishing. Theoretically this is explained by the fact that fishing removes larger individuals, and indirect effects can lead to increases of their smaller prey. There might be a parallel argument here if meaningful acoustic surrogate species groups can be defined (Table 2). Further studies are required to demonstrate and evaluate the usefulness of such acoustic indices of diversity and multifrequency dominance curves to describe community changes and to set reference points.

Food web functioning

Abundance indices for key species groups can be related to food web changes in ecosystem functioning (Table 2, Livingston et al. 2005). In many food webs, gross anatomical differences in organisms accompany changes in trophic level. For example, a generic food web has phytoplankton, zooplankton, forage fishes, piscivores, apex predators, and humans as individual levels. Acoustic methods are generally successful at classifying acoustic backscatter to trophic level (e.g. Goss et al. 1998, Kang et al. 2002, Korneliussen & Ona 2003, Jech & Michaels 2006, De Robertis & Cokelet in press, Ressler et al. in press). Acoustic methods are less successful at separating species, or 'intra-trophic-level' classification, and this is an area of intense research in fisheries acoustics. Expected changes in trophic dynamics under the impact of fishing depend on the trophic position of these species and the trophic level at which fishing occurs (Rochet et al. 2010). For example, 'fishing down' the food web (a gradual change in the trophic level of commercial landings from high to low; Pauly et al. 1998) should be detectable using acoustic methods. Similarly, for the expected impacts of changes in environmental conditions, future research might enable relative reference points to be derived for this indicator.

Predator–prey relationships structure food webs on different spatio-temporal scales. Using high-resolution acoustic information, Benoit-Bird & Au (2003b) showed that spinner dolphins followed the diel horizontal and vertical migration of their nekton prey; key to this behavioural study was the simultaneous observation of both predators and prey. More general predator–prey patterns are observable on a larger spatio-temporal scale. Grémillet et al. (2008) detected a spatial mismatch between zooplankton and small pelagics (sardine and anchovy) off the coast of South Africa. They interpreted this as the consequence of a regime shift which has modified the ecosystem. In the Bay of Biscay the mesoscale (dozens of km) spatial distribution of anchovy displayed significant correlation with plankton communities commonly found in river plumes and in the southern coastal areas (Petitgas et al. 2006). Thus changes in spatial overlap at different spatio-temporal scales might indicate ecosystem changes, which could be subsequent to changes in environmental conditions. However, as large-scale spatial overlap between fish predator–prey pairs can vary strongly among years (Kempf et al. 2010), conclusions regarding general food web changes might have to be based on several species. As noted previously, various indices of spatial overlap exist (see review in Woillez et al. 2007), including the global index of co-location proposed by Bez & Rivoirard (2000); utilizing data from acoustic surveys, the larger-scale spatial overlap between species (fish) or species groups (zooplankton) could be estimated. The increase of fishing pressure on one species or set of species might be expected to reduce the spatial overlap with other species since it decreases the overall spatial distribution range of that group. Effects of environmental conditions are more complex and potentially less intuitive. This is because, as environmental conditions change, they may affect the spatial distribution and abundance of multiple species but not necessarily in the same way for each species. Acoustic surveys during periods of acute environmental stress, such as hypoxia, have provided more clear insight into overlap of species or trophic levels and potential impacts to food webs. Taylor & Rand (2003), Taylor et al. (2007), and Hazen et al. (2009a) have shown that vertical distributions of fish are strongly affected by stratification and hypoxia, whereas their zooplankton prey have higher tolerance and possibly use the hypoxic zones as a refuge from predation.

CONCLUSIONS AND RECOMMENDATIONS

Acoustic sampling methods have clear advantages as well as limitations. Their usefulness in monitoring the abundance of commercially important pelagic fishes and zooplankton is well established. To support EBM, the application of these techniques to other important species and species groups should be explored, keeping in mind that resources for additional survey efforts are limited. The techniques described here are most effective for pelagic and semidemersal species. Backscatter classification, groundtruth sampling, and determination of size and taxonomic composition of dominant acoustic scatterers must be pursued with as much rigor as possible by developers and users of acoustic methods. Sampling with complementary technologies such as nets, trawls, and optics to define size, species, gender, maturity, and age composition will continue to play an important role. A clear understanding of the capabilities of acoustic measurements will determine how useful any indicators derived from these data will be. For example, acoustic data can be categorized as good, fair, or poor, as follows:

Good: calibrated acoustic backscatter, robust classification of targets, established target-strength models for organisms, and conversion of backscatter into ecologically relevant units (e.g. biomass or abundance by size and taxon). This is the case for a scientific acoustic survey.

Fair: calibrated backscatter, good description of the dominant acoustic targets and how this target composition varies over time and space. This would be the case for acoustic backscatter from a mixture of midwater micronekton measured by vessels of opportunity, accompanied by net sampling of the composition of the scattering layers.

Poor: uncalibrated backscatter, targets unknown. This would be the case for acoustic data from vessels of opportunity or buoys with no complementary sampling and no way to infer the composition of the backscatter based on prior knowledge of or comparisons with similar ecosystems. It is currently nearly useless for developing indicators for EBM.

Our recommendations for development and application of acoustic indicators for EBM may be summarized as follows:

(1) Extend acoustic indices of biomass and abundance to other species and species groups in the ecosystem. The most commonly used indicator in fisheries stock assessment and management is biomass, which is used for stock modelling and is evaluated relative to a reference point that depends on the management objective. There is no reason why these and other potential stock or trophic-level indicators cannot be carefully extended to other species and species groups.

(2) Explore the use of acoustic methods for indexing properties other than biomass and abundance. The same acoustic data used for biomass estimation can be used to describe other properties of fish populations, such as spatial distribution, occupancy, body length, and habitat conditions, all of which may become more important in EBM than they have been in single-species management. Diversity and food web considerations are clearly gaining in importance, and it therefore seems timely to develop acoustics-derived indicators for food webs and assemblages. We have provided ideas for future research on this topic.

(3) Develop reference points for indicators so that they can be properly interpreted for EBM. Two major challenges remain: (1) to clearly define the goals of EBM, and (2) to establish acceptable reference points for potential indicators (other than stock biomass). With regard to the second challenge, especially, we propose that empirical reference points should be defined for new indicators, and the behaviour of those indicators under different hypothetical pressures on the ecosystem (fishing and climate change) should be tested using the best information available. For example, an indicator of fish-prey (e.g. zooplankton) abundance derived from acoustic data should be evaluated against a predefined abundance level that corresponds either to a certain point in the available time series that presents specific characteristics, or to a critical level of biomass. Expected changes in this index due to the variation in the abundance of predators, to fishing, and to environmental changes should also be taken into consideration. As new information and additional observations are gathered, these reference points and scenarios should be re-evaluated and revised in order to ensure that the indicator is being interpreted correctly in its EBM context. Comparative studies of similar indicators, reference points, and models used for EBM in different ecosystems will be useful.

The synthesis of technique, measurement, and application that we propose here is something that scientists who develop and use acoustics technology to study marine organisms, as well as analysts and modellers who use acoustic data for assessment and management, must work together to achieve.

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Appendix 1. Construction of Fig. 1: Spatio-temporal scope of a single observation by various sampling devices and sensors

All values in Fig. 1 are the minimum and maximum volumes and time required for a single observation with the sampling devices and sensors are listed below. We do not account for repeated measurements over space and time. Polygons in Fig. 1 were drawn such that the upper right corner represents maximum spatial and temporal values and the lower left corner the minimum spatial and temporal values.

Active acoustics

Maximum volume and time was derived from the Ocean Acoustic Waveguide Remote Sensing (OAWRS) system (Makris et al. 2009). Horizontal extent is approximately 100 km in diameter. Vertical extent is dependent on water depth. For this estimate, we assumed 100 m. Two-way travel time for this observation is ~70 s. We did not include basin-scale or ocean-scale measurements such as those conducted to monitor climate change (Baggeroer et al. 1998). Minimum volume was derived from the Dual-frequency IDentification SONar (DIDSON; Sound Metrics). The DIDSON uses acoustic lens technology to acquire high-resolution acoustic images. The DIDSON system can transmit on the order of 10 pings s^{-1} (0.1 Hz). Volume is based on a 14 × 0.3° beam with 1.5 cm range resolution at 1 m range.

Visual optics

Visual optics includes cameras and video systems. Maximum sampling volume is based on a wide-angle lens (96 × 78°; Deep Sea Power and Light Super SeaCam 5000) and detection of objects out to 30 m. Sampling volume is modelled as pyramidal (V = Bh/3, where B is the area of the base and h is the distance). Minimum sampling volume is assumed to be 5 mm^3. The maximum frame rate for acquiring data is ~30 frames s^{-1}.

Laser technologies

Laser technologies consist predominantly of the laser line scanner (LLS; Yoklavich et al. 2003) and Light Detection and Ranging equipment (LIDAR; Churnside et al. 2001). The LLS scans a laser beam in the across-track direction, acquiring a 2-dimensional image of targets in the water column and on the sea floor. The LLS has a 70° swath; its sampling volume depends on the height of the system above the seafloor, but it is towed as close to the bottom as ~3 m. In constructing Fig. 1 we used a 4 m swath and 7 mm along-track resolving scale. LIDAR essentially generates a column of light from an airborne vehicle (usually an airplane) that illuminates targets in the water. LIDAR can penetrate to about 50 m in clear water; a 10 ns pulse generates a 'column' 5 m in diameter.

Trawl

Trawls for fishing come in a wide variety of types, and are fished for a wide variety of purposes and in a wide variety of habitats. It is therefore difficult to set a minimum and maximum. However, there are commonalities among trawls for scientific uses. As examples, we selected a bottom trawl from the northeast United States for the minimum, and a large pelagic trawl used in Iceland (Reynisson & Sigurdsson 1996) for the maximum. The 'Yankee 36' net has been used for approximately 40 yr in the northeast United States for fisheries-independent sampling (Azarovitz 1981). Tow duration was 30 min at about 3.8 knots (1.9 m s^{-1}). The mouth opening was ~2 m vertical × 10.5 m horizontal. A Gloria-type Hampidjan pelagic trawl was used to sample deep-water oceanic redfish *Sebastes* spp. (Reynisson & Sigurdsson 1996). A nominal opening when towed at 3 knots (1.5 m s^{-1}) is ~70 m vertical by 95 m horizontal. Tow duration was set at 60 min.

Zooplankton sampling

Several types of sampling gear are used to collect zooplankton, but they fall into 3 general categories: (1) conventional gear, (2) multiple net, and (3) electronic optical (Sameoto et al. 2000). Sameoto et al. (2000) provide a summary of the resolving scale and operating ranges of these types of gear.

For the zooplankton net, the minimum was derived by taking the resolving scale of a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) at 1 m^2 and towing at 1 m s^{-1} for 30 min. The maximum was derived by taking the resolving scale of the larger MOCNESS (3 m × 3 m) and towing at 1 m s^{-1} for 60 min.

For the optical sensors, the minimum was derived by taking the spatial resolving scale of a video plankton recorder (VPR, 0.01 m vertical × 5 m horizontal), acquiring data at 2 frames s^{-1} (0.5 Hz), and towing at 5 knots

Appendix 1 (continued)

(2.5 m s^{-1}). The maximum was derived by taking the maximum spatial resolving scale of an optical plankton counter (1 m × 1 m), acquiring data at 1 frame s^{-1}, and towing at 5 knots (2.5 m s^{-1}).

Pumps

Pumps are used to sample zooplankton and ichthyoplankton, including fish larvae. The minimum was derived from the resolving scale of a pump (0.1 m × 0.1 m), and sampling at 1 time s^{-1} on a vessel moving at 10 knots (5 m s^{-1}). The maximum was given in Sameoto et al. (2000) as 2.8 m^3 min^{-1}.

Water bottles

As the name suggests, water bottles are used to capture water samples for chemical and biological (e.g. zooplankton and phytoplankton) analysis. The minimum is 1×10^{-3} m^3 and the maximum is 1 m^3. We assume 1 s per sample.

Physical environment sensors

Sensors to measure the physical environment (e.g. temperature, conductivity, pressure, light attenuation, turbulence, etc.) are generally point measurements. We estimate the sampling volume of these to be approximately 1 cm^3.

Satellite

Satellites provide wide-area coverage at fairly high resolution in a single snapshot. Satellite measurements do not penetrate below the surface and we set this limit to 1 m depth. Barbini et al. (2006) provide range and resolution of 3 satellite systems for ocean measurements: SeaWiFS, MODIS, and MERIS. MODIS has the finest resolution, at 0.25 km. SeaWiFS has the maximum footprint, covering a 2.8 km swath. We do not include satellites that can image an entire hemisphere.

Table A1. Minimum and maximum sampling volumes and time required for a single observation by different sampling technologies

Sensor	Volume (m^3)		Time (s)	
	Min.	Max.	Min.	Max.
Active acoustics	1.9×10^{-5}	7.9×10^{11}	1.0×10^{-1}	6.7×10^{1}
Visual optics	1.3×10^{-7}	3.2×10^{4}	1.0×10^{-2}	3.0×10^{-2}
Trawl	7.2×10^{4}	3.6×10^{7}	1.8×10^{3}	3.6×10^{3}
Zooplankton nets	1.8×10^{3}	3.2×10^{4}	1.8×10^{3}	3.6×10^{3}
Zooplankton optics	6.3×10^{-2}	2.5×10^{0}	5.0×10^{-1}	1.0×10^{0}
Pumps	5.0×10^{-2}	2.8×10^{0}	1.0×10^{0}	6.0×10^{1}
Water bottles	1.0×10^{-3}	1.0×10^{0}	1.0×10^{0}	1.0×10^{0}
Laser	8.8×10^{-2}	9.8×10^{2}	1.0×10^{-2}	3.3×10^{-2}
Physical sensors	1.0×10^{-6}	1.0×10^{-6}	1.0×10^{-1}	1.0×10^{0}
Satellite	6.3×10^{4}	7.8×10^{6}	4.4×10^{-2}	9.0×10^{-1}

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