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Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Quo Vadimus

Marine ecosystem acoustics (MEA): quantifying processes in the sea at the spatio-temporal scales on which they occur

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Sustainable management of fisheries resources requires quantitative knowledge and understanding of species distribution, abundance, and productivity-determining processes. Conventional sampling by physical capture is inconsistent with the spatial and temporal scales on which many of these processes occur. In contrast, acoustic observations can be obtained on spatial scales from centimetres to ocean basins, and temporal scales from seconds to seasons. The concept of marine ecosystem acoustics (MEA) is founded on the basic capability of acoustics to detect, classify, and quantify organisms and biological and physical heterogeneities in the water column. Acoustics observations integrate operational technologies, platforms, and models and can generate information by taxon at the relevant scales. The gaps between single-species assessment and ecosystem-based management, as well as between fisheries oceanography and ecology, are thereby bridged. The MEA concept combines state-of-the-art acoustic technology with advanced operational capabilities and tailored modelling integrated into a flexible tool for ecosystem research and monitoring. Case studies are presented to illustrate application of the MEA concept in quantification of biophysical coupling, patchiness of organisms, predator–prey interactions, and fish stock recruitment processes. Widespread implementation of MEA will have a large impact on marine monitoring and assessment practices and it is to be hoped that they also promote and facilitate interaction among disciplines within the marine sciences.

Keywords: acoustics, assessment, ecology, ecosystem-based fisheries management, ecosystem models, physical–biological coupling, recruitment processes, spatio-temporal scaling.

Introduction

After observing the connections between sea surface temperatures along the coast of Western Norway, and subsequent biological changes in the Barents Sea, Helland-Hansen and Nansen stated "*We think that these discoveries give us the right to hope that by continued investigations it will be possible to predict the character of climate, fisheries, and harvests, months or even years in advance*" (Helland-Hansen and Nansen, 1909). This represents an early conceptualization of what we now refer to as fisheries oceanography.

Since Johan Hjort developed his recruitment hypothesis (Hjort, 1914), fisheries scientists have struggled to understand the drivers of variability in the population dynamics of commercially important fish and shellfish populations. Fisheries oceanography has sought to understand the influence of the physical environment on these processes. Fisheries scientists, utilizing data from commercial fishing, developed survey tools and population models to assess the status of harvested stocks and to set future (sustainable) catch levels. The inability of marine ecologists to collect data on the spatial and temporal scales that are possible in terrestrial and intertidal environments has limited the development of a more process-oriented fisheries oceanography that incorporates mainstream ecological theory (see Stergiou and Browman, 2005).

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Ecosystem-based fisheries management (EBM) has been widely adopted by stewardship agencies in an attempt to more effectively manage the direct and collateral impacts that fishing and other human activities impose on the oceans (Bianchi and Skjoldal, 2008; McLeod and Leslie, 2009; Link, 2010; Kruse *et al*., 2012). EBM also represents an (as yet unrealized) opportunity to incorporate more ecological theory into fisheries oceanography.

Fisheries oceanography has typically been divided into the traditional trophic control paradigms of bottom-up and top-down forcing. However, it has increasingly been acknowledged that trophic forcing is dynamic and may shift considerably in time and space (e.g. Cury *et al*., 2000; Frank *et al*., 2007). A natural extension of Hjort's fisheries oceanography paradigm is, therefore, the move towards an *ecosystem oceanography* (*sensu* Cury *et al*., 2008): the study of interactions among ecosystem components and drivers at the level of the population, the foodweb, and the ecosystem. Ecosystem oceanography aims to understand each organizational level by confronting model results with the empirical reality expressed in the data. We must, therefore, build models that incorporate the key ecological processes and carry out subsea observations on spatial and temporal scales that can inform these models. Unfortunately, this has proven impossible to achieve with classical sampling methods and equipment.

Operationalizing *ecosystem oceanography* requires models linked to synoptic observations and sampling of the ocean's biological and physical characteristics (see, e.g. Handegard *et al*., 2012b; Demer *et al*., 2009). Hans Lassen, a former Head of the ICES Advisory Programme, states that the data demanded by the ecosystem approach cannot possibly be met because of the costs involved with the use of present technology. He foresees new technologies taking over: "*Or would a technological breakthrough in LIDAR or hydroacoustics (e.g. multifrequency techniques) be the way forward?…* ***I believe that these and many other technological changes will be seen in the not too distant future*** "(ICES Inside Out, 2010, No. 4, p. 2). In this context, Koslow (2009), Trenkel *et al*. (2011), and Handegard *et al*. (2012b) explore the possibility of simultaneously collecting physical and acoustic information about the identity and distribution of organisms to integrate the two and assess biophysical coupling at previously inaccessible spatio-temporal scales (e.g. Godø *et al*., 2012; Kaartvedt *et al*., 2012).

The reintroduction of ecology into fisheries oceanography through the EBM makes this a timely effort. On a general level, ecology can be defined as, "the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance" (Krebs, 1972; Begon *et al*., 1986). This definition focuses on the organism and, once the organism is detected and classified, its abundance can be determined by investigating its spatial and temporal distribution. In the sea, acquiring such knowledge highlights three crucial observational challenges: *detection, identification, and enumeration*. Understanding variation in abundance and distribution requires interpretation of inter- and intra- specific interactions, as well as biophysical coupling and physical forcing on the spatial and temporal scales at which these interactions occur. This leads to the fourth challenge, *coverage*, i.e. our ability to observe ecosystem components, and their interactions. To date, this has been impossible for operational reasons. Therefore, efficient sampling strategies combined with mathematical and statistical modelling have gradually become indispensible tools with the ability to combine observations of physics, individuals, and interactions at appropriate scales of time and space.

Historically, fisheries oceanography began as a natural science focused on making basic exploratory observations. Only recently has it focused on assessing patterns and processes. However, this modern focus has highlighted the limits imposed by traditional capture-based sampling methods. Henry Stommel first described the inefficiency of oceanographic surveys that do not take into account that patterns and dynamics must be observed at appropriate temporal and spatial scales (Stommel, 1963). His thinking has been incorporated into marine ecology and the original three-dimensional Stommel diagram, which visualizes variability in physical properties, has also been used to visualize the various scales upon which abundance varies in plankton communities (Haury *et al*., 1978 and see Figure 1). The challenges associated with appropriate spatio-temporal sampling in relation to observing key features of the ecosystem have been thoroughly described (see overview in Vance and Doel, 2010). As stated by Herman and Platt, "the sampling grid has to be at least as fine-scaled as the scale of the process of interest" (Herman and Platt, 1980, p. 204). Several specific examples that illustrate this follow.

It is commonly assumed that the growth rate and survival of fish larvae depends primarily upon food availability (which is not the same as prey abundance) and predation (see, e.g. Pepin, 2004; Houde, 2009; Hare, 2014). However, this has not yet been properly resolved or validated in the field as traditional sampling gear aggregate predators and prey over volumes and times much larger than those at which these processes occur (see, e.g. Pepin, 2004; Houde, 2008). Global as well as local circulation models, which are used for studying the impact of climate change, operate on hundreds of meters to hundreds of kilometre grid resolutions. These are orders of magnitude larger than those required for ecosystem process studies. Currently, predictions of large-scale climate models, as well as ecosystem assessment models, depend substantially on unvalidated assumptions about the scaling of patterns and processes. Importantly, as stated by Levin (1992), "the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology" (p. 1943). The marine ecosystem acoustics (MEA) concept establishes observation systems that fill this data requirement gap.

MEA will achieve this goal by (i) building an observation system with acoustics as the main tool; (ii) combine that with enhanced deployment and operational capabilities; and (iii) tailor the output for use in modelling in an integrated platform that generates information resolved to taxon and collected at previously inaccessible spatio-temporal scales.

Thus, the MEA concept bridges the gap between single stock assessment and management, and methods for assessment, prediction, and management practice of harvested ecosystems in accordance with EBM. The data stream produced by MEA will enable representation of the population characteristics (identity, size, number, biomass, behaviour) of the main components of marine ecosystems. Following Levin (1992), a main challenge for the modelling component is "retaining essential information without getting bogged down in unnecessary detail" (p. 1944), i.e. moving from fine scales to broad scales, and *vice versa*, without losing essential information. Under EBM, the focus must be to maintain the quantification details needed to understand and assess exploited stocks without being confounded by the details of the marginal processes behind it. The MEA sensors produce a complex data stream that limit the viability of the MEA concept unless simulation models are developed that exploit the potential

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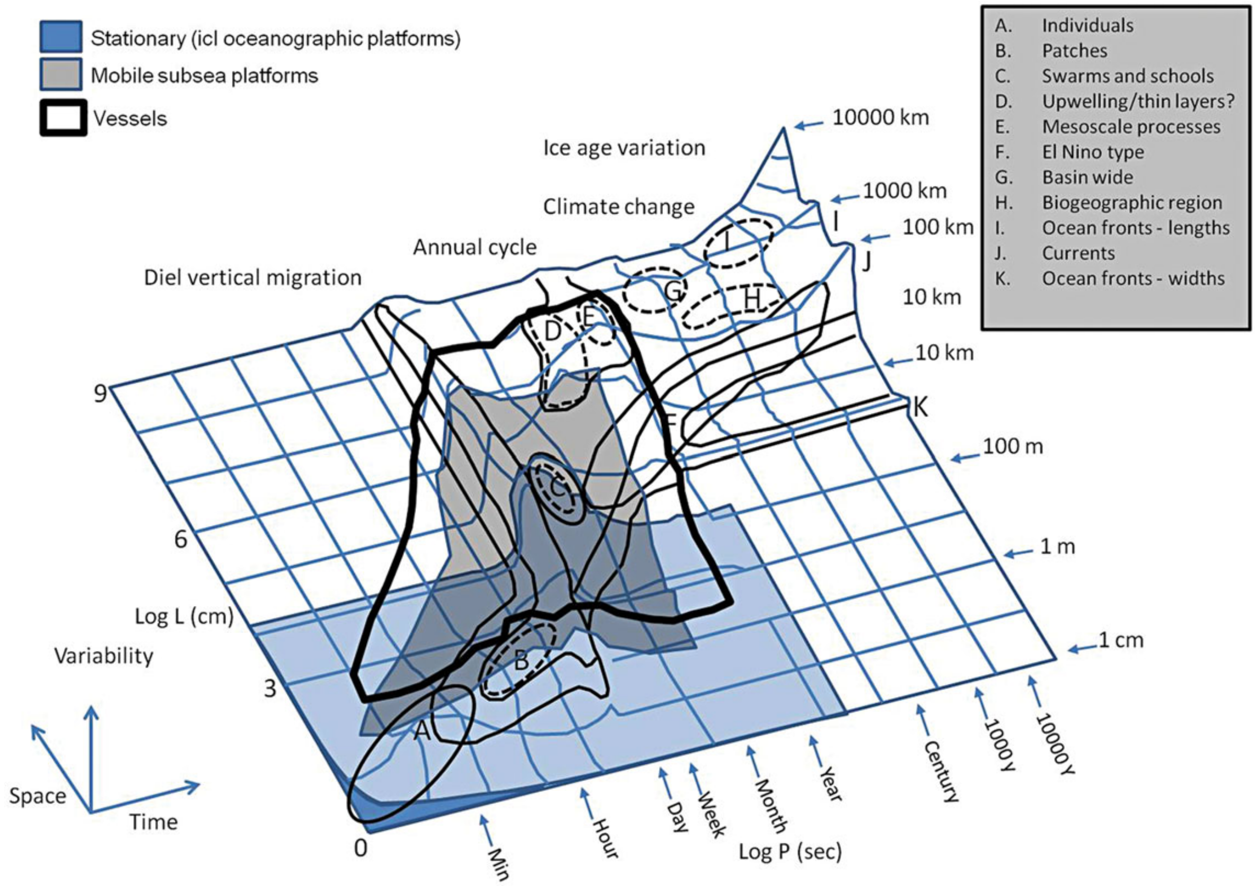

Figure 1. Modification of the Stommel diagram adopted from Haury *et al.* (1978). The surface illustrates time–space variation in plankton and higher trophic level biomass. Phenomena of importance to ecosystem understanding and assessment, and their extension in time and space are indicated on the top of the variability surface and are identified by capital letters. The diagram is extended to illustrate the use of various platforms under the MEA concept; their coverage potential, overlap and uniqueness in time and space. Stationary here includes stationary and oceanographic platforms. Vessels include vessel and vessel operated tethered platforms.

of the acoustics and operational technologies, and *vice versa* (Handegard *et al.*, 2012b). Furthermore, the limited time–space coverage of ocean observations associated with the deployment of research vessels and/or moored instrument packages severely constrains our parameterization and prediction capabilities. Improved and increased application of unstructured acoustic data from ships of opportunity will, therefore, also be important. This endeavour will benefit from the ongoing development of tools and approaches to analysing very large datasets ("big data"; e.g. Schadt *et al.*, 2010; Halevi and Moed, 2012; Levy *et al.*, 2014; Soranno and Schimel, 2014).

In short, advances in acoustics have, in principle, made it possible to collect information on marine organisms of all sizes (fish eggs and larvae, zooplankton, and larger) by identifying and sizing them, and by observing them at previously inaccessible spatial and temporal scales. In achieving this, MEA would respond to basic challenges in ecology as well as in fisheries science and this paper aims to describe how and why this might be possible in the long term. We next describe how the opportunities offered by this sensor technology can be operationalized.

Operationalizing the MEA concept

MEA requires a balanced and efficient use of acoustic sensor technology combined with appropriate operational skills and an active and coordinated feedback loop with the development of process models. This is described in detail in the sections that follow.

Sound in the ocean is analogous to light in the atmosphere: just as the atmosphere is transparent to light, so is the ocean transparent to sound. In the ocean, sound propagates readily, while light is rapidly absorbed and otherwise diffracted by a multitude of small-scale heterogeneities of which sound, with a much longer wavelength, is relatively unaffected. This recognition has permeated research in underwater sound over the past century. It was early discovered that fish could be detected by echolocation, and the presentation of the first echograms of spawning skrei in Lofoten, by Oscar Sund in 1935 (Sund, 1935), was among the findings that stimulated the development of fisheries acoustics. By 1960, techniques for acoustic quantification of fish had been developed (Dragesund and Olsen, 1965) and these continue to be developed and refined so that it is now possible to determine the distribution and abundance of fish stocks using acoustics (e.g. Simmonds and MacLennan, 2005).

Recent advances in acoustics present new possibilities in assessment and management. Remote classification of target categories using multiple frequency scientific echosounders is a promising technique that is currently used but is still under development (Kloser *et al.*, 2002; Korneliussen and Ona, 2002). The expanded observation volume of new scientific multibeam echosounders and

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sonars (Trenkel *et al.*, 2008; Ona *et al.*, 2009), operating at ultrasonic frequencies, makes it possible to quantify the abundance and school structure of organisms near the surface (Misund *et al.*, 2005; Ona *et al.*, 2006). Although expanding the high-frequency range using broadband technology is still in its infancy, there is the potential to enhance spatio-temporal resolution down to 1 cm and 1 s as well as increase the accuracy of species or target category separation.

Expanding bandwidth towards lower frequencies facilitates studies of organismal abundance and collective behaviour over distances of up to 100 km (Makris *et al.*, 2009). All of these improvements will generate massive amounts of new information in marine science. However, our ability to exploit these technical advances in an operational ecosystem oceanography depends on: (i) efficient post-processing and seamless flow of acoustics data from observation platforms to users, (ii) models tailored to the available data, (iii) systems for integrating acoustic data from different platforms, and (iv) researchers trained to address the vast quantity and diversity of these data.

Alternative platforms are being developed that enable *in situ* observation of plankton and fish at the resolution upon which processes occur (Godø *et al.*, 2005; Onsrud *et al.*, 2005). Flexibility in platform and sensor combinations moves observation systems for fisheries oceanography towards those used for physical oceanography (Handegard *et al.*, 2012b). Such observations are vital to the quantification and modelling of stock distribution and abundance, migration, and the critical life history events that determine recruitment.

The most advanced biophysically coupled fisheries oceanographic models have been developed using observations made at spatio-temporal scales that do not match those on which key productivity-determining processes occur (e.g. predation; starvation; fine-scale distribution; recruitment; Pepin, 2004; Houde, 2008). To make further progress, observation systems that resolve these processes, and routinely integrate the data collected into process and ecosystem models, are required.

We herein present MEA as an approach to achieve this objective. The MEA concept utilizes emerging opportunities in *acoustic sensor technologies* combined with advanced *operational capabilities*, tied together with tailored *modelling* designed to address basic scientific questions in marine ecology and fisheries oceanography as well as fill the knowledge and data gaps required to operationalize EBM.

Acoustics sensor technology

Spatial resolution is obtained by moving the acoustic sensor, by using multiple spatially distributed sensors, or by tracking the organisms within the acoustic beam. Under the MEA concept, resolution will be expanded to permit identification of individuals at centimetre scales all the way to processes taking place on scales of tens of kilometres. The tools and techniques that are currently available to accomplish this are briefly described below.

Higher frequencies and associated shorter pulses and wavelengths resolve the sampling volume better than lower frequencies. Sonars in the low-frequency band resolve schools of fish at scales of up to 100 km (Makris *et al.*, 2006, 2009), while echosounders with frequencies ~100 s of kHz yield centimetre-scale resolutions. Broadband technology that uses pulse compression techniques can further enhance resolution to millimetre scales in the high-frequency band (see, e.g. Stanton, 2009). Split-beam echosounders, discrete frequencies as well as broadband, allow target tracking of individuals (Brede *et al.*, 1990; Handegard *et al.*, 2005). High-frequency, broadband systems with split-beams also enhance resolution to the millimetre scale through matched filtering methods, so that echoes from smaller targets, such as copepods, can be extracted and tracked *in situ* at short range. Enhanced resolution enables target tracking algorithms for single individuals to perform better when particle density is high, thereby permitting behaviour studies of individuals inside schools or patches (e.g. Handegard, 2007). Ping rate operated during cruise transects determines the resolution of sampling. For example, patches of zooplankton and juvenile fish may be small (Benoit-Bird *et al.*, 2013) and a high ping repetition rate might be needed to properly resolve their distribution. Importantly, under such circumstances, plankton nets sample volumes far larger than the patches and, therefore, will not provide an accurate picture of the spatial distribution of the organisms that they capture.

Temporal resolution. High temporal resolution can be obtained by increasing ping rates during cruise transects, yielding enough pings on individuals or groups to resolve their distribution and behaviour patterns. In deep water, ping rate is limited by the travelling time of sound back and forth to the bottom or to the maximum survey depth. Ping rate may also be increased by using multi-pulse techniques that code the transmitted signal to allow several pulses to be used simultaneously. Long-term data for studying and quantifying important biological processes such as diel or seasonal cycles (Figure 2) or climate impacts on marine life require stationary systems (Genin *et al.*, 2005; Godø *et al.*, 2005; Kaartvedt *et al.*, 2009).

Identification by species and size is a key challenge for MEA**.** Identification of the targets in acoustic records has, to date, been dependent on simultaneous sampling using capture gear. Such sampling is now being improved through visual techniques that continuously image individuals during trawling, thus resolving observation over the depth range sampled (Deep Vision, Rosen and Holst, 2013). This might become an important technique for development of identification methods for independent acoustic remote sensing. Such methods can improve realism in assessment through continuous and accurate acoustic species identification. Some of the acoustic technologies available to accomplish this are described below.

Fisheries acoustics has moved from single frequency to multiple frequency analysis (Trenkel *et al.*, 2011) to exploit the emerging methods to identify single species or taxonomic categories of species (Horne, 2000; Kloser *et al.*, 2002; Korneliussen and Ona, 2002; Lavery *et al.*, 2007; Korneliussen *et al.*, 2008) and the size of individuals (Johnsen *et al.*, 2009) without the need for capture sampling. The recent development of quantitative scientific broadband systems will enable comparison of acoustic backscattering over a more continuous frequency spectrum. This will greatly improve the possibility to categorize targets to the level of species or taxonomic groups (Stanton, 2009; Lavery *et al.*, 2010; Stanton *et al.*, 2010). The richer information from individual targets that are present in the broadband echo can also be used to extract target size. Extending bandwidth towards lower frequencies (500 Hz to 20 kHz) enables studies of swimbladder resonance phenomena in fish as a tool for size and species identification (Holliday, 1972; Love, 1978; Løvik and Hovem, 1979; Jagannathan *et al.*, 2009; Godø *et al.*, 2010). Split-beam technology is useful, not only for spatial resolution (see p. 10), but also to allow identification of individual size through analysis of acoustic target strength using target strength–length relationships obtained empirically. In some cases, behavioural characteristics of the target can also aid in species identification.

Abundance/biomass. Acoustic backscattering can be converted into biomass and making such measurements for relatively long periods can provide insights into biophysically coupled processes. However, some basic technical issues must be solved before

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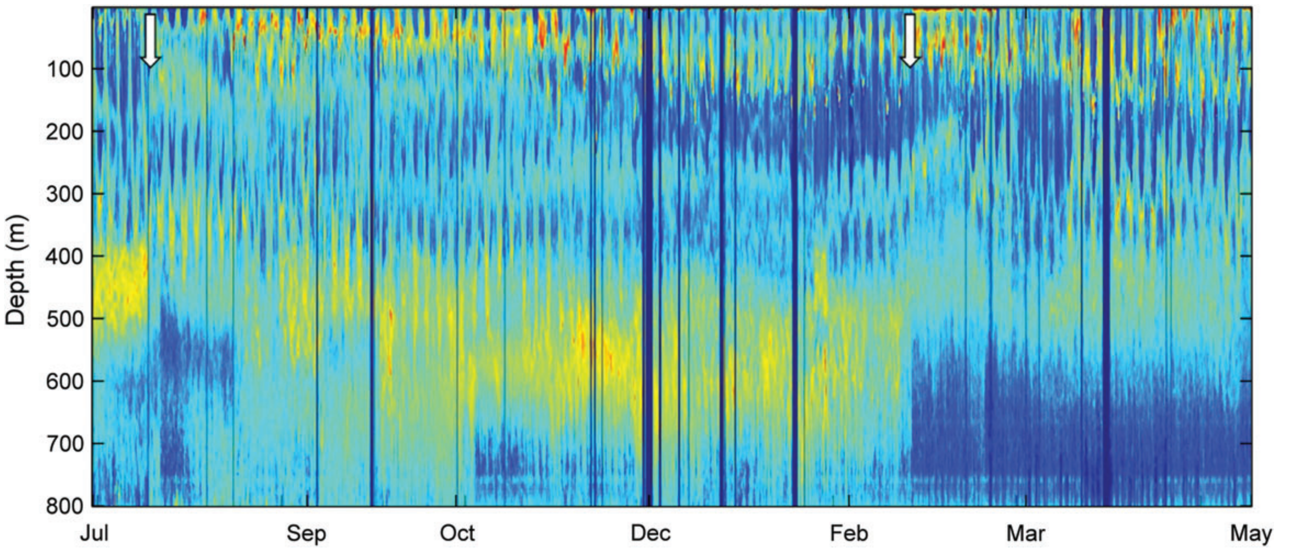

Figure 2. Seasonal variation in acoustic backscatter (smoothed over time) at a location on the Mid-Atlantic Ridge. Data are collected according to a mission plan leaving gaps of days between observations. Abrupt changes taking place in August and February–March (arrows) are probably caused by physical–biological influences on the acoustic backscatter associated with the movement of the Sub Polar Front (Opdal *et al.*, 2008) over the position of the acoustic unit.

meaningful biomass and process information can be obtained from acoustic backscattering.

As for any sensor technology, very careful calibration of instrumentation is required to obtain quantitative information from acoustics (Foote *et al.*, 1987, 2005). Careful and frequent calibration allows for measurements to be compared over time and among vessels or other acoustic platforms. Backscattering of marine organisms is affected by the orientation of the target, more so at higher frequencies than at lower. In other words, the behavioural characteristics of the recorded individuals affect the density measured. Normally, an average orientation is assumed. MEA aims to improve the measurement of backscattering by developing behaviour models that relate variation in fish behaviour to variation in backscatter (Holmin *et al.*, 2012). This will reduce the variability of the density measurements. The tools for doing this are improving continuously, as exemplified by the recent calibrated multibeam sonars and enhanced resolution in target tracking by split-beam broadband acoustics (Stanton, 2009; Ona *et al.*, 2011). A basic requirement for acoustic density estimation is knowledge of acoustic target strength. The enhanced resolution and modelling possibilities described above create a strong framework for *in situ* observation of target strength for taxon of smaller sizes and at higher densities.

Processes. Under MEA, a combination of the technology, tools, and approaches described above will permit systematic observation and quantification of processes such as species and trophic interactions and biophysical coupling. Although advances in acoustics have taken place with varying motivation and goals, they clearly demonstrate the potential of the technology with respect to the main issues—detection, identification, and enumeration. There are, however, challenges and difficulties that must be surmounted before these new technologies can be applied to full effect. These are taken up next.

Operational skills

Most of the acoustic technology solutions described above are typically operated from vessels. This creates operational limitations such as the extent of spatial and temporal coverage possible during surveys. Also, the use of higher frequencies limits the range of acoustic sampling since higher frequencies sample only a limited depth when vessel-based. Thus, to achieve the MEA objective of sampling on spatial and temporal scales relevant to the processes being observed, a suite of vessel- and non vessel-based platforms is required.

Below we describe how advanced operational solutions can compensate for inherent limitations in the acoustic technology and, thereby, permit us to sample at high spatial and temporal resolutions.

The vessel has been, and will probably remain, the single most important platform. In particular, the capabilities of research vessels to effectively operate alternative platforms, as described above, will be crucial. Further, fishing fleets are becoming advanced acoustic platforms (Karp, 2007). New vessels are occasionally designed with input from scientists so that they are essentially acoustic research vessels with respect to technology, noise characteristics, and laboratory, office, and cabin space. Involvement of the fishing industry in assessment and management of marine resources is both a political objective and an operational necessity to meet the requirements of EBM.

Vessel operated tethered platforms such as towed vehicles and profiling devices operate over large bandwidths and cover the whole depth range with identical volumes and bandwidths. They are powerful tools for uniform acoustic characterization of the water column. They can be towed or deployed vertically from a stationary vessel. Additional sensors, e.g. temperature/salinity and imaging cameras, can aid identification of organisms and the associated physical environment. Tethered systems operated from survey vessels overcome the range limitation of high frequencies and provide acoustic characterization of the full water column. These systems mirror or even surpass the performance of stationary and movable subsea platforms (described below), but are limited by the requirement for a vessel (Ona and Pedersen, 2012).

Stationary platforms allow for observations without the spatial confounding resulting from vessel movements. Sensors can be

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located anywhere in the water column depending on the process of interest. Such platforms are equipped in a manner similar to profiling platforms but normally with fewer frequencies. They support the collection of information on temporal variability on scales of seconds to years. Thus, they might become important tools for assessing the impact of climate change. Multiple examples of stationary systems that produce high temporal resolution data at depth exist, both anchored buoys (Doksæter *et al*., 2009) and cabled bottom-mounted systems (Godø *et al*., 2005; Kaartvedt *et al*., 2009; Urmy *et al*., 2012; http://love.statoil.com). Typical applications for such systems are quantification of processes such as diel rhythms in vertical migration, predator–prey interactions, swimming speed (Klevjer and Kaartvedt, 2011), tail beats and phase (Handegard *et al*., 2009), and changes in acoustic properties of target species over time.

Autonomous moving subsea platforms are systems that collect acoustic data with advanced technology and transfer them in real time or near real time to a nearby vessel or data centre. They can be surface or submerged drifters equipped in a manner similar to stationary systems. They can also be autonomous underwater vehicles (AUV) with their own propulsion and navigation systems. Due to high power consumption and limited battery capacity, these platforms are most often used in experimental work of limited duration. Typically, they are used in studies of fish behaviour (e.g. vessel-induced behaviour), or studies of biophysical coupling or other studies requiring high spatial resolution. The transducers may point in various directions and collect data over various depth ranges according to the objectives of the study, and may include organisms that are inaccessible to most other sampling techniques (e.g. under ice—see Brierley *et al*., 2002). Typically, such platforms can support observations of density distribution patterns and the behavioural characteristics of surface organisms that are distributed, for example, in a vessel's "blind zone" (e.g. herring and mackerel feeding at surface above the vessel transducer depth).

Oceanographic platforms like moorings and floats may host acoustic sensors. They must be designed without compromising the quality of biomass measurements, although they have size restrictions allowing only use of higher frequencies with associated range limits, and power limitations restricting sampling rates and operational lifespan (although advances are on the way here too). The capital and operating costs will be much lower than traditional systems and, therefore, they can be deployed in large numbers allowing high spatio-temporal coverage. The development of this category of acoustic platform is currently lagging behind some of the others and, as a result, these platforms are not yet commonly used for biological/ecological studies. Nevertheless, such platforms might become an important tool to enable relevant monitoring of oceanic ecosystems (Handegard *et al*., 2012b). They are suitable for systematic vessel-based monitoring and/or specific process studies. Oceanographic acoustic platforms support two important roles in future monitoring. First, reduced purchase and operational costs makes spatial coverage realistic through a launch programme similar to the Argo buoy floats (http://www.argo.ucsd.edu/). Second, they enable simultaneous collection of physical and biological information over long periods of time, which is required to provide observational input to complex ecosystem process models.

The potential of acoustic sensors cannot be realized without exploiting the opportunities offered by advanced operational skills. The resulting data stream elevates the complexity of the data to a level that makes interpretation and utilization difficult. To compensate for this, a modelling approach is mandatory. This is elaborated upon in the next section.

Modelling

Modelling not only secures the integrity and consistency of the "big data" collected using acoustic technology, but also represents the common frame of reference for the multidisciplinary work taking place under the MEA concept: modellers will challenge the technology components with their specific needs for data with which to parameterize the simulations and new opportunities in acoustic technology will drive the development of modelling. MEA's ambition is to ensure that field data are collected and treated so as to satisfy the requirements of advanced ecosystem models.

The ecosystem oceanography component of EBM requires models linked to observations on the ocean's biological and physical characteristics (McClatchie *et al*., 2012), and on a wide range of spatial and temporal scales. MEA incorporates this through active model development that exploits the opportunities offered by acoustics and, conversely, by employing models to direct technology development. Two basic challenges associated with the MEA concept can be solved through modelling. First, it is a basic challenge to set up a flexible monitoring programme that spans the wide range of spatial and temporal scales that it is now possible to sample with acoustic technology. Second, EBM requires quantitative understanding of ecosystem dynamics and processes as a foundation for integrated assessments (Link and Browman, 2014). A simple example is how predator–prey interactions between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) are assessed from combined acoustic-trawl information in the Barents Sea. The collected stomach data of cod and the information on distribution overlap of the two species is used as a basis for advice on total allowable catches assessing impacts on stocks from both fishing and predator–prey interactions (Bogstad and Gjøsæter, 2001; Johannesen *et al*., 2012).

The MEA approach offers opportunities to observe ecosystem dynamics and properties across a wide range of temporal and spatial scales. For example, temporal fine-scaled observations (e.g. individual fish behaviour) usually span a limited spatial scale, whereas observations on coarse temporal scales span larger spatial scales (e.g. satellite data) with crude resolution. An associated challenge is that fine-scale observations are resource demanding and wide geographical coverage is neither practically achievable nor economically viable. To address this, intercalibration and integration of observations across sensors and platforms require tailored models to infer the role of the fine-scale (time and space) processes on larger scales [see citation of Levin (1992) above]. This can be achieved using statistical models, where the fine-scaled observations are (ideally random) subsamples of the large-scale system, and proper survey designs combined with modelling can combine information over the relevant spatial and temporal scales. One specific example is the potential to combine stationary acoustics with acoustic observations from transects. Modelling diel impact on density distribution patterns of marine organisms from the stationary observations and adjusting the transect data therefore will enable separation of spatial and temporal distribution impacts; a basic requirement for understanding ecosystem function. Additional usage of unstructured data from "ships of opportunity" may greatly expand the pool of observations (Handegard *et al*., 2012b). Further, to obtain a quantitative understanding of ecosystem dynamics, the tailored observation-modelling framework of MEA needs models that fully utilize the observation systems. The

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amount of information available from the various types of platforms and acoustic sensors goes beyond what can be handled by existing models, and further development of models that respond to the potential of new observations is essential. Similarly, acoustic observation approaches must be developed according to the needs of models, including both testing of assumptions and estimation of model parameters.

Models can be built to inform integrated assessment needs of an ecosystem, similar to that of traditional stock assessments models to set fishing quotas, where the observations can be assimilated with the models and used to predict key properties for the assessment. However, the concept goes beyond parameterization of models relevant to the assessment. By implementing competing hypotheses of ecosystem processes, the models can be used to predict the observations which enable testing of the contrasting hypotheses. This will, in turn, provide understanding of the key processes in the ecosystem and eventually ecosystem function.

We have emphasized that full utilization of the data collection in MEA cannot be realized without a strong modelling component. Modelling for EBM requires a tight interaction with the assessment and management community and cannot be specified in general terms under MEA. Such interaction is essential to secure that models produce useful information and, *vice versa*, so that the assessment and management community is made aware of the potential of MEA to generate relevant data and validate models.

Case studies demonstrating the strength and potential of the MEA approach

The credibility of a new concept/approach to a research question requires demonstrations that illustrate its viability and realism. We have chosen some basic challenges associated with EBM to demonstrate that flexible solutions combining *acoustic technology* with *operational skills* and *modelling*—that is, MEA—can move fisheries oceanography beyond what has been possible using capture technology.

Understanding productivity-determining processes and ecosystem function

"What we cannot do is describe the world in the absence of any prior understanding of it, and in the absence of any theory" (Harré and Secord, 1972, p. 163). Our ability to describe the underwater world is basically expanded with MEA as a tool for understanding ecosystem function through insight into processes at all scales from individual behaviour to meso- and large-scale circulation dynamics. In this example, we want to illustrate that acoustic technology enables collection of wide range of data which supports understanding of ecosystems but which currently are given limited attention by ecology and modelling.

Physical–biological coupling is a basic driver of ecosystems. Since acoustics images distribution patterns in the sea as they occur, it can provide insight into such interactions. For example, vessel-based and moored echosounders image internal waves and thin layers which influence the distribution patterns of plankton and, therefore, the larger organisms that prey upon them (Holliday, 1972; Farmer and Armi, 1999; Benoit-Bird, 2009; Kaartvedt *et al.*, 2012). At larger scales, Godø *et al.* (2012) demonstrated how vessel-based acoustics enables mapping of the density structure in mesoscale eddies and how the phenomenon shapes the ecosystem and stimulates higher trophic marine life: the physical concentration of food or food production produces a habitat for higher trophic levels that otherwise would not exist. Similarly, Zwolinski and Demer (2012) and Zwolinski *et al.* (2011) demonstrate how acoustics and associated oceanographic observations can be used to characterize the pelagic habitat of fish in the Californian current.

Patchiness of organisms determines predation success and survival of organisms at higher trophic levels, but traditional net sampling techniques are unable to assess the real size of patches and their distribution in time and space. Knowledge of such patterns is crucial to build basic understanding of how these distribution patterns cascade through higher trophic levels as demonstrated by several studies using acoustics (Ressler *et al.*, 2012; Benoit-Bird *et al.*, 2013).

Predator–prey interactions are another basic ecosystem process where acoustics may support the generation of fundamental new knowledge. As an example, predator–prey interactions have been evaluated in the Barents Sea based on trawl-based point samples. Combining this with information from whale observations and seabirds allows for a better understanding of predator–prey interactions (Johannesen *et al.*, 2012). However, the predator–prey interactions are often fine-scale processes, and acoustics addresses this at more appropriate scales than trawl indices, not least due to the vertical resolution offered. This is exemplified through whale–herring interactions (Nøttestad and Axelsen, 1999), and also simultaneous recording of single individual *predators and prey* is possible with split-beam systems (Onsrud *et al.*, 2005) and high-frequency imaging systems (Handegard *et al.*, 2012a), demonstrating the potential of acoustics over more conventional approaches to resolve fine-scale trophic interaction processes. A good example of a predator–prey interaction process is the behavioural impact on small mesopelagic fish, the silvery lightfish (*Maurolicus muelleri),* in the presence of a predator. From a long-term study using a cabled submerged stationary platform with an echosounder, the vertical distribution of the small mesopelagic fish *M. muelleri* was observed to change dramatically and very rapidly in response to a predator. An example of this reaction is shown in Figure 3—a scattering layer ascribed to juveniles of this species descends tens of metres upon encountering predators. Further, the vertical distribution of *M. muelleri* has been studied extensively, with acoustic observations revealing a clear relation to light levels (Giske *et al.*, 1990; Balino and Aksnes, 1993; Staby and Aksnes, 2011). Subsequent modelling has addressed the vertical distribution in terms of trade-offs between feeding and predation risk, both being expressed in terms of the light conditions (Rosland and Giske, 1997; Staby *et al.*, 2013). These long-term acoustic observations suggest that additional variables may be included which can be quantified through observations, exemplifying the potential of the coupled modelling–observation approach. Similarly, acoustic observations have revealed whales feeding on mesopelagic fish (Figure 4, Benoit-Bird and Au, 2009a, b; Godø *et al.*, 2013).

Understanding the drivers of variability in fish stock recruitment

Recruitment to most large fish stocks is thought to be determined by a combination of predation, starvation, and displacement away from appropriate nursery grounds during the early life history stages (e.g. Houde, 2009). With the observation capabilities described above, and the resolution possibilities described for the acoustic technologies, MEA observation methods can be tailored to not only observe interactions between fish larvae and copepods, and fish larvae and their predators, but also to quantify these interactions using broadband and split-beam technologies. This would

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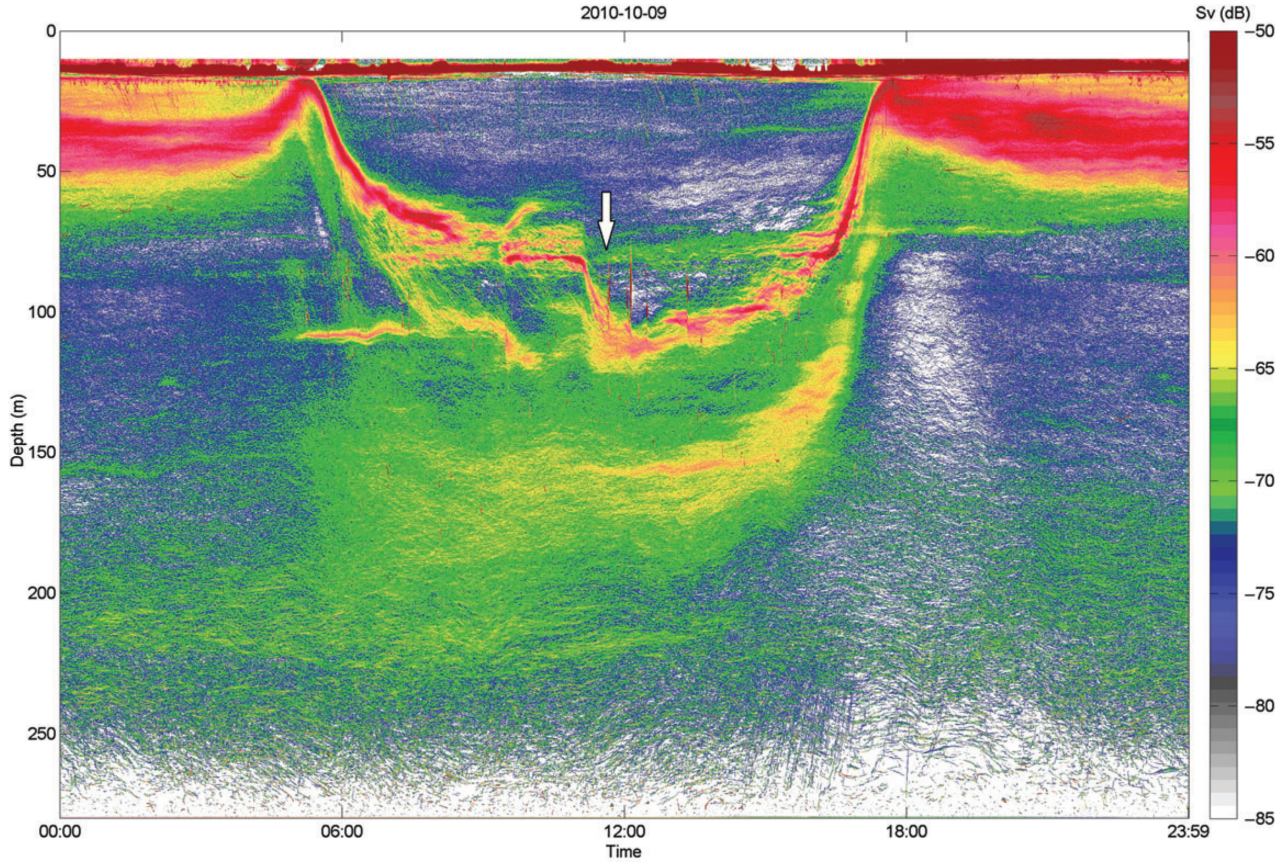

Figure 3. Echogram capturing the diel vertical migration of a small silvery lightfish (*Maurolicus muelleri*) layer impacted by schools of predators (white arrow) at 100 m depth at about 12:00 UTC. Note how the depth distribution of prey changes substantially after contact with the predator.

be facilitated by interpreting the movement patterns observed acoustically with fine-scale observations made in the laboratory (e.g. Browman and O'Brien, 1992; Abrahamsen *et al*., 2010; Browman *et al*., 2011; Vollset *et al*., 2011). Further, with operational skills as a tool for designing a sampling regime for larvae during the period from first feeding to the nursery grounds, essential information for quantitative drift models, which are currently based upon assumptions, can be assessed (see Johansen *et al*., 2009). Such a distributed intensive sampling programme is becoming realistic through the utilization of low-cost oceanographic platform acoustics. Attempts to predict distribution patterns of larvae based on such particle models fail if they do not consider behavioural aspects (Johansen *et al*., 2009; Ospina-Alvarez *et al*., 2012; Sundelof and Jonsson, 2012; Staaterman and Paris, 2014). In a long-term perspective, when quantitative observations of behavioural characteristics with appropriate resolution through tailored technology are possible, and these are combined with models, it will be feasible to more thoroughly and realistically test the prevailing hypothesis of Hjort, Cushing, and others (reviewed by Hare, 2014).

Censusing fish stocks using MEA

Assessing fish stocks using acoustics requires precise abundance measurements and correct identification of the acoustic traces. Both issues belong to the basic acoustic technology solutions described above. Identification is currently done predominantly by trawl sampling. Trawls accumulate information over large volumes and provide neither species nor size information at the spatial or temporal scales provided by acoustics. A renewal of fish stock assessment therefore requires further development of acoustic identification techniques, so as to avoid degradation of acoustically measured details by crude resolution and selective trawls. The acoustic probing platform with built-in optical instruments for identification and the Deep Vision trawl system (mentioned above) are examples of how the identification challenge can be addressed.

Acoustic-trawl surveys combine information from net sampling and acoustics to generate indices of abundance that are used in stock assessment (Aglen, 1994). Challenges for a well-designed survey are often associated with biased observations caused by various processes (Godø and Wespestad, 1993), including relative changes in sampling gear selectivity, acoustic blind zones (Totland *et al*., 2009), vertical distribution, and avoidance behaviour of the focal species (Olsen *et al*., 1983; De Robertis and Handegard, 2013). As an example, new scientific sonars and modelling efforts that combine detailed sonar information with a behaviour model before combination with echosounder data are promising, as discussed by Holmin *et al*. (2012). Such approaches may provide a platform for merging the data from the various sensors and ultimately help overcome some of the obstacles associated with interannual variability in survey indices.

Implementing MEA

Present marine research and monitoring employs a combination of acoustic technology solutions and simple operational skills to

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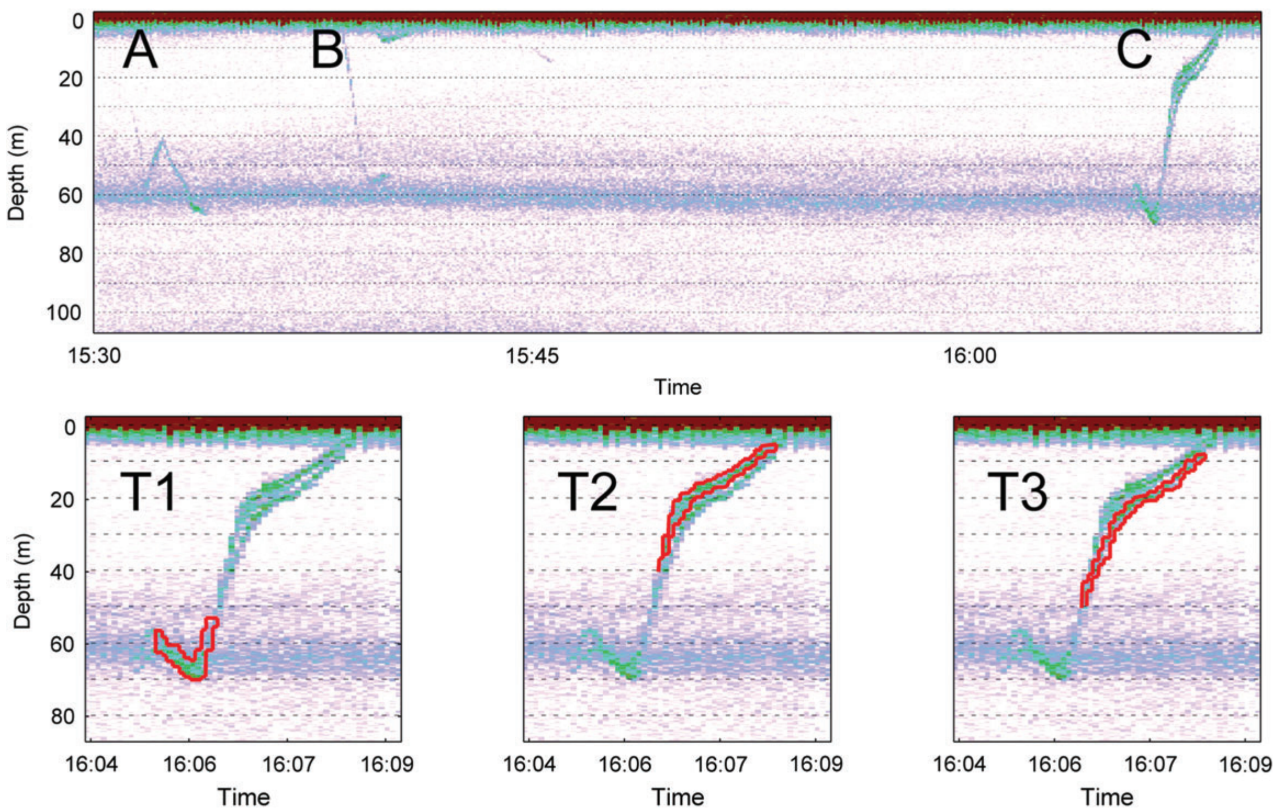

Figure 4. Whale diving behaviour as recorded by stationary acoustics. Upper panel: Echogram capturing layer of mesopelagic fish at 60 m depth and diving whales recorded as vertically moving traces (A, B, C). Lower panel: Details of whale track C. Red boxes show the separated track as indicated by target tracking algorithms. The black marks identify accepted single targets according to the detection criteria defined for the algorithm. The red box in T1 indicates a single individual, whereas separation of the signal into two individuals occurs in the red boxes of T2 and T3. The tracks in T2 and T3 probably refer to detected density differences when the acoustic signals pass into and out of the whale body. The distance between them thus reflects the size of the animal [the figure is adopted from Godø *et al.* (2013) where further details can be found].

Table 1. A schematic illustration of how combinations of acoustic solutions and operational skills can support some of the key challenges of ecosystem-based management (EBM).

Acoustics solution / Operation skills / Challenge to be solved	Species id	Spatial resolution	Temporal resolution	Quant. behaviour	Quant. Interactio
	a b c d	a b c d	a b c d	a b c d	a b c d
Vessels					
Vessel operated tehtered					
Autonomous subsea platforms					
Stationary					
Oceanographic (mooring, floater)					

The key challenges of EBM are grey scale-coded, with the size of the grey bar in each cell indicating the importance of that specific combination of acoustics solution and operational skill to solve the given challenge. The grey scale coding scheme is: ecosystem function, a; fish stock recruitment, b; fish stock assessment, c; ecosystem assessment, d. For example, stationary platforms provide high temporal resolution (horizontal bar covers the column) of importance to fish stock recruitment (identified by size of bar in column b).

address the needs of fisheries science, marine ecology, and EBM (Table 1). A stronger reliance on acoustic systems, combined with an expanded and designed use of operational systems—that is, MEA—is required to meet the challenges presented from the left to the right side of each cell in Table 1. Implementation–operationalization of the MEA concept would occur as follows:

(i) Establish an operational data storage and processing framework that enables accessibility and merging/fusion of information at the various spatial and temporal scales. This is a prerequisite for the MEA approach and requires immediate action to ensure that existing data can be used to efficiently develop new concepts.

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(ii) Define the variables that must be observed, and at what temporal and spatial scales, to understand and model productivity-determining processes. This step must be implemented in close cooperation with ecosystem modellers to ensure that the information produced, and its format, can be readily input into models.

(iii) Following from (i), develop and deploy observation systems (combinations of acoustic solutions × operational systems) and ensure that the data that they produce are relevant to, and useful for, biophysically coupled ecosystem models. Here, it is essential to start with clear priorities based upon existing knowledge (or the lack thereof), keeping in mind Levin's (1992) statement about "…retaining essential information without getting bogged down in unnecessary detail".

(iv) Evaluate and adjust the observation framework according to the outcome of (i)–(iii) and improve the cost-efficiency of observation systems by developing a dynamic interaction between the quantitative observation and modelling framework.

(v) Establish a long-term monitoring framework that includes observation systems, operational infrastructure, operational routines/procedures, and models that permit data production and analysis that follow from the needs of EBM.

(vi) Develop cross-disciplinary educational programmes that produce scientists with the required knowledge and skill so that MEA's three components can be seamlessly integrated.

Clearly, achieving all the above will require a systematic approach in more than one institution and will not occur overnight. However, the potential in the approach justifies the effort that will be required to make it a reality.

Concluding remarks

A basic challenge of both fisheries science and ecology, and something that is at the heart of successfully implementing EBM, is empiricising productivity-determining processes, biophysical coupling, and trophic interactions (see, for example, North *et al.*, 2009). Observing such processes—at the spatial and temporal scales on which they occur—is impossible with classical observation methods but is within our grasp with existing acoustic technology (Godø, 1999; Beamish and Rothschild, 2009). Numerical models of ecosystem processes have also made great advances but are missing an empirical basis (e.g. Peck *et al.*, 2012; Peck and Hufnagl, 2012; Griffith and Fulton, 2014). Coupling the acoustics-based observational capacity with ecosystem modelling is the raison d'etre of the MEA approach.

Fisheries science and marine ecology have developed independently in support of different scientific questions and objectives. However, fisheries science needs ecology to meet the requirements of EBM. Concurrently, these challenges from fisheries science will improve the empirical base used to test the core concepts and hypotheses of marine ecology and fisheries oceanography (see Hare, 2014). Thus, by necessity, EBM is forcing fisheries science towards a closer connection with marine ecology and fisheries oceanography. The MEA approach would provide a foundation that would drive basic steps forward for both fields and will stimulate more interaction between them. MEA could also reduce the gap between terrestrial and marine ecology (see Stergiou and Browman, 2005) by decreasing the current disparity in observation abilities in terms of space–time resolution between terrestrial and marine environments. In this sense, MEA would represent a breakthrough in fisheries science and marine ecology.

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