Ecological Insights from Pelagic Habitats Acquired Using Active Acoustic Techniques

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Abstract

Marine pelagic ecosystems present fascinating opportunities for ecological investigation but pose important methodological challenges for sampling. Active acoustic techniques involve producing sound and receiving signals from organisms and other water column sources, offering the benefit of high spatial and temporal resolution and, via integration into different platforms, the ability to make measurements spanning a range of spatial and temporal scales. As a consequence, a variety of questions concerning the ecology of pelagic systems lend themselves to active acoustics, ranging from organism-level investigations and physiological responses to the environment to ecosystem-level studies and climate. As technologies and data analysis methods have matured, the use of acoustics in ecological studies has grown rapidly. We explore the continued role of active acoustics in addressing questions concerning life in the ocean, highlight creative applications to key ecological themes ranging from physiology and behavior to biogeography and climate, and discuss emerging avenues where acoustics can help determine how pelagic ecosystems function.

INTRODUCTION

The Largest Living Space on the Planet

Organisms dynamically interact with each other and with their habitat, including the biotic, chemical, and physical components that together make up an ecosystem. To study these interactions, ecologists [a term introduced by Haeckel (1866)] combine an understanding of behavior, physiology, evolution, and earth science to quantify the "economy of nature" and, sometimes, our role in it.

Marine pelagic ecosystems make up the largest living space on the planet. These systems have several features that are in striking contrast to those we are familiar with as air-breathing, terrestrial animals. First, the food chain does not begin with large, relatively long-lived plants that are highly structured and anchored in space, providing both food and cover; instead, it begins with microscopic phytoplankton that have doubling times of hours or days, provide little in the way of structure, are consumed completely rather than grazed, and are constantly moving with the physical medium. As a result, pelagic ecosystems change quickly and are associated with water masses and structures rather than geography. In the ocean, a tight coupling exists between the spatial and temporal scales of physical processes, such as fronts, eddies, and gyres, and the scales of the organisms and biological processes they influence; this is in strong contrast to terrestrial systems, where physical processes in the atmosphere, such as storms, droughts, and climatic events, tend to occur at much smaller spatial scales and shorter temporal scales than the biological processes they affect (Steele 1991). These differences between marine and terrestrial systems provide a range of fascinating questions for ecological investigation but also pose methodological challenges to the marine ecologist.

Using Sound in the Sea

A significant challenge for those interested in studying life in the ocean is the limited penetration of light, which makes optical tools ineffective at sampling over large volumes and great ranges. Organisms in the ocean take advantage of limited light and are often physically and behaviorally adapted to hide "in plain sight"—the only real means of hiding in a habitat that lacks cover. Many animals also exploit the rapid and efficient transmission of sound in water for communication and sensing, features that are relevant for scientific exploration of the marine habitat. Sometimes such scientific study is achieved through the reception of natural sounds (passive acoustics). Another technique that takes advantage of sound transmission in water, termed active acoustics, includes both producing sound and receiving the resulting response. Most commonly, this means producing a pulse of sound and listening for the echoes resulting from sound being backscattered by organisms, objects (e.g., the bottom), or other discontinuities in the medium (e.g., density changes resulting from the water column structure). Measurement of the time delay of the received acoustic signal and knowledge of the local speed of sound in seawater allows calculation of the distance of targets, which is the principle underlying sonar (originally an acronym for sound navigation and ranging), and examination of the intensity of the returning sound reveals information about the sources of the scattering.

The use of active acoustic techniques for studying life in the ocean began in the 1920s and 1930s with the first echo detection of fish (Kimura 1929) and the first plotting of the acoustic energy data on a time-versus-depth plot, known as an echogram (Sund 1935). Rapid development of sonars and other acoustic tools during the Second World War led to the discovery of extensive layers that migrate vertically each day between the midwater depths of the world's oceans and the surface (Johnson 1948), collectively referred to as the deep scattering layer. The discovery of

the animals that make up these features and description of their acoustic properties led to great advances in our understanding of life beneath the surface. From the first applications of active acoustic tools to life in the ocean, it was clear that they would have considerable impact on our ability to find, identify, and target species of commercial value in the ocean. Fishermen were soon employing echo sounders (Hodgson 1951, Hodgson & Fridriksson 1955), and in the 1960s, acoustic tools designed specifically to study animals in the ocean began to play a role in the counting and, ultimately, management of commercial stocks (Dragesund & Olsen 1965, Fernandes et al. 2002).

The Current State of Active Acoustic Techniques

Today, an increasingly large variety of active acoustic approaches are available for studying life in the ocean (**Figure 1**). These generally share the advantages of rapid sampling with high spatial and temporal resolution and coverage, are noninvasive and nonextractive, work over a range of environmental conditions (e.g., darkness and fog), and in many instances can allow truly synoptic observations of multiple animal types and/or of physical processes. However, they are generally unable to detect the smallest organisms that make up the base of the food chain, and because they are indirect, they provide relatively low taxonomic resolution. Other challenges include the fact that the sounds produced can be detected by some animals, the systems are power hungry and generally costly, and the data sets are large and can be complex to interpret, thus requiring advanced knowledge and computational tools. The exact choice of method depends strongly on the nature of the ecological questions to be addressed. No handbook is available for ecological acoustics, but interested newcomers are referred to the sidebar (A Primer on Acoustic Data Analysis Methods) and will find references covering the range of technologies available, operating principles, and underlying theories concerning sound propagation in the Related Resources section at the end of this article.

A central aspect of active acoustics is interpreting the intensity of the received signal, which is determined by a combination of multiple physical parameters (such as source level and signal loss during propagation) and by factors associated with the nature of biological scatterers present. The efficiency with which an individual organism scatters sound varies with its acoustic properties (e.g., whether it bears a gas inclusion such as a swim bladder or has hard parts such as a shell or bony skeleton), as well as with its size, shape, behavior (e.g., orientation relative to the acoustic source and receiver), and potentially other parameters such as its physiological condition. Scattering also varies strongly with frequency—different types of organisms exhibit characteristic frequency responses of great value for remote inference of community composition using multifrequency, broadband, and wide-band echo sounders (**Figure 2**)—and with the abundance of the different types of animals present. The overall received signal is thus a complicated function of the abundance, species composition, and size distribution of organisms present and can be further complicated by the contributions of scattering from nonbiological sources (e.g., turbulent microstructure). A great deal of research effort has gone into identifying particular species or types of organisms in the acoustic record and converting acoustic returns to accurate estimates of biomass.

Studies using active acoustics for fisheries science and stock assessments (a discipline often referred to as fisheries acoustics) and those that use acoustics to study the interactions among organisms and their environment face similar needs in interpreting acoustic data, often acquired using the same acoustic instruments and similar techniques but focusing on very different questions. The key question for stock assessment is how many fish are in the ocean, which necessarily emphasizes accuracy, precision, and repeatability over time because small changes in results can have significant management implications. These constraints are often ameliorated in ecological

Echo sounder: a general device employing the principle of sonar; sound is emitted from, and received by, a single transducer

Single-frequency echo sounder: an echo sounder that transmits acoustic pulses centered at a single frequency

Multifrequency echo sounder: an echo sounder that employs a range of discrete frequencies to capture the frequency response of organisms present

Broadband echo sounder: an echo sounder that transmits pulses that vary in frequency over their duration, providing enhanced and continuous characterization of frequency responses

Wide-band echo sounder: an echo sounder that encompasses multiple broadband or even narrowband (i.e., single-frequency) pulses using multiple transducers to widen the overall frequency content

studies, where the focus is on much broader questions, such as how life in the ocean works and why it came to be that way. These are the central questions for all ecologists studying the ocean, regardless of technique, and in the case of acoustics, they can often be addressed in ways that are robust to uncertainties of the sort that are unacceptable in stock assessment.

a

1. Autonomous underwater vehicle (AUV)
2. Unmanned surface platform
3. Ship
4. Profiler
5. Mooring

1. Copepods
2. Euphausiids (krill)
3. Pteropods
4. Fish school

5. Diving seabird
6. Whale
7. Individual fish
8. Squid

b

1 Copepods

4 Fish schools

5 Diving seabird

30 m

1.5 km

1 Copepods   5 Seabird   4 Fish school

10 m

30 m

−71 −65 −59 −53 −47 −41 −35
120-kHz volume backscattering
strength (S_v, dB re 1 m^{-1})
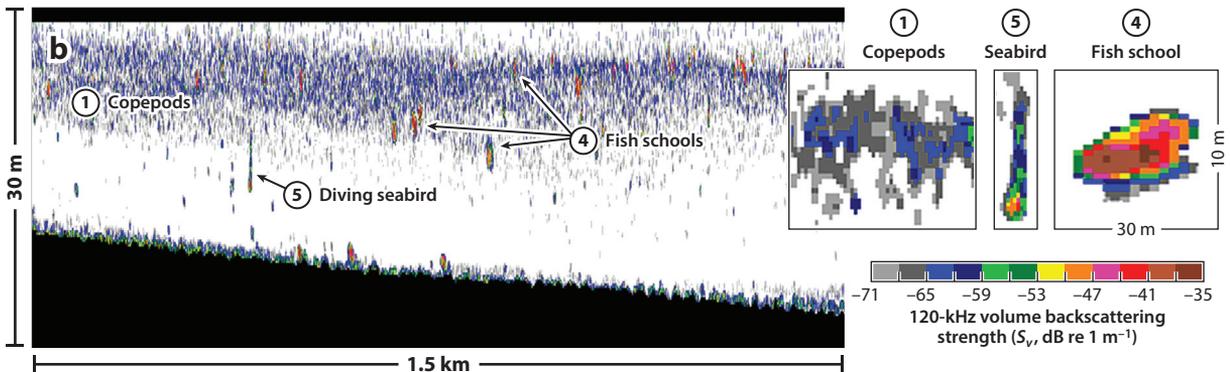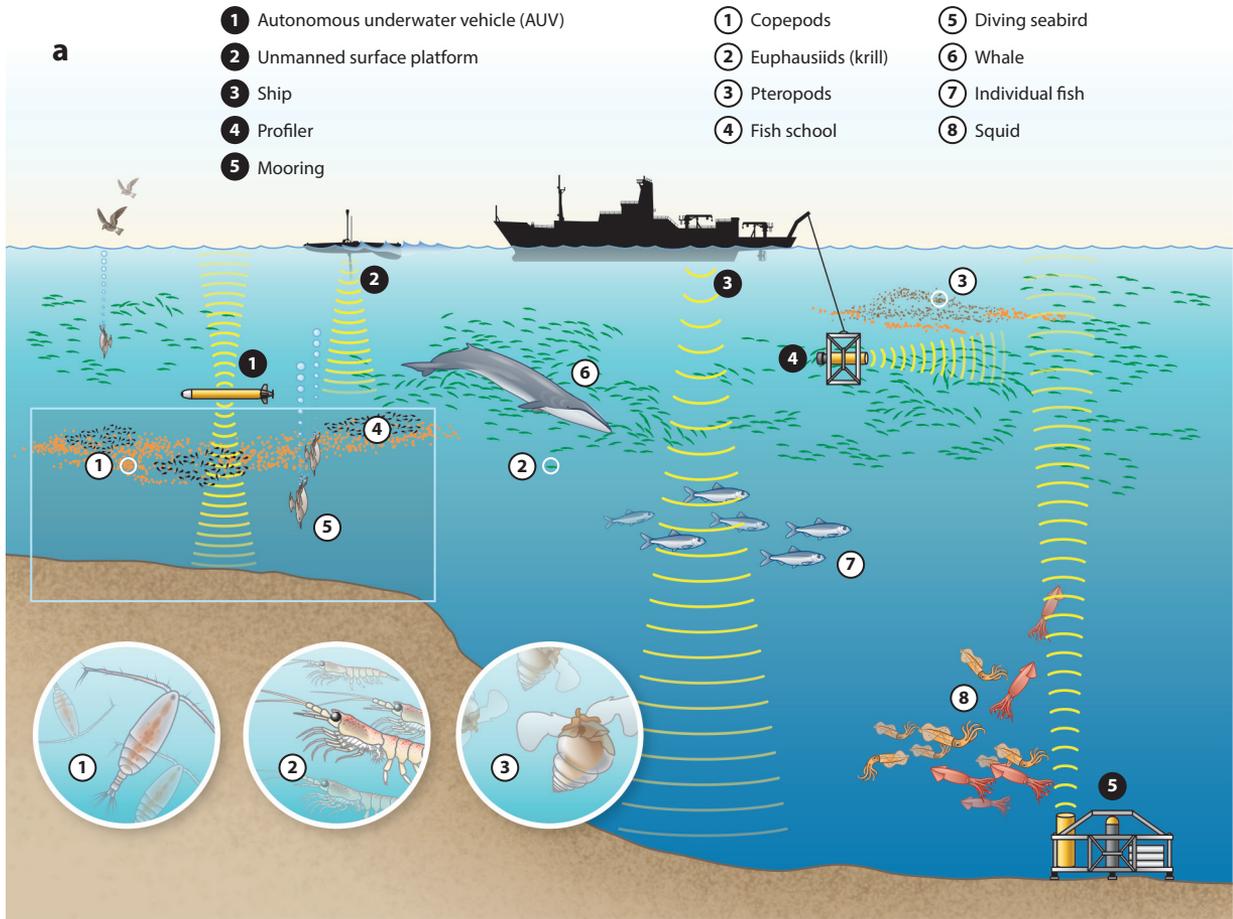
Acoustic Studies of Ecosystems in a Time of Explosive Growth

Studies of noncommercial species go back to the beginning of active acoustic sampling (e.g., Edwards & Livingstone 1960). However, since about the year 2000, there has been rapid and exponential growth in the number of studies using active acoustics to address broad, ecological questions about life in the ocean. This shift is evident in the nature of presentations made at symposia focused on active acoustics sponsored by the International Council for the Exploration of the Sea at roughly seven-year intervals (Fernandes et al. 2002). At the first meeting, held in 1973, only 1 out of approximately 50 presentations was classified as relating animals to their environment. This low representation of ecological presentations persisted until 2002, when ecological topics accounted for 20% of presentations. This proportion increased rapidly to approximately 50% in 2008 and then to approximately 75% in 2015, in part as a result of the push toward ecosystem-based management along with growth in acoustic studies outside of applied efforts.

It is within the context of this recent explosive growth that we explore the role acoustics has played in addressing questions about how life works in the ocean and what role this approach can play in generating integrated ecological theories. We structure this discussion not by method or chronology but rather by identifying key themes in the field of ecology and highlighting the carefully designed, often creative applications of acoustic techniques and their integration with other approaches.

BIOGEOGRAPHY AND LARGE-SCALE SPATIAL DISTRIBUTION: WHERE DO WE FIND ANIMALS IN THE OCEAN?

Understanding the spatial distribution of organisms in relation to underlying forcing mechanisms constitutes a central problem in marine ecology, and indeed, ecology is occasionally defined as the study of the distribution and abundance of organisms and associated underlying interactions (Krebs 1972). Much early work in the nascent field of marine ecology in the late nineteenth and early twentieth centuries focused on biogeography, describing the ranges and delimitations of species over broad geographic scales. Correspondingly, some of the earliest applications of acoustics to marine zooplankton combined acoustic observations of pervasive scattering layers in the open ocean with more sparse direct sampling using nets or visual observations in order to make inferences about the distribution of zooplankton over large geographic regions (Barham 1966, Barraclough et al. 1969). Intriguingly, a recent return to acoustic approaches to biogeography

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Figure 1

(*a*) Examples of acoustic tools (*solid circled numbers* with *curved yellow lines* indicating acoustic waves) and the wide variety of animals (*open circled numbers*) that they can be used to study, ranging from zooplankton to marine mammals. A large and increasing variety of tools are available with varying capabilities for single-target detection (dual- and split-beam as opposed to single-beam tools), frequency content (defined by absolute frequency and number, i.e., single-frequency as opposed to multifrequency or broadband tools), number of beams (single-beam as opposed to multibeam tools), degree of autonomy, size, and so on. As exemplified by the studies reviewed in this article, different technologies are more or less suited to particular organisms and questions, though cost can necessitate trade-offs in data quality. Traditional shipboard systems are increasingly complemented by an innovative assortment of profiled, moored, and autonomous platforms such as vehicles, moorings, and floats, allowing a range of spatial and temporal scales to be considered. These must be carefully and creatively integrated to match the scales of interest with the capabilities of the instruments and platforms. (*b*) An example of acoustic data, representing the shaded rectangle in panel *a*. This echogram shows data from a 120-kHz echo sounder inside an autonomous underwater vehicle (Moline et al. 2015). Acoustic data can span orders of magnitude and hence are typically plotted on color scales in logarithmic form in decibels (dB). Both the main echogram and the detailed views extracted from it are shown using the same scale. Both the quantitative backscatter data and the morphometrics of echo distributions can be used to identify key targets, including the bubble streams left behind by diving seabirds, schools of fish, and layers of mesozooplankton.

A PRIMER ON ACOUSTIC DATA ANALYSIS METHODS

Collecting underwater acoustic data involves carefully selecting the instrument, platform, and experimental design, after which data are processed and interpreted to arrive at derived quantities of biological relevance, such as animal abundance. Relative to fisheries assessments, the required degree of rigor of individual steps can often be reduced in ecological studies by carefully posing questions that are robust to sources of uncertainty. Typical steps include the following:

1. *Signal conditioning:* Noise, interference, and any other unwanted echoes (e.g., the bottom in many applications) must be removed. Data must have sufficient signal-to-noise ratios (i.e., the signal from desired targets must exceed all sources of ambient, electrical, and system noise within the desired sampling range) and minimal interference from other acoustic sources within the sampled frequency band.

2. *Signal processing:* To arrive at quantitative results, intensity data are calibrated (Foote et al. 1987) and integrated over range bins and/or multiple pings (i.e., echo integration) or are beamformed to provide the target location within the acoustic beam for individual scatterers, allowing measurement of absolute echo intensity, referred to as target strength.

3. *Visualization:* Data are typically displayed in ways that allow intuitive interpretation. A great deal of research effort has focused on methods that account for the multiple orders of magnitude spanned, three- or four-dimensional nature of survey data, frequency content, influence of water motion, and other issues characteristic of acoustic data.

4. *Classification:* Echoes from target organisms of interest typically must be discriminated from other sources of scattering, achieved through a combination of approaches:

    a. *Frequency content:* Known frequency responses from theoretical scattering models and/or empirical studies can be compared with measurements made at a series of discrete frequencies (Jech & Michaels 2006, Korneliussen et al. 2008) or over a broad and continuous frequency band (Lavery et al. 2010a, Stanton et al. 2010). Operational frequencies or bands are best chosen to maximize the information content of the frequency response (see **Figure 2**).

    b. *Echo distributional characteristics:* Known differences among organisms in other factors manifest in the acoustic data—such as the shape or depth of aggregations or behavior patterns of individuals—can be used to infer species composition (Horne 2000). These characteristics can also in themselves be the object of ecological study.

    c. *Independent ground-truthing:* Complementary, direct sampling methods of greater taxonomic resolution, such as nets or optical systems, are typically employed (reviewed in McClatchie et al. 2000).

5. *Estimation of ecologically meaningful quantities:* When quantities such as animal abundance or biomass are required, acoustic measurements at individual frequencies can be scaled based on knowledge of the expected scattering intensity of one animal (i.e., its target strength). When multiple frequencies are available, mathematical inversions can be used to solve for the abundance of animals of particular sizes or types (Holliday 1977). In both approaches, some knowledge of the target strength of individual organisms is required. Target strength values are derived from empirical measurements as well as theoretical, physics-based scattering models.

over large scales in the open ocean has now been made using fishing vessels and other vessels of opportunity to study micronektonic fishes, documenting patterns of variability across ocean basins and associations with temperature and primary production (Escobar-Flores et al. 2013, Irigoien et al. 2014, Kloser et al. 2009). With suitable echo sounders (standard equipment on many oceanographic and fisheries research vessels) and opportunities afforded by commercial and fishing industry vessels, such observations are feasible from nonacoustic cruises and have been advanced as an important potential contributor to integrated ocean observing systems.

With the publication of Stommel's (1963) seminal work drawing attention to the importance of scale in oceanography, a major emphasis in marine ecology came to focus on understanding scales of variability in the spatial distribution of marine organisms and associated forcing mechanisms, which can often operate at different scales (Haury et al. 1978). A key strength of acoustic methods lies in their fine spatial resolution, and the fact that data can be collected nearly continuously from a moving vessel (or other platform) provides an opportunity to examine the processes influencing organismal distribution across spatial scales. As a consequence, a large body of literature has developed examining acoustic estimates of the abundance or biomass of particular species or taxa, made over spatial scales ranging from tens of kilometers to ocean basins, relative to observations of environmental features that allow inference of the underlying processes; mostly these are derived from ship-based surveys that utilize scientific echo sounders and increasingly employ multifrequency approaches. Where necessary information on scatterer composition or target strength has been lacking, quantities such as patch area (Ressler et al. 2005) or simply volume backscattering have also been considered. Substantial insight has thus been gained into the broad-scale distribution of organisms such as fish and euphausiids relative to large-scale bathymetric features (e.g., banks and shelf breaks; Ressler et al. 2005), hydrography quantified via concurrent observations (e.g., water masses, currents, and degree of water column stratification; Lawson et al. 2008, Wiebe et al. 1996), and circulation features often assessed via satellite observations (e.g., persistent fronts, mesoscale eddies, and gyres; Behagle et al. 2014, Ichii et al. 1998). In addition to acoustic estimates of abundance and biomass, other acoustically derived quantities capitalizing on the wealth of information in acoustic data sets have been considered in such studies of organismal distribution, including various metrics describing patchiness and estimates of animal length based on multifrequency inversions (Lawson et al. 2008, Lebourges-Dhaussy et al. 2014). Acoustic analyses of animal distribution have also contributed to statistical and, in some cases, predictive coupled biophysical models of distribution relevant to management (Johansen et al. 2009).

Based on the large body of work in theoretical ecology examining the problem of pattern and scale in organismal distribution (Levin 1992), some studies have sought to examine variability in distributions quantified acoustically in light of theoretical expectations. Departures in the Fourier transform spectrum of Antarctic krill (*Euphausia superba*) spatial distribution from the theoretical predictions of the Kolmogorov spectrum for turbulence evident in concurrent measurements of temperature and fluorescence, for instance, have shown that zooplankton exhibit stronger patchiness at small scales than expected from physical processes alone (Weber et al. 1986). Spectral analysis has been employed less often in recent years, but with advances in computational capabilities and mathematical approaches such as wavelet analysis, it offers a profitable avenue for further exploration—identifying, for example, the scales of hot spots of biological activity across trophic levels (Bertrand et al. 2014). Similarly, ecological theories concerning organismal distribution in heterogeneous habitats have enjoyed a great deal of success in a variety of systems and offer an attractive framework for considering the fitness of individuals in relation to acoustically quantified patterns of distribution. For example, at least in some years, sprat (*Sprattus sprattus*) distribute themselves in the Baltic Sea in a fashion that maintains constant body condition (an index of fitness), consistent with expectations of the ideal free distribution concept (Casini et al. 2014).

BIOPHYSICAL INTERACTIONS: HOW DOES THE ENVIRONMENT DRIVE DISTRIBUTION OF ANIMALS IN THE SEA?

At smaller spatial scales, many studies have been able to take a more mechanistic approach to examining the role of physical processes in aggregating organisms and their prey as well as the interaction of organismal behaviors with flow regimes, in large part because the resulting

aggregations are often dense with distinct edges, lending themselves well to acoustic characterization. Many organisms aggregate in regions of abrupt bathymetry, and acoustic observations together with hydrographic and current observations (often integrated with biophysical models such as individual-based models coupled to circulation models) have been used to understand the interaction of biological and physical processes underlying animal aggregations. For example, a combination of vertical movements and behavioral responses to small-scale shear associated with turbulent flow has been implicated in the aggregation of *Euphausia pacifica* along the sill of a fjord (Ianson et al. 2011). Similarly, vertical movements interacting with circulation patterns and bathymetric constraints are believed to lead to euphausiid aggregations in canyons (where retentive eddies can exist at depth) and regions of upwelling and differential flow direction with depth such as the Saint Lawrence River estuary (Allen et al. 2001, Greene et al. 1988, Mackas et al. 1997, Simard et al. 1986, Sourisseau et al. 2006). Tidal phase has also been shown to affect the aggregation structure of Antarctic krill (Bernard & Steinberg 2013), explaining differences observed in distances traveled by foraging penguins between diurnal and semidiurnal tidal regimes (Oliver et al. 2013). Similar processes involving topographically induced upwelling and retentive
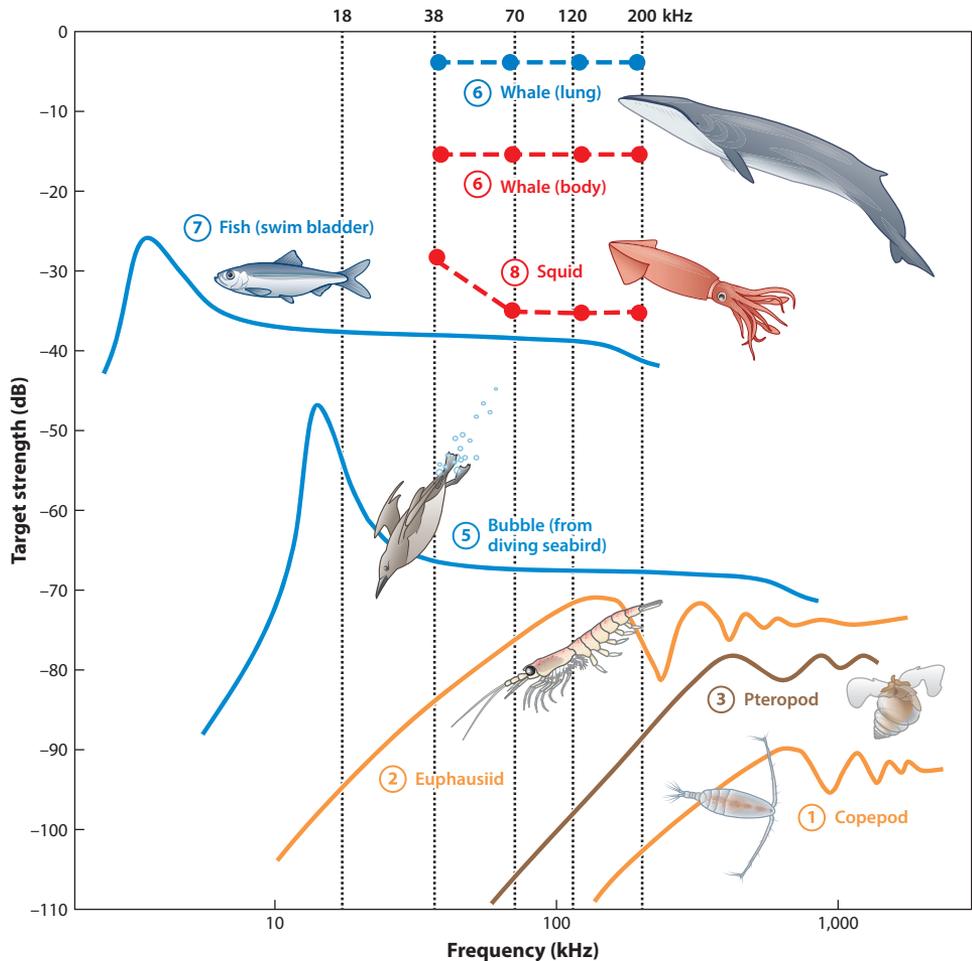
eddies at seamounts have been shown to enhance primary production, ultimately leading, in a process sometimes referred to as trophic subsidy, to the increased production of higher trophic levels and the occurrence of fish aggregations commonly observed acoustically (reviewed in Genin 2004). It should also be noted, however, that such studies of animal aggregations focus on strongly scattering organisms, and it is typically necessary to ignore the roles and contributions of weakly co-occurring organisms, sparsely distributed individuals outside of aggregations, and even strongly scattering organisms at long ranges where noise thresholds preclude effective sampling.

Dense aggregations of zooplankton occupying vertical scales on the order of 1 m and horizontal scales of kilometers, typically referred to as thin layers, constitute another form of aggregation where the fine vertical resolution of acoustic observations has enabled key insights into the underlying biological and physical drivers. Concurrent hydrographic observations have indicated that these layers form at the pycnocline in relatively quiescent time periods and are disrupted by winds, advection of new water masses, and upwelling of waters low in oxygen (Cheriton et al. 2007), with the structure of the layers further impacted by zooplanktivorous fish (as revealed by three-dimensional sonar; Benoit-Bird 2009). Indeed, predation by fish on zooplankton that leads to holes in aggregations, evident in simultaneous acoustic observations of both trophic levels, appears to be a generalizable mechanism for generating or intensifying patchiness in zooplankton distributions (Genin et al. 1988).

Studies of biophysical interactions have often been especially successful when both the physical concentrating mechanism and the organisms can be observed acoustically, because the biological response and physical forcing can then be examined at the same scales. Internal waves, for example,

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Figure 2

Frequency responses characteristic of the different types of animals shown in **Figure 1**, utilizing the same circled numbers (figure design follows the style of A. Lavery; for detailed explanations of underlying theory, measurements, and applications, see the works listed in the Related Resources section at the end of this article). Dashed lines denote curves derived from empirical observations; solid lines indicate predictions based on physics-based scattering models validated through empirical measurements. The vertical dotted lines show typical sampling frequencies (18, 38, 70, 120, and 200 kHz). The line colors indicate animal types (or parts of animals) that are similar kinds of acoustic scatterers. Fluid-like scatterers (*orange lines*) show a characteristic steep increase in the Rayleigh scattering regime and an oscillating plateau in the geometric regime, and measurements made at frequencies that span the transition between regimes provide great power for identifying organism types; shown here are responses characteristic of (①) a 2-mm copepod and (②) a 35-mm euphausiid. The overall shapes of the frequency responses for these two organism types are similar, but note the shift to greater target strength levels and lower frequencies typical of the larger taxon. Shell-bearing scatterers (*brown line*) exhibit a frequency response with a shape similar to that of fluid-like organisms but with a greater magnitude for similarly sized individuals resulting from the greater efficiency of scattering from the hard shell; shown here is a response characteristic of (③) a 1-mm shelled pteropod (i.e., a thecosome). Gas-filled structures (*blue lines*) display strong resonant peaks of great value in discriminating sources of scattering; shown here are responses characteristic of (⑤) a small bubble such as might be produced by a diving seabird, (⑥) air-filled whale lungs, and (⑦) a swim-bladder-bearing fish (the curve shown here is representative of an ∼23-cm herring). Large organisms that do not have gas inclusions, such as fishes without swim bladders (e.g., mackerel) or squid, and even parts of large animals such as whale bodies (⑥), behave as fluid-like scatterers (*red lines*), but the contribution to target strength of hard parts such as bones or cartilage can lead to complicated frequency responses, as shown here for (⑧) a 46-cm squid. Acoustic studies often consider volume backscattering strength, which represents the summed contributions (i.e., target strengths) of all animals present normalized to the sample volume. For a given size and type of animal, the frequency response of volume backscattering will preserve the shape of the target strength curves shown here but will differ in magnitude depending on the numerical density of animals. When multiple organisms of different acoustic types and sizes are present, the frequency response of volume backscattering can become complicated and often more challenging to interpret.

manifest themselves in acoustic data as displacements of animal layers or of scattering from physical density discontinuities in the water column. Initial studies employing analog single-frequency echo sounders primarily to image internal waves (Haury et al. 1979) were followed by more sophisticated explorations of the relative importance to observed multifrequency (and, more recently, broadband) scattering of organisms in comparison with the turbulent microstructure generated by the wave itself (Lavery et al. 2007, 2010b; Warren et al. 2003). Ultimately, such studies have paved the way for ecologically oriented examinations of the role of internal waves in structuring the distribution of zooplankton and thereby influencing the distribution of zooplanktivorous fishes and piscivorous seabirds (Bertrand et al. 2014).

Similarly, acoustic observations of the vertical distribution of epipelagic animals presumably intolerant of hypoxia in the eastern South Pacific off Peru, a region characterized by a strong and shallow oxygen minimum zone, have been used both to infer the depth of the upper limit of the oxygen minimum zone and to examine the compression of vertical habitat for Peruvian anchovy (*Engraulis ringens*) caused by variability in this depth (Bertrand et al. 2010). Secondary vertical circulation cells, either tidally generated or wind driven (i.e., Langmuir) and involving alternating regions of upwelling and downwelling between cells, can also concentrate organisms and hence are another physical process that is manifest in acoustic data, as horizontal banding over spatial scales of tens of meters (Pershing et al. 2001, Wiebe et al. 1996). It is likely that many more such physical processes exist that are revealed in the acoustic data directly and remain to be explored.

As instrumentation for characterizing such physical processes and biophysical models used to explore the response of animals to flow fields continue to develop, opportunities for studies of biophysical interactions will grow. There is also likely unfulfilled potential in existing data streams; for example, acoustic Doppler current profilers (ADCPs) are standard instrumentation on research vessels and on many moorings that provide measurements of particle motion (assumed to be passive) and hence of current velocities, but within some animal aggregations, these measurements are indicative of animal movements. Only limited efforts have been made to mine this information fully, combining ADCP observations of currents (outside of aggregations), animal movements (within aggregations), and backscattering (indicative of animal abundance, though not a quantitative measure of biomass in many ADCPs) to quantify the role of directional and random movements in generating and maintaining aggregations (Zhou & Dorland 2004) and potentially contributing to mixing (Pujiana et al. 2015).

TEMPORAL DYNAMICS: WHEN, WHY, AND HOW DO ANIMALS MOVE?

Similar to the breadth of spatial scales over which acoustic observations can be made from moving platforms, observations made from single locations such as moorings or a stationary vessel allow phenomena to be resolved across a range of temporal scales. Studies using the backscattering signal from upward-looking ADCPs on moorings to characterize the vertical distribution of scattering layers over diel time periods, and in particular to quantify variability in the regular diel vertical migration undertaken by many zooplankton and other organisms, were among the earliest of these applications (Plueddemann & Pinkel 1989). ADCPs remain common instrumentation on moorings deployed to examine physical processes over durations of weeks to years. In addition to the resulting measurements of currents, the backscattering signal intended originally as a diagnostic of signal quality has been used profitably to characterize temporal variability in scatterer abundance; observations from moored ADCPs in the Arabian Sea, for instance, indicated seasonal variation in diel vertical migrations and acoustically estimated biomass associated with the monsoonal cycle

and concomitant upwelling (Ashjian et al. 2002). Similarly, zooplankton biomass inferred from ADCP time series measured at the Bermuda Atlantic Time-Series Study (BATS) station revealed temporal variability associated with spring blooms, the passage of mesoscale eddies, and hurricanes (Jiang et al. 2007). More recently, scientific echo sounders have been installed on moorings and observatories, allowing long-term observation of scattering communities, and have led to the development of a variety of metrics (density, dispersion, etc.) used to examine temporal patterns and periodicity in pelagic fauna based on quantitative interpretations of intensity (Urmy et al. 2012)

Perhaps less exploited has been the contribution of acoustic observations to studies of biogeochemistry. Acoustic estimates of the biomass of zooplankton and fish can be used to estimate the production of fecal pellets and contributions to downward carbon export (i.e., passive flux of sinking particles), as well as the vertical migration of organisms that leads to carbon being consumed (through predation) and freed (through respiration and excretion) at different depths, resulting in the active flux of carbon to the deep sea. Speculations have been made linking time-series observations of zooplankton biomass estimated acoustically to variability in vertical carbon and nitrogen export (Jiang et al. 2007) and sediment trap flux (Hernández-León et al. 2002). Direct observations of euphausiid fecal pellet flux have been made using a moored upward-facing echo sounder, suggesting a novel means of quantifying this component of the carbon cycle (Rostad & Kaartvedt 2013). Acoustics has also been part of the sampling complement of large, interdisciplinary programs examining carbon vertical flux, particularly in the Southern Ocean (Turner & Owens 1995), and has been used to constrain certain parameters in biogeochemical models (Priddle et al. 2003). Most recently, Bianchi et al. (2013) assessed the amplitude of diel vertical migrations observed with shipboard ADCPs in relation to the depth of the oxygen minimum zone and employed these data in a global model of coupled ocean circulation and biogeochemistry, examining the intensification by vertical migrators of oxygen deficits at depth. Although studies directly linking acoustic observations of animal abundance, vertical movements, and fecal pellets to biogeochemistry have been few, they offer a potentially valuable avenue of investigation to advance understanding of marine biogeochemistry and the complexities of the biological carbon pump (Doney & Steinberg 2013).

CLIMATE SCIENCE: HOW DO ECOSYSTEMS RESPOND TO CHANGE?

Acoustic methods can provide important information when studying the effects of climate variation on marine ecosystems, both via single-location time-series observations and using spatial surveys conducted regularly over multiple years. In the equatorial Pacific, time-series observations made at broadly separated stations (140°W and 170°W) revealed variability in ADCP backscattering at lunar, seasonal, and interannual timescales, suggesting that El Niño events lead to variability in the seasonal extent of the oligotrophic warm pool evident in scatterer abundance (Radenac et al. 2010). A long tradition of acoustic surveys for assessment of commercially exploited species, often with time series spanning decades, has allowed multiple studies of fluctuations in abundance relative to indices of natural climate variability in various regions, including Antarctic krill relative to the El Niño–Southern Oscillation and Southern Annular Mode (Fielding et al. 2014) as well as anchovy and sardines in the Humboldt Current System off western South America relative to temperature and El Niño events (Gutierrez et al. 2007). In some instances, acoustics can also help disentangle the relative importance of fishing compared with long-term, climate-related sources of variability in abundance, as was the case for Pacific sardine (*Sardinops sagax*) in the northeast Pacific, where combined acoustic and trawl surveys have suggested that stock declines in recent

years stem from an interaction between increasing exploitation rates and a cold oceanographic regime unfavorable to the sardine population (Zwolinski & Demer 2012). Similarly, acoustics has contributed to identifying the behavioral and other adaptations underlying the emergence of the bearded goby (*Sufflogobius bibarbatus*) as the dominant forage fish species in the northern Benguela upwelling system off Africa following the collapse of the sardine fishery and associated shift to a jellyfish-dominated system (Utne-Palm et al. 2010).

Such examinations of natural patterns of climate variability can also provide insight into the possible future effects of directional climate change. Acoustic studies of the distribution of fish and their zooplankton prey in relation to ice cover and temperature in the Arctic, for example, likely provide clues to the changes to come as these habitat characteristics change in the next few decades (De Robertis & Cokelet 2012, Hollowed et al. 2012). As acoustic time series continue to lengthen and the environmental impacts of climate change in the form of temperature changes, ocean acidification, and reduction of sea ice continue to accrue, evidence of the effects of climate change on ecosystems will undoubtedly be found directly from acoustic observations, providing insight into the mechanistic underpinnings.

PHYSIOLOGY: WHAT HAPPENS INSIDE AN ANIMAL WHEN ITS ENVIRONMENT CHANGES?

One way organisms respond to their environment over both short and long timescales is via physiological changes, for example, by packing on extra fat when feeding conditions are good or entering a rest stage when they are not. Understanding the physiological adjustments organisms make to survive and reproduce successfully in their ever-changing environments can provide insights into the conditions themselves as well as the physiological constraints of the animal. Like animal type and size, the physiological condition of animals has an effect on their acoustic scattering. Changes in stomach fullness and reproductive state can affect the shape of an animal or the shape of internal organs such as the swim bladder (Machias & Tsimenides 1995), and changes in lipid content and stomach contents can affect an animal's density and sound speed (Greenlaw & Johnson 1982), all of which can affect acoustic scattering. Changes in swim-bladder size in fish that move vertically in the water over short time periods have been assessed acoustically in situ (Diachok 2000, Halldorsson 1983). Although much attention has focused on how physiological state might affect target strength variation and thus the accuracy of biomass assessments, outside of measurements of the dynamics of fish swim-bladder volume (Gauthier & Rose 2002b, Thompson & Love 1996), there are few examples of studies that exploit variation in acoustic scattering to understand physiological responses to the environment.

Ex situ studies show that it is possible to make use of variance in physiological condition to acoustically estimate the energy content of animals more quickly and easily than traditional laboratory measures (Benoit-Bird & Au 2002). Energy budgets are key to understanding ecological systems because variation in the transfer of biotic energy is a key contributor to population dynamics and community structure (Lindeman 1942). Acoustic approaches have the potential to contribute to our understanding of the complex physiological responses of animals to highly variable conditions at scales that traditional approaches cannot. Although some physiological changes may affect entire communities, making it possible to see their effects in traditional acoustic surveys, approaches that allow acoustic measurements of individual animals are more likely to provide information on gut fullness or energy content. A variety of approaches—including lowering echo sounder transducers (Kloser 1996); using broadband, multiangle acoustics coupled with imaging (Roberts & Jaffe 2007); and using underwater acoustic cameras (Iida et al. 2006)—have

been utilized to make in situ acoustic measurements of individuals and, sometimes, their internal structures. If tools like these could be utilized to provide indicators of physiological variables, they could lead to important advances in our understanding of behavior as well as ecosystem processes.

LIFE HISTORY STRATEGIES: WHAT ARE THE TACTICS FOR SURVIVAL?

Physiological changes in an organism (such as storing lipids before winter) and behaviors like diel vertical migration can be part of an animal's life history strategy, that is, its lifetime pattern of growth, differentiation, storage, and reproduction. A life history strategy can be thought of as the mechanism by which the environment and the organism interact to determine an animal's fitness, a central idea in evolutionary and ecological theory. Migration is a nearly universal strategy in the animal kingdom, one that acoustics has played an important role in understanding at timescales ranging from daily excursions to once-in-a-lifetime spawning movements. One of the first applications of echo sounding was the discovery of the deep scattering layer and the description of diel vertical migration (Barham 1966), a common behavior thought to be a strategy that balances the need to find food in rich surface waters against the need to avoid visual predators (Enright 1979). Moored echo sounders have revealed the relationship between seasonal migration timing and physical conditions within an upwelling system (Kaltenberg et al. 2010). Careful acoustic exploration has revealed the locations of hidden oceanic spawning regions and associated spawning migrations (Rose 1993), and the addition of acoustic tools has enhanced our understanding of the critical transition from riverine spawning grounds to the ocean by juvenile anadromous fish (Brodeur et al. 2003).

Acoustic tools have provided information on other hidden locations animals use, revealing new aspects of their survival strategies. Acoustics on an autonomous underwater vehicle allowed sampling of previously inaccessible areas beneath the ice in the Antarctic, revealing the importance of the ice edge to krill (Brierley et al. 2002). Krill hide from some predators while utilizing the algae that bloom in this dynamic region in the summer, explaining the aggregations of krill-eating whales observed in this zone. Finding ways to avoid predators in open water, where there is no natural cover, is key for the survival of animals, particularly when they must reduce their energy expenditures. Acoustics has allowed researchers to examine an important strategy that copepods use to hide from predators: overwintering at depth (Bagoien et al. 2001). Exploiting a key strength of acoustics, namely the ability to examine multiple organism types simultaneously, has revealed how seasonally migrating fish predators influence the timing of copepod spawning and descent, ultimately affecting the number of generations per year (Kaartvedt 2000). Sampling of multiple animal types using acoustics also played a role in identifying how predator avoidance and foraging strategies change as a function of time of day. For example, zooplankton, fish, and dolphins all focus on one depth and are very active at dusk, but each group uses quite different tactics through the rest of the night (Benoit-Bird & McManus 2014).

Movements of organisms need not be regular or predictable to be important to an animal's success. During an El Niño event, echo sounder surveys combined with direct sampling revealed that Humboldt squid trade their usual gigantism and high fecundity in rich coastal habitats for small size and rapid reproduction in less productive deep waters, resulting in a near doubling in biomass, all in response to a climatic mode switch (Hoving et al. 2013). This finding highlights the fact that life history traits are not fixed but are responsive to the environment, potentially over a range of timescales. The increasing availability of extensive, regular surveys performed for fisheries stock assessments coupled with the ability of carefully designed acoustic sampling to address processes over a range of scales makes it likely that researchers will continue to document

such responsive allocations of an individual's resources (i.e., time, effort, and energy expenditure) among competing life functions in other marine animals.

BEHAVIORAL ECOLOGY: HOW AND WHY DO ANIMALS RESPOND TO ENVIRONMENTAL STIMULI?

The way in which an animal acts in response to a particular situation or stimulus is the component of its life history strategy thought of as behavior. The behavior of an animal results from the integration of its evolutionary history, genes, development, physiology, anatomy, and environment. Studying behaviors such as migrations, mate choice, food gathering, and predator evasion provides insight into each of the forces that shape an animal's life. Acoustics has played a role in revealing both the causal mechanisms underlying marine animal behavior (the "how" or proximate questions) and the survival or fitness value of behaviors (the "why" or ultimate questions) over a range of spatial and temporal scales. For example, split-beam and multibeam echo sounders have been used to measure the swimming behavior and velocity of individual animals ranging in size from centimeter-long zooplankton to greater-than-meter-long squid. These studies also acoustically characterized the swimming patterns of these animals to identify the drivers of the observed behavior—suggesting, for instance, that zooplankton use active swimming against vertical currents within a frontal feature for depth maintenance (Genin et al. 2005), that avoidance of visual predators is a key factor driving the primarily oblique swimming of vertically migrating krill (De Robertis et al. 2003), and that avoidance of competition with conspecifics during feeding drives the complex spiral swimming paths of squid (Benoit-Bird & Gilly 2012). Handegard et al. (2009) looked even more finely at swimming behavior, using a split-beam system to estimate fish tail-beat frequency and make inferences about swimming energetics. More commonly, acoustics has been used to track the net velocity of a group of animals either over short timescales, exploiting Doppler shifts in the acoustic signal created by the movement (Holliday 1974, Zhou & Dorland 2004), or over longer timescales, by observing the net directed movement of biomass using echo sounders, for example, during diel migration (e.g., Benoit-Bird & Au 2004, Kringel et al. 2003).

One question that has long intrigued researchers is why animals exhibit sociality, spending some or all of their lives moving together in a group; this behavior pits our understanding of evolution acting on the individual against our perception of an unselfish, synchronous group. Because of their conspicuousness both visually and acoustically and their importance to many fisheries, groups of fish (called shoals or, when organized and polarized, referred to more specifically as schools) have received much attention. Multiple studies have addressed how fish aggregate and examined this behavior's survival value for aggregations that range in scale from a few meters across to tens of kilometers and that can be persistent or form and disband within minutes. The acoustic tools used to study schools vary widely with the scales to be addressed and the nature of the ecological question. Simple echo sounders deployed from ships have been used to document patterns of school clustering (Petitgas et al. 2001) and to identify daily temporal patterns in fish aggregations, indicating that pelagic fish generally aggregate in distinct schools at dawn and disperse into more loosely organized shoals at dusk, often accompanied by a diel shift in vertical distribution (Blaxter & Hunter 1982, Gauthier & Rose 2002a), which is thought to maximize the trade-off between food acquisition and risk from visual predators. Time series of such measurements from moorings show that the story can be more complicated; the combined effects of prey availability and water column depth influence the efficiency of school formation, leading to aggregations that do not break down in synchrony with the diel pattern (Kaltenberg & Benoit-Bird 2009).

Multibeam systems—that is, those with a fan or array of narrow beams sensitive enough to detect the relatively weak scattering from biological targets—have played an important role in

examining fish aggregations because of their ability to add at least one dimension relative to single-beam echo sounders (Gerlotto et al. 1999). Comparative analysis of these kinds of measurements across taxa has led to the conclusion that aggregation shape in the ocean is highly conserved, providing individual group members an optimum between predator avoidance and oxygen acquisition (Brierley & Cox 2010). However, repeated observations of a single school with a multibeam sonar over the course of an hour revealed how dynamic the shape, size, depth, and internal density of a school can be over a short period of time (Weber et al. 2009), and similar observations over three days showed complex school dynamics as fish balanced the trade-offs of spawning and access to mates against predation risk (Axelsen et al. 2000). Multibeam echo sounders can sometimes reveal the structure within schools of fish, demonstrating that large aggregations are in fact made up of small groups of individuals that maintain contact (Gerlotto et al. 2010). This observation supports findings from other approaches, providing insight into the behavioral rules used by animals that result in collective behavior while refining our understanding of the importance of the individuals within the group.

Observing the largest-scale fish aggregations requires a different approach to using multiple beams. Ocean acoustic waveguide remote sensing employs a relatively low-frequency broadband signal while exploiting the potential for sound to propagate over long ranges via trapped modes in the ocean, a technique that can instantaneously and continuously create a two-dimensional horizontal image of fish within a 100-km-diameter area (Jagannathan et al. 2009). This approach has revealed that spawning aggregations of herring form rapidly when a critical population density is achieved and that this darkness-mediated process is driven by a small number of leaders, with rapid information transfer occurring horizontally in waves (Makris et al. 2009). Coupling acoustic observations at scales from the individual to tens of kilometers with distribution models, acoustic models, and theories about emergent behavior (e.g., Viscido et al. 2004) will contribute to creating a global framework for understanding congregating behavior.

PREDATOR-PREY INTERACTIONS: HOW DO ANIMALS FIND FOOD WHILE PREY AVOID BEING EATEN?

Living in groups strongly impacts the ecological and evolutionary dynamics of the individuals within the aggregations as well as those of their predators, prey, and competitors. Multibeam echo sounders and multibeam acoustic camera observations have played an important role in revealing the dynamic properties of interactions between groups of prey and their predators, providing measurements of prey density, the direction of their movement, and the distance of individual prey from each other and from predators, often simultaneously with measurements of predator attack angle, velocity, and dynamics. Repeated observations over time represent the key strength of this approach because they provide the opportunity to observe and quantify dynamic behavior in a way analogous to studies above water, allowing both intuitive, visual assessment once the complex and voluminous data stream is analyzed and connection to the extensive theory developed for other grouping animals, such as birds, insects, and ungulates. Fish schools under attack by marine mammals, seabirds, or fish have been acoustically observed to reduce their interindividual spacing and split into smaller groups, sometimes re-forming behind the attacking predators (Axelsen et al. 2001, Handegard et al. 2012, Nøttestad & Axelsen 1999, Nøttestad et al. 2002b). Zooplankton under attack by fish predators exhibit similar responses (Benoit-Bird 2009). These responses are thought to be a result of the so-called selfish herd, in which individuals seek to use others in the group for cover while maintaining the maximum distance from the approaching predator. Observations of the predators have shown that both fish and marine mammal predators often use social behaviors themselves to attempt to overcome these defenses, swimming in coordinated

formations (Handegard et al. 2012) and even cooperating to push prey to the surface (Nøttestad et al. 2002a) or into much denser aggregations (Benoit-Bird & Au 2009) to facilitate effective, efficient prey capture.

Multibeam systems are not the only tools used to simultaneously observe predators and prey. The most common approach has been to combine visual surveys of air-breathing predators with an echo sounder or (more recently) a multibeam sonar survey of the prey field, with the resulting data often further integrated with measures of the habitat. These efforts have examined predator and prey interactions at much larger spatial and longer temporal scales, revealing behavioral processes underlying interactions, for example, that predators can exploit the interaction between their prey and the physical habitat (Coyle 1992) and that krill swarms consistently become more spherical in response to a variety of air-breathing predators (Cox et al. 2009). Studies combining visual and acoustic observations have helped researchers make significant progress in understanding the role of food in driving patterns of animal distributions and population abundances. For example, we now know that air-breathing predators in a variety of systems are remarkably selective in choosing how the prey they eat are distributed, preferring dense, shallow patches regardless of their size or total biomass (Benoit-Bird et al. 2013a, Croll et al. 2005).

Echo sounders in combination with passive acoustic localizations of vocalizing animals or observations of animals carrying behavior-recording (Benoit-Bird et al. 2013b, Hazen et al. 2009) or acoustically transmitting (Josse et al. 1998) tags have also revealed details of predator-prey interactions; these approaches are not reliant on animals coming to the surface, potentially expanding examination beyond air-breathing predators. Underwater tagging technology in particular is advancing rapidly, with tags decreasing in size while increasing in capabilities and carrying new sensors (including both passive and, soon, active acoustics). These advances are enabling researchers to characterize the behavior of animals as well as the habitat surrounding them and are spawning new statistical and visualization techniques for their analysis (Bograd et al. 2010). Studies integrating tags with acoustics have given a glimpse of the possibilities for integrating animal behavior with studies of prey and physical environments. The strengths of this approach—the overlap in resolution possible between these tags and acoustics, the ability for the tags to provide context concerning the water surrounding a tagged animal, and the ability to use acoustics to describe the areas the tagged animal did not choose while letting that animal lead researchers to interesting areas—hint at the potential for carefully designed integration of tagging and acoustics to reveal the secrets of interactions beneath the water's surface.

In addition to quantifying prey, echo sounder surveys can sometimes directly observe the overlap of predator and prey, providing truly synoptic measures, as illustrated in **Figure 3**. Echo sounders have revealed diving depths and the patterns of underwater prey selection in a

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Figure 3

An echogram recorded from a calibrated split-beam echo sounder on a stationary vessel in the Gulf of California, showing how three trophic levels (sperm whales eat squid, which in turn consume myctophids and krill) can be examined synoptically. The underlying numerical data have been converted into an echogram image, displaying acoustic volume backscattering strength in logarithmic form (i.e., in decibels) via the color scale; below the image, a large range of quantitative measures relevant for studying the ecosystem have been extracted from the processed data using a variety of techniques described in footnotes. These data show differences in behavior between differently sized squid, with the smallest squid found in schools and the largest found deepest. These size differences also correlate with different escape velocities when squid were approached by a predator, a diving sperm whale. The whale observations highlight consistency in the surfacing behavior of two individual whales. Combined, such data can facilitate studies of behavior; enable examination of physiological limitations; provide inputs to bioenergetics models; and, when coupled with physical environmental variables measured simultaneously, allow identification of the responses of animals to features such as the oxygen minimum zone. Data collection details are provided in Benoit-Bird & Gilly (2012).
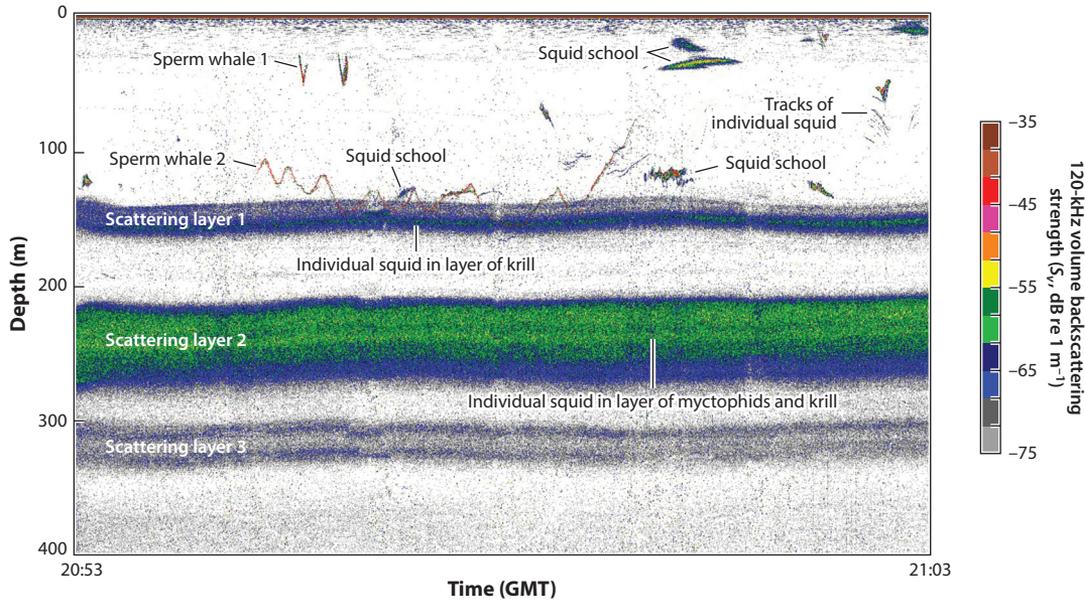
Sperm whales

Whale 1
Target strength[a] = −8 dB (0 to −11.8)
Dive 1: Duration = 16 s
    Bottom depth = 56 m
    Ascent and descent rates = 7 m/s, little variance

16 s near surface[b]
Dive 2: Duration = 16 s
    Bottom depth = 56 m
    Ascent and descent rates = 7 m/s, little variance

Whale 2
Target strength[a] = −7.6 dB (−1.1 to −10.4)
Dive 1 (undulating): Duration = 6.5 min
    Bottom depths = 126, 138, 147, 147, 147, 158, 157 m
    Main dive descent rate = 2.3 m/s, ascent rate = 1.3 m/s
    Rates of depth change within the event = 0.2 to 2.6 m/s

54 s near surface[b]
Dive 2: Duration = 15 s
    Bottom depth = 26 m
    Ascent and descent rates = 7 m/s, little variance

Squid

Schools
Mean density of individuals[c] = 0.84 squid/m^3 (0.47 to 1.17)

Individuals leaving schools
Mean length[d,e] = 47 cm (41 to 53)
Maximum instantaneous escape velocities[a] = 21 m/s (17 to 28)
Sustained escape velocities[a] = 5 m/s (3 to 7)
Complex ascending paths[a]

Schools in krill layers
Mean density of individuals[f] = 0.014 squid/m^3
Mean length[d,e] = 56 cm (51 to 61)

Schools in myctophid/krill layers
Mean density of individuals[f] = 0.003 squid/m^3
Mean length[d,e] = 64 cm (59 to 72)

Prey

Scattering layers
Mean density in layer 1[c,g] = 0.35 individuals/m^3 (0.01 to 0.87)
Mean density in layer 2[c,g] = 0.41 individuals/m^3 (0.11 to 2.8)

[a]Split-beam echo sounder allows target localization and tracking and measurement of target strength.

[b]Visual observations from ship-tracked whales at the surface.

[c]Echo energy integration combines acoustic volume backscattering when individuals are too close to be independently resolved with estimates of individual target strength to estimate animal density.

[d]Target strength was converted to length using empirically established relationships.

[e]Ground-truthed using depth-targeted squid capture.

[f]Echo counting.

[g]Ground-truthed using depth-targeted net trawls.

variety of air-breathing predators, including seabirds (Brierley & Fernandes 2001), marine mammals (reviewed in Benoit-Bird et al. 2009), and fish (Kaartvedt et al. 1996). Using echo sounders, Kaartvedt et al. (1996) described the vertical patterns of zooplankton and planktivorous and carnivorous fish, revealing the important role that water optical conditions driven by phytoplankton have in releasing planktivores from visual predators. This study found that there was a strong overlap between planktivores and krill in areas of high primary productivity but that the planktivores hid near the bottom in other circumstances, a behaviorally mediated connection between productivity and ecosystem processes. Also using echo sounders, Swartzman et al. (1994) simultaneously examined the school characteristics of adult and juvenile walleye pollock, revealing the importance of biophysical interactions in mediating cannibalism in these individuals where they co-occur.

INTERACTION WEBS: BOTTOM UP, TOP DOWN, OR INDIRECT FORCING?

The investigation of links and interactions among organisms has revealed much about the factors driving population change and community composition since Elton (1927) first described the concept of food webs. Combining observations of these interactions with prolific theoretical developments has helped reveal how systems function and how bottom-up forces such as nutrient availability (White 1978) and top-down forces such as predators (Hairston et al. 1960) underlie observed patterns. In pelagic marine systems, data from acoustic surveys are frequently incorporated into mass-balance models of food web dynamics (e.g., Santora et al. 2013), primarily as biomass estimates. The biomass estimates in these models are critical for determining ecosystem efficiency, biogeochemical cycling processes, and linkages between systems typically modeled separately (Irigoien et al. 2014) as well as for determining management regions, targets, and metrics (Allain et al. 2012). Incorporation of acoustic measurements into existing food web models has raised questions about the processes incorporated into these models. For example, in the waters off Scotland, models assumed bottom-up-limited fish populations. However, acoustic measurements, trawls, stomach contents, and feeding parameter estimates instead revealed the importance of recruitment and fishing mortality, a top-down factor often not considered in traditional food webs (Reilly et al. 2013). Similarly, acoustic assessments of mesopelagic fish biomass suggest that energy transfer efficiency in the open ocean may be much higher than previously estimated (Irigoien et al. 2014).

Direct analysis of acoustic measurements of biomass over time along with knowledge about species interactions has also revealed the mechanisms linking species. For example, interannual comparisons of acoustic biomass estimates revealed the potential of pollock to be a significant top-down control on euphausiids in the Bering Sea (Ressler et al. 2012), providing key details to inform the existing, primarily bottom-up, climate-driven conceptual and numerical models that have been developed for this system. Over longer timescales, interannual variations in the horizontal and vertical distribution of key prey in the Bering Sea explain the breeding success of nearby seabirds (Kokubun et al. 2008). Highly resolved, month-long stationary acoustic observations of the biomass of multiple trophic levels have helped to reveal that resource limitation mediated by the dynamics of spatial patches regulates the structure of Hawaii's nearshore food web (Benoit-Bird & McManus 2012, 2014). Bottom-up processes connecting phytoplankton, zooplankton, micronekton, and spinner dolphins (*Stenella longirostris*) were driven not by biomass but rather by the distribution of organisms at specific times of day, providing a way to incorporate the heterogeneity so typical of pelagic ecosystems into the concept of food webs.

Food web concepts have more recently been generalized to interaction webs, including not only trophic links that consider the flow of energy but also interactions such as competition,

cooperative behavior, and indirect effects in structuring ecosystems. These interactions are often measured using experiments not possible in pelagic habitats and thus are just beginning to be explored in the open sea. However, the combination of acoustics to measure prey and concurrent observations of predators, including the use of advanced movement-recording tags, has allowed researchers to investigate competition in sympatric species that utilize the same resources. In part by using acoustic observations, Friedlaender and colleagues found differences in feeding performance (Friedlaender et al. 2014) and modeled niches (Friedlaender et al. 2009, 2011) in air-breathing, krill-consuming predators (seals, whales, and penguins) in the Antarctic that suggest strategies to minimize competition among these predators. Indirect effects—that is, those that occur at two or more links from the primary interaction—have been demonstrated using annual acoustic surveys of a pelagic system. Following the removal of cod and other large-bodied benthic predators, the abundance of these animals' prey increased markedly while the abundance of zooplankton decreased and phytoplankton increased, fitting the predictions of a trophic cascade and illustrating the potential that cod have to play a keystone role in the western Atlantic (Frank et al. 2005). Although the mechanisms behind the restructuring observed in that ecosystem were demonstrated with nonacoustic methods of fishery-independent stock assessment, the increasing availability of time series of acoustic data from a broad range of species around the world will make it possible to demonstrate these important relationships elsewhere in ways that have previously been challenging. By going beyond describing the flow of energy, interaction webs, which combine empirical investigation of interactions with a prolific branch of ecological theory and process models, can explain observed patterns of organism distribution and abundance and provide a fundamental understanding of how organismal interactions shape the ocean.

OUTLOOK

Challenges and Opportunities

As evidenced by the studies highlighted above, active acoustic techniques can offer unique insight into a broad range of topics in marine pelagic ecology. The emphasis of this discussion has been on the ecological questions addressed rather than the specific acoustic technologies, but technological innovations, in terms of both instrumentation and platforms, have played and will continue to play a large role in facilitating new ecological insights. The long-standing challenges associated with taxonomic resolution and acoustic discrimination of organism type as well as data visualization and processing (including the handling of ever-increasing volumes of data) will likewise continue to be addressed through innovative experimental designs along with new tools and methods of data analysis. Furthermore, as emphasized in many of the examples presented here, active acoustics is just one tool in the arsenal available to marine scientists; many of the greatest insights have resulted from creative integration of multiple, complementary sampling devices and platforms, and such multidisciplinary approaches will remain important for addressing the multiorganism, multiscale problems found in the ocean.

New developments in the use of active acoustics for fisheries and ecosystem assessment and management will also continue to contribute to studies of marine ecology. These related disciplines have a long tradition of exchanging ideas and insights, which will only increase as fisheries agencies move toward ecosystem-based management and the field of fisheries acoustics continues to expand in scope to encompass broader assessments and observations of marine ecosystems (Godø et al. 2014), the development of new ecosystem indicators (Trenkel et al. 2011), and the development and use of new platforms and integrated systems for ocean observation (Greene et al. 2014,

Handegard et al. 2013). Similarly, advancements in the field of acoustical oceanography continue to push forward measurements of the physical habitat at scales similar to those of the biological measurements made with acoustics (Lavery et al. 2010a,b). Although many of these studies have focused on the separation of physical and biological sources of scattering, with each group of scientists trying to separate signals from their intended targets from the noise generated by the other (Warren et al. 2003), data analysis advancements and ongoing collaborations between groups can also lead to greater understanding of how animals respond to and influence their habitat.

Current, Emerging, and Future Directions

Pelagic ecosystems differ from their terrestrial counterparts, notably in the structure of food webs and the scales at which physical forces and biological responses operate. This contrast affords particular insight for generating new, general ecological theories. Multiple general concepts in ecology have originated from pelagic systems, including ecological stoichiometry, trophic cascades, and the match/mismatch hypothesis (Menge et al. 2009). Active acoustics plays an important and growing role in this developing understanding of pelagic ecology. The ability to obtain time series over species groups ranging from zooplankton to top predators, directly observe interactions among species groups, and capture heterogeneity of processes in space and time (in some cases as a result of other ongoing efforts, including stock assessments and ocean observing programs) places acousticians in a position to contribute to the fundamental understanding of how biological processes shape the ocean. Increasingly, the role of active acoustics in marine ecology has shifted from describing patterns and making inferences about the structuring influences to examining ecological processes directly and mechanistically. Studies of individual species or taxa followed later by examinations of pairwise interactions are now paving the way for integrated studies of complex webs involving multiple types of organisms and their environment.

Acoustic observations offer opportunities to address new problems by measuring ecologically relevant quantities, including many beyond those that are immediately obvious, such as species abundance. At the same time, emerging societal problems such as climate change and biodiversity loss pose research challenges requiring greater ecological understanding of natural processes such as the carbon cycle and ecosystem stability. Together, these provide new and exciting opportunities for active acoustics. For instance, although the use of acoustics to monitor biodiversity might initially seem counterintuitive because of the coarse taxonomic nature of the resulting data, making active acoustic measurements over long time periods and then integrating them with other, more taxonomically resolved data types has been advanced as an important approach for this monitoring (Duffy et al. 2013) and could be used to investigate the forces underlying changes in biodiversity and ecosystem resilience. Similarly, current interest in the carbon cycle associated with climate change provides a stimulating opportunity for active acoustics to bring enhanced ecological insight to biogeochemistry through observations of diel vertical migration and hence active carbon flux (Doney & Steinberg 2013) and through new approaches such as the acoustic observation of sinking fecal pellets, a possibility that was entirely unanticipated until recently (Rostad & Kaartvedt 2013).

The field of ecology benefits from a rich theoretical basis, which can provide compelling and testable hypotheses concerning the functioning of pelagic ecosystems. The challenge thus lies in identifying such hypotheses and emerging opportunities and in developing creative approaches to address them, capitalizing on acoustic and other complementary methods. We hope that the discussion presented here will provide continued stimulation to help drive the field forward, fostering the next decade of innovative inquiry into existing, emerging, and unforeseen avenues of ecological investigation.

SUMMARY POINTS

1. The use of an increasingly diverse array of active acoustic tools and associated platforms to address ecological questions in marine ecosystems, often as a complement to a suite of other approaches, is growing rapidly.

2. A wide range of species can be studied with active acoustics, including zooplankton, gelatinous organisms, fish, squid, marine mammals, and seabirds.

3. Acoustic methods are noninvasive and nonextractive, and they allow fine-spatial-resolution data collection continuously and often truly synoptically from multiple animal types and sometimes their associated physical conditions over a range of environmental conditions.

4. Acoustics can be used across a broad range of spatial and temporal scales, contributing to studies of animal physiology, life history strategies and behavior, population dynamics and distributions, biophysical interactions, climate, community stability and responses to change, biodiversity and ecosystem health, ecosystem interaction webs, and more within these opaque, four-dimensional pelagic systems.

5. Acoustic methods are generally unable to detect the small organisms that make up the base of the food chain and typically provide relatively low taxonomic resolution; however, imaginative approaches and innovative combinations of complementary tools can overcome these limitations.

6. Unlike acoustic assessment of fisheries stocks, there is no handbook for using acoustics to study ecosystem processes; the choice of field and analytical methods must be carefully selected to match the ecological question in ways that are robust to sources of uncertainty.

7. Creativity in experimental design, equipment choice, and deployment approach along with integration with ecological theory derived in both marine and terrestrial systems as well as collaboration and input from related outside disciplines will continue to drive the field forward.

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