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Review Article

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Applications and analytical approaches using imaging sonar for quantifying behavioural interactions among aquatic organisms and their environment

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For many aquatic animals, distributional patterns, trophodynamic relationships, and reproductive activity are driven by complex biotic and abiotic ecosystem interactions that influence behaviour. Linking behavioural information to environmental stimuli and stressors can, therefore, help to anticipate population and ecosystem responses to changing conditions and inform management. However, behavioural information is challenging to obtain because many sampling gears do not provide adequate spatial or temporal resolution, or potentially alter behaviours. Traditionally, most behavioural studies have been laboratory experiments, while behaviour *in situ* has often been inferred indirectly. Advancements in imaging sonar technology enable the study of *in situ* behaviours with the potential to address many understudied relationships. In this review we discuss applications of imaging sonar among a meta-analysis of 155 studies of aquatic organisms in their environments. We evaluate the performance of imaging sonar for studying inter- and intra-specific interactions, associations with complex and sensitive habitats and low-visibility environments, and to evaluate traditional fisheries sampling gears. We examine the data processing and analytical methods used to refine taxonomic resolution, manage time use and autocorrelation through sub-sampling, extract behavioural metrics applied to ecological processes, and for automating abundance estimates and image classification with the goal of providing a resource for researchers.

Keywords: acoustics, adaptive resolution imaging sonar (ARIS), behaviour, dual-frequency identification sonar (DIDSON), fish, meta-analysis review.

Introduction

Understanding the behavioural responses of organisms to their social environment or abiotic factors is a fundamental objective of many aquatic ecological studies and can provide important information for fisheries and protected species management. Habitat selection based on suitability or preference, social structure, reproduction, and predator–prey interactions are integral to linking populations and communities at the ecosystem level (Baltz *et al.*, 1998). Studies that relate aquatic animal behaviours to ecosystem processes can help to determine how organisms respond and adapt to change with implications for resiliency to stressors, ability to compete, and evolution. Additionally, information about animal interactions collected using different harvest or sampling gears is important for population or stock assessments (Rose *et al.*, 2005; Rakowitz *et al.*, 2012; Handegard *et al.*, 2017a; Kang *et al.*, 2020; Smith *et al.*, 2021a). Behavioural information can, however, be a challenge to obtain because many sampling methods do not provide the necessary spatial or temporal resolution, or potentially alter natural behaviours during sampling. Here, we address the utility of imaging sonar as a tool for studying aquatic animal behaviour *in situ*.

Experiments conducted in controlled settings have led to important advancements contributing to the growing comprehension of patterns in fish behaviour (Magurran, 1986; Pitcher *et al.*, 1988; Brown *et al.*, 2006; Rieucau *et al.*, 2016; Munnelly *et al.*, 2021). A contemporary challenge to further the understanding of the mechanisms and functions of behaviour under natural conditions is to acquire reliable quantitative measurements of aquatic organisms' behaviour *in situ* (Rieucau *et al.*, 2015; Reeves *et al.*, 2018). The most common techniques for sampling aquatic organisms have traditionally used extractive gears, such as traps, nets, trawls, dredges, hooked gear, piscicides, or stunning by electric shock. While effective, these techniques can only be used to infer certain behaviours, such as habitat use, or predator–prey interactions indirectly. In addition, some non-extractive techniques, such as diver surveys or remote video arrays, intrude upon the natural setting and can alter behaviours of the organisms present. Continued development of non-extractive and minimally intrusive data collection techniques (e.g. visual methods, hydroacoustics, and genetics) and analytical approaches have enabled behavioural research within environments not previously possible (Frias-Torres and Luo, 2009; Handegard *et al.*, 2012; Jůza *et al.*, 2013; Staines *et al.*, 2022). In particular, sonars are non-extractive and are often minimally intrusive to the targeted organisms and study area while additionally providing high spatial resolution. These features help to

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reveal detailed fine-scale associations that can greatly influence broad-scale distribution patterns throughout the ecosystem.

Among recent innovations allowing non-extractive sampling technologies, the use of imaging sonar, developed by Sound Metrics Corporation in 1999, was first recognized as a fisheries survey tool by Belcher *et al.* (2001, 2002) and Moursund *et al.* (2003), and the first applied use of imaging sonar in an ecological study was published by Tiffan *et al.* (2004). Imaging sonars such as the dual-frequency identification sonar (DIDSON) and the adaptive resolution imaging sonar (ARIS; Sound Metrics Corp.), the BlueView (Teledyne Marine Technologies Inc.), Oculus (Blueprint Subsea), Gemini (Tritech International Ltd), Flexview (Kongsberg Maritime Inc.), Imagenex (Imagenex Technology Corp.), and the Echoscope (Coda Octopus Inc.) use multi-beam high-frequency (0.7–3.0 MHz) sound waves (also known as ultrasound) to produce near video-quality images while requiring relatively low power consumption. Like other hydroacoustic equipment, these so-called "acoustic cameras" are not limited by turbidity (Belcher *et al.*, 1999) or light-related visibility constraints, and the relatively high sampling rate and volume of imaging sonar facilitates its use for rapidly surveying large areas of variable bathymetry and habitat complexity without impacting the environment (Pavlov *et al.*, 2009; Becker *et al.*, 2011a; Grabowski *et al.*, 2012; Able *et al.*, 2014; Rakowitz *et al.*, 2014, 2017; Lankowicz *et al.*, 2020; Henderson *et al.*, 2023; Olson *et al.*, 2023). In addition, as most species cannot detect the echoed frequencies (Narins *et al.*, 2013 and references therein, Velez, 2015), community-level quantitative and behavioural information can be obtained without the built-in selectivity biases of traditional sampling gears, or the effects of attracting or deterring some species. The high operating frequencies of imaging sonars produces imagery with a fixed number of samples, allowing for high spatial resolution at the cost of range (Mueller *et al.*, 2010). The increased pixel resolution results in an improved ability to resolve numerous targets along the X and Z polar plains (the range and the azimuth) simultaneously (Kupilik and Petersen, 2014) and the ability to detect fine morphometric and behavioural details, such as body length, shape, and orientation (Burwen *et al.*, 2010; Tušer *et al.*, 2014; Lin *et al.*, 2016; Cook *et al.*, 2019; Daroux *et al.*, 2019; Helminen *et al.*, 2020), and well-defined tail-beat patterns (Mueller *et al.*, 2010; Tiffan *et al.*, 2010; Kang *et al.*, 2011; Kirk *et al.*, 2015; Helminen *et al.*, 2021). Thus, imaging sonars can provide a powerful means to accurately sample fish, and other nekton density at short range (albeit from a 2-dimensional field of view), including information that can help identify animals to lower taxonomic levels and allow tracking of fine-scale swimming patterns. Other models have recently been developed for use by recreational fishermen to target game fish, including the LiveScope (Garmin Ltd), MEGA Live Imaging (Johnson Outdoors Inc.), and the ActiveTarget (Lowrance), which require proprietary chart-plotter interfaces, but could provide cost-effective alternatives for some research applications (Gutiérrez-Estrada *et al.*, 2022; Neeley *et al.*, 2023).

Many non-extractive sampling methods, such as underwater video and hydroacoustics, allow for the collection of a large amount of observational behavioural data and share the common prohibitive aspect that data processing is labour intensive. Recently, automated tracking procedures have been used to reduce the processing effort required to extract metrics of fish behaviour from video (Rieucau *et al.*, 2018), echosounder (Handegard *et al.*, 2017b), and imaging sonar hydroacoustics data (Handegard *et al.*, 2012; Shahrestani *et al.*, 2017; Tsao *et al.*, 2019; Lankowicz *et al.*, 2020; Shen *et al.*, 2023). For instance, background removal and threshold filtering techniques that are not available for video are useful methods in automated processing of sonar imagery. Automated procedures have also been developed to classify ensonified "objects" based on shape or movement pattern recognition algorithms (Mueller *et al.*, 2008; Tong *et al.*, 2009; Han *et al.*, 2009a, b; Mizuno *et al.*, 2016; Jing *et al.*, 2018a; Shen *et al.*, 2023) and machine learning techniques (Redmon and Farhadi, 2018; Kandimalla *et al.*, 2022; Feng *et al.*, 2023). Additionally, inter- and intra-species behavioural interactions can be assessed within high-density shoals where individual fish tracking becomes impossible by using techniques that track net movement across pixel cells (Handegard *et al.*, 2012, 2017b, Rieucau *et al.*, 2016). However, from the information processing perspective, the current imaging sonars available have major limitations compared with other sensors, such as cameras and hydrophones, including the lack of a common data format and difficulty acquiring raw data files, which adds difficulty to sensor integration (Cotter *et al.*, 2017; Polagye *et al.*, 2020; Cotter and Polagye, 2020a), and real-time data processing to avoid collecting burdensome volumes of low-information data (Cotter and Polagye, 2020a, b). In many instances, manual processing remains necessary to extract information from imaging sonar footage (Han and Uye, 2009). In such cases data sub-sampling is often the most practical solution to reducing the processing effort and often does not reduce the precision in representing the elements of the data with high spatial correlation, such as abundance (Xie and Martens, 2014; Boswell *et al.*, 2019).

There are other limitations of imaging sonar in addition to labour intensive processing. Taxonomic resolution and biomass estimates rely on image quality and cannot be improved using methods commonly used for processing echosounder data, such as differences in backscatter across varying frequencies (e.g. decibel differencing and broadband scattering), or target strength of highly reflective internal tissues such as swim bladders (Burwen *et al.*, 2007; Mueller *et al.*, 2008; Frias-Torres and Luo, 2009; Han *et al.*, 2009a, b; Jones *et al.*, 2021). Further, imaging sonar resolution is limited by several factors, including the inability to differentiate multiple targets occurring at the same range (the X polar plane) within the same beam (the Z polar plane along the azimuth) but occupying different elevations (the Y polar plane), which are combined into a flat surface during the 2-dimensional imaging process (Belcher *et al.*, 2002; Christ and Wernli, 2013; Capoccioni *et al.*, 2019). An exception to this is the Ecoscope by Coda Octopus Inc., which is currently the only 3-dimensional imaging sonar. Related to this issue, organisms on substrate can blend in unless the sonar is carefully oriented with a shallow grazing angle to the bottom or other structure to produce acoustic shadows of organisms present, or if the organisms are moving (Belcher *et al.*, 2002; Langkau *et al.*, 2012; Connolly *et al.*, 2022). This can reduce detection of organisms associated with complex bottom features if they occur at the same range, as well as by producing the added complication of acoustic sidelobe interference. Sidelobe interference occurs when beams intercept high-density objects that generate strong returns from the outer edges of adjacent beams within the array to create noise that can mask lower return features or organisms. This is particularly common along the bottom, resulting in the acoustic "dead zone" that is more pronounced in single- and split-beam echosounders, but still affects imaging sonar (Holmes *et al*., 2006). In addition, imaging sonars are impaired by bubbles and suspended, high-density sediments like sand which reduces the utility of imagery collected in rough conditions, particularly in the upper water column (Maxwell and Gove, 2007). Bubbles and suspended sand can act as unwanted sources of reverberation within the sampled water volume or within the water that floods the imaging sonar between the transducer and the lens despite the otherwise high performance of imaging sonar in turbid conditions (Dahl *et al*., 2001; Maxwell and Gove, 2007). Motion artefacts can also obscure resolution in part because individual frames are constructed of a series of transmit–receive cycles, leading to slight temporal differences within a single image (Helminen and Linnansaari, 2021). As a result, fast-moving targets can produce fragmented returns, and stationary objects can appear fragmented if the sonar is operated from a moving platform. All of these factors influencing resolution require experience to recognize by image annotators and are subjective.

Also of note are some limitations that can be mitigated through survey design. The high frequencies used by imaging sonar and the negative effects of geometric spreading on range resolution reduce the intensity at range and, therefore, the effective maximum detection range (Mueller *et al*., 2008), while the narrow origin of the beam, and inability to fully ensonify targets within ~1 m (where the beam array is not fully formed) impairs nearfield detection (Rose *et al*., 2005; Han and Uye, 2009). Accessory lenses available for some models can be used to refine the field of view (FOV; e.g. the telephoto, concentration, and spreader lenses by Sound Metrics Corp.), although these general effects are inherent, and footage within 1–2 m of the sonar is often not useful (Maxwell and Gove, 2007). Correct positioning of the sonar is essential for optimizing its performance to meet the study objectives (Martignac *et al*., 2015), and readily adjustable or remotely operated rotating mounts are other helpful accessories in this regard. The most widely used orientation involves positioning the sonar horizontally to provide a forward X- by lateral Z-dimension view of either the bottom or a cross-section of the water column that lacks resolution in the vertical Y dimension. Another useful orientation is positioning the sonar between 30 and 60° downward to provide a vertical X by lateral Z 2-dimensional view of the water column that lacks resolution in the forward, Y dimension. A third option is to rotate a horizontally positioned imaging sonar 90° to either side so that the Z polar plane of the beam array produces a vertical FOV, lacking resolution in the lateral, Y dimension. Finally, it is worth mentioning that the imaging sonars available are non-autonomous and remote deployment requires integration with a computer system and power supply (Francisco *et al*., 2022). In this regard, remote imaging sonar deployment has the same logistic challenges of remote video using traditional light-focusing cameras, but at a higher starting expense. These considerations must be carefully weighed by the researcher in the context of the study objectives and environmental conditions.

Through a meta-analysis, we surmise, to the best of our knowledge, 155 peer-reviewed publications (published through 2022) that have used imaging sonars to study freshwater (91 studies), estuarine, or marine (65 studies) aquatic animal behaviours *in situ* (Figure 1). We review the primary findings or novel aspects of 13 studies published in 2023 that were not included in the meta-analysis and discuss an additional 57 papers related to technical aspects of imaging sonar without ecological applications that were also excluded from the formal meta-analysis. Finally, we acknowledge, but do not consider 14 additional papers that used imaging sonar to study the behaviour of aquatic organisms *in situ* for which no English translation was available (Tong *et al*., 2009; Yang *et al*., 2010; Lee *et al*., 2014; Zhou *et al*., 2014; Guo *et al*., 2015; Mo *et al*., 2015; Zhang *et al*., 2017, 2018; Shen *et al*., 2018; Jing *et al*., 2018b, 2019; Huang *et al*., 2020; Schmidt and Schletterer, 2020, 2020). Considered together, all of the above studies have had a wide reach, having been published across 68 peer-reviewed scientific journals, the top five being the *Journal of North American Fisheries Management*, *Fisheries Research*, *Transactions of the American Fisheries Society*, *Estuaries and Coasts*, and the *Journal of Great Lakes Research*. These studies have collectively accumulated 4785 citations, an indication of the impact this technology has had to date.

Relevant literature was searched in Google Scholar (https://scholar.google.com/first access: 16 March 2020; final access: 24 September 2023) using combinations of the following search terms: (A) "acoustic camera", "acoustic lens sonar", "multibeam forward-looking sonar", "forward-looking sonar", or "imaging sonar"; (B) "abundance", "behaviour", "behaviour", "biomass", "fish", or "target"; and (C) the specific sonar model names listed above. Full-text reviews were carried out to identify studies with an *in situ* ecological component for inclusion in the meta-analysis. Studies of organisms within net pens or tanks were considered *in situ* if the organisms were monitored within the artificial environment or they included interactions with the natural environment, but purely experimental studies were excluded. Studies using mechanical-scanning sonars, which are sometimes referred to as imaging sonars, such as Tsao *et al*. (2019) were also excluded. We cross-referenced the literature cited, and the subsequent literature citing each study to find additional papers (the number of papers identified through cross-referencing was not tracked). Other references using imaging sonar were included to support those relevant topics discussed. Our main objective was to show not only how imaging sonar can be used, but how this methodology has been employed to further the current knowledge in fisheries science and aquatic ecology. The information provided here will highlight the existing research gaps and help to guide future study design and data processing strategies to quantify relevant metrics of fish and other aquatic animal behaviours.

To our knowledge, three known existing reviews of imaging sonar applications for studying wildlife include Martignac *et al*. (2015), Wei *et al*. (2022), and Sibley *et al*. (2023a). Martignac *et al*. (2015) presented imaging sonar as an excellent fish counting tool in river and stream studies, compared imaging sonar among other sampling gears, and provided a summary of technical specifications, including applied operational guidelines. Wei *et al*. (2022) reviewed the uses of imaging- and side-scan sonar, the analytical challenges of processing sonar data manually, and automated processing approaches. Sibley *et al*. (2023a) discussed abundance quantification, capacity for measuring species richness, and size information with an emphasis on high species diversity and habitat complexity applications. All three prior reviews thoroughly compared the studies evaluating the accuracy and precision of length

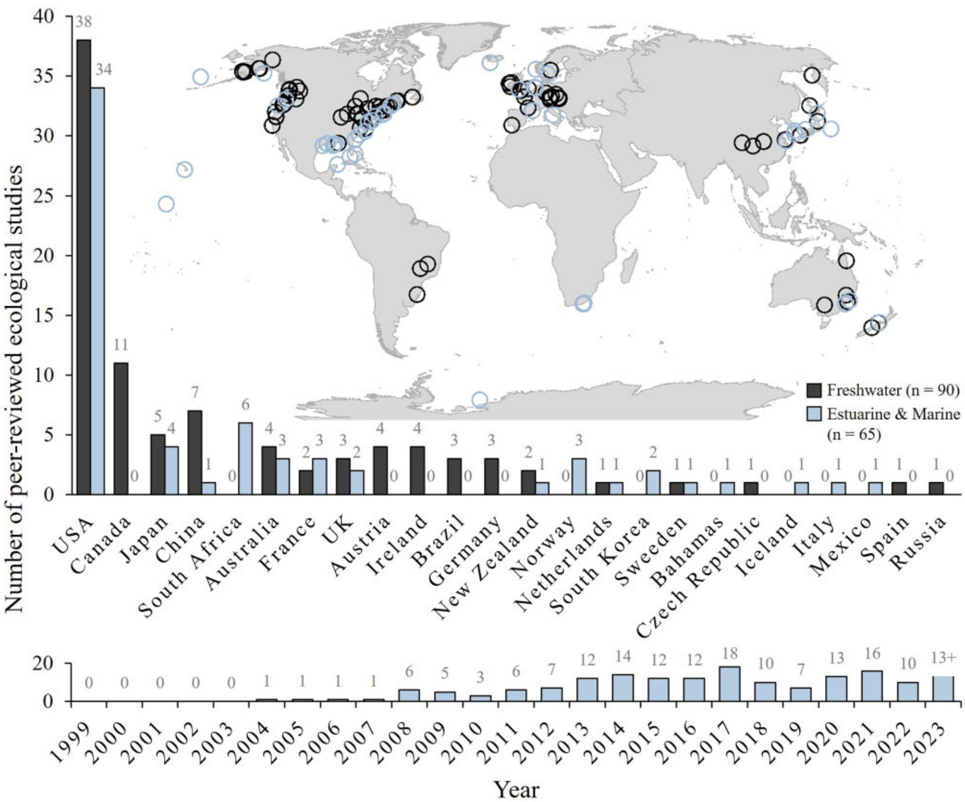

Figure 1. The number and distribution of *in situ* studies using imaging sonar to study aquatic organisms in freshwater (black bars) and estuarine or marine environments (blue bars). Locations of studies are indicated by black and blue circles on the global map. The timeline shows the number of ecological studies using imaging sonar published by year since the technology was first developed in 1999.

measurements from imaging sonar. Our review builds upon Martignac *et al.* (2015) with references to 226 additional studies that have used imaging sonar since 2015, or which have occurred in ponds, lakes, estuaries, and marine environments outside the scope of their work. We also build upon the work of Wei *et al.* (2022) and Sibley *et al.* (2023a) through inclusion of a quantitative meta-analysis detailing how imaging sonar data has been used, including references to 125, and 114 additional studies published within peer-reviewed scientific journals, respectively. Herein, we first address the auspicious ecological and fisheries applications of imaging sonar and emphasize the utility of imaging sonar for providing quantifiable behavioural information, which can be used to address a number of ecological questions. Finally, we discuss the challenges of and approaches for processing imaging sonar data to extract this kind of information.

Applications of imaging sonar to address research gaps

The study of inter- and intra-species interactions

Foremost among the sampling advantages provided by imaging sonar is the high resolution of the acquired acoustic data (see Table 1 for a comparison of technical specifications). The frame rate can be configured between 2 and 21 frames s^{-1} (depending upon the sonar model and distance from the sonar transducer), with a downrange resolution of 2–160 mm. This allows for the detection of multiple small targets along the same bearing to provide a 29–130° horizontal by 14–20° vertical cone-shaped FOV to a distance of 5–120 m from the sonar (depending upon the frequency). Size and spatial information, such as object length, distance from the sonar transducers, and proximity to other objects for all ensonified targets are additionally extractable. The image quality depends on the sound frequency and the number of acoustic beams emitted by the imaging sonar for a specific operational mode, as well as physicochemical properties (e.g. salinity, temperature, and pressure) of the water through which the signal is being propagated due to their effects on sound velocity. The shorter wavelength or pulse duration at higher frequencies produces higher quality images that can depict details such as fins, but at the cost of a decreased effective range, with downrange resolution decreasing with increasing distance and frame rate (Parsons *et al.*, 2017). Lower frequencies rely increasingly upon tissues with more highly reflective properties, such as swimbladders (Foote, 1980). To date, at least five studies have used 0.7 MHz DIDSON, one has used 0.72 MHz Gemini, six have used 0.9 MHz BlueView, one has used 1.0 MHz Simsonar, 29 have used 1.1 MHz DIDSON, three have used 1.1 MHz ARIS, one has used 1.1 MHz LiveScope, seven have used 1.2 MHz DIDSON, 93 have used 1.8 MHz DIDSON, 18 have used 1.8 MHz ARIS, and 12 have used 3.0 MHz ARIS (Table 2; "Sonar" column, keyword: "MHz").

The ability to resolve multiple targets at a fine spatial scale is important for differentiating various groups within ensonified assemblages or communities and for observing and quantifying individual, or collective behavioural patterns in gregarious species (Handegard *et al.*, 2012; Rieucau *et al.*, 2015, 2016, 2017b). The relatively high downrange resolution not

Table 1. A summary of the technical specifications for imaging sonars of at least 0.7 MHz for reference among key acquisition parameters from past studies or planning new ones. Range resolution decreases with increasing frame rate and distance due to the additional time required to send and receive the acoustic signal and transmit the imagery over ethernet, so they are often fixed relative to one another. The vertical width of the beam array, or FOV, is the same as the vertical aperture for these 2-dimensional sonars and can be adjusted using accessory lenses. The 3-dimensional Ecoscope PIPE CIVS is an exception. Models developed for shallow-water, recreational fish finding that require proprietary chart-plotter interfaces, and have non-submersible transceivers, but which could be useful for research include the Panoptix LiveScope, Hummingbird MEGA Live, and ActiveTarget series. Unspecified values are listed as "UNS" and models out of production are marked "OOP".

Sonar model	Frequency (MHz)	Beam number	Horizontal beam width (°)	Vertical FOV (°)	Beam spacing (°)	Horizontal FOV (°)	Nominal range; depth range (m)	Range resolution (mm)	Frame rate (frames s^{-1})
Micron Gemini	0.72	128	0.7	20	UNS	90	50; 300	8–UNS	UNS
Gemini 720ik 360°	0.72	1 536	1.0	20	UNS	360	120; 300	4–UNS	UNS
ActiveTarget	0.8	UNS	UNS	UNS	UNS	UNS	UNS; not submersible	UNS	UNS
Hummingbird MEGA Live	0.8	UNS	UNS	25	UNS	45	38; not submersible	UNS	UNS
BlueView-M	0.9	512	1.0	20	0.18	90	100; 1 000	13–UNS	UNS–25
BlueView-Mk2	0.9	768	1.0	12	0.18	130	100; 1 000	13–UNS	UNS–25
Simsonar (OOP)	1.0	96	UNS	20	UNS	130	UNS; 50	4–UNS	UNS
ARIS Defender, Explorer, and Voyager 1200	0.7 or 1.1	48	0.6 or 0.4	14	0.3 or 0.6	29	80 or 35; 100, 300, and 4 000	3–30 or 3–24	3–15 or 8–15
Imagenex	1.1	480	1.5	15	0.16	80	30; 300	1–60	3–40
Panoptix LiveScope	1.1	UNS	UNS	20	UNS	135	15; not submersible	UNS	UNS
Ecoscope PIPE CIVS	0.9–1.15	384 × 384 × 9	45	45	0.11 × 0.11	45	20; 40, 250, 600, or 3 000	16–UNS	5–50
DIDSON-LR (OOP)	0.7 or 1.2	48	0.6 or 0.4	14	0.6	29	80 or 35; 100, 300, and 4 000	20–160 or 5–40	2–21 or 4–21
Gemini 1200ik	0.72 or 1.2	512 or 1 024	0.25 or 0.12	20 or 12	0.18 or UNS	120	120 or 50; 350	4–UNS or 2.4–UNS	UNS
Oculus M750d	0.75 or 1.2	512	1.0 or 0.6	20	0.25	130	120 or 40; 500, 1 000, or 4 000	4–120 or 2.5–40	6–15
Flexview HF	0.7, 0.95, 1.2, or 1.4	256 or 512	1.0, 0.8, 0.65, or 0.55	30, 27, 21, or 18	0.55 or 0.27, 0.55 or 0.27, 0.29 or 0.15, and 0.12 or 0.06	140, 140, 75, or 45	100, 70, 50, or 30; 300	10–60, 10–30, 10–30, or 10–15	4–30, 2–30, 5.5–30, or 4.7–30
M3 HR	0.7, 0.95, 1.2, or 1.4	256 or 512	1.0, 0.8, 0.65, or 0.55	30, 27, 21, or 18	0.55 or 0.27, 0.55 or 0.27, 0.29 or 0.15, and 0.12 or 0.06	140, 140, 75, or 45	100, 70, 50, or 30; 300	10–60, 10–30, 10–30, or 10–15	4–30, 2–30, 5.5–30, or 4.7–30
DIDSON-Std (OOP)	1.1 or 1.8	48 or 96	0.4 or 0.3	14	0.6 or 0.3	29	35 or 15; 100, 300, and 4 000	10–80 or 2.5–20	4–21
ARIS Defender, Explorer, and Voyager 1800	1.2 or 1.8	96	0.4 or 0.3	14	0.3	29	35 or 15; 300; 100, 300, and 4 000	3–30 or 3–24	7–15 or 8–15
Oculus M1200d	1.2 or 2.1	512	0.6 or 0.4	20 or 12	0.25 or 0.16	130 or 60	40 or 10; 500, 1 000, or 4 000	2.5–40 or 2.5–10	6–15

Table 1. Continued

Sonar model	Frequency (MHz)	Beam number	Horizontal beam width (°)	Vertical FOV (°)	Beam spacing (°)	Horizontal FOV (°)	Nominal range; depth range (m)	Range resolution (mm)	Frame rate (frames s^{-1})
BlueView-130 M	0.9 or 2.25	768	1.0	20	0.18	130 or 90	100 or 10; 1 000	130–UNS or 6–UNS	UNS–25
Blueview-130 Mk2	0.9 or 2.25	768	1.0	12 or 20	0.18	130	100 or 10; 1 000	13–UNS or 6–UNS	UNS–25
Blueview-130/45 Mk2	0.9 or 2.25	768 or 256	1.0	12 or 20	0.18	130 or 45	100 or 10; 1 000	13–UNS or 6–UNS	UNS–25
Oculus M3000d	1.2 or 3.0	512	0.6 or 0.4	20	0.25 or 0.1	130 or 40	30 or 5; 500, 1 000, or 4 000	2.5–40 or 2–5	6–15
ARIS Defender, Explorer, and Voyager 3000	1.8 or 3.0	128	0.3 or 0.2	15	0.25	30	15 or 5; 300; 100, 300, and 4 000	3–19	6–15

Table 2. Notes from *in situ* studies of fish behaviour using imaging sonar. Unspecified information is marked, "UNS".

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Able *et al.* (2013)	Mobile 1.8 MHz DIDSON	424 138 m transects	All	Fish abundance, length, school frequency, size, and spacing; size-guild analysis; community composition	Habitat (distance to pier) and annual comparison, spatial and depth distribution; influences of diurnal patterns, tide, and light in an estuary in the USA (NY)	Mean from 2–3 independent manual counts; all occurrences transect^{-1} ($n = 424$); hooked-gear and net ground truth
Able *et al.* (2014)	Mobile 1.8 MHz DIDSON	114 5–30 s transects	All	Fish abundance and length; school frequency, size, spacing, and degree of order; swim direction, depth and milling activity; size-guild analysis; community composition; associations with debris	Spatial and depth distribution along an urban shoreline in an estuary in the USA (NY)	Mean from 2–3 independent manual counts; all occurrences transect^{-1} ($n = 114$); principal components analysis for behaviour-based identification net, visual observation, and trap ground truth
Accola *et al.* (2022a)	Mobile 1.8 MHz DIDSON	536 transects	All	Pacific salmon abundance	Habitat comparison and depth distribution; influence of light in an estuary in the USA (WA)	Manual; all occurrences transect^{-1} ($n = 536$); video ground truth
Accola *et al.* (2022b)	Mobile 1.8 MHz DIDSON	412 transects	All	Pacific salmon abundance	Habitat and annual or seasonal comparison, and depth distribution; influence of diurnal patterns and light in an estuary in the USA (WA)	Manual; all occurrences transect^{-1} ($n = 412$); no ground truth
Artero *et al.* (2021)	Stationary and mobile 0.9 MHz BlueView	24 h	All	Goliath grouper abundance and length	Habitat and annual or seasonal comparison, spatial distribution on the continental shelf of French Guiana	Manual; all occurrences 15-min deployment^{-1} ($n = 96$); hooked-gear ground truth
Auster *et al.* (2013)	Stationary 1.8 MHz DIDSON	3.2 h	All	Fish length; vertical distribution; size-guild analysis; community composition	Habitat comparison, spatial distribution, threat avoidance, predation, on the continental shelf of the USA (GA)	Manual; MeanN 12-min period^{-1} ($n = 16$); visual observation and video ground truth
Baumann *et al.* (2016)	Stationary 1.8 MHz DIDSON	8 h	1 min	Fish abundance	Habitat (artificial habitats and a control site) and annual or seasonal comparison in 2 lakes in the USA (NC)	Manual counts; MeanN of 2 summed sets of 4 random frames deployment^{-1} ($n = 60$); sub-sampling; no ground truth
Becker and Suthers (2014)	Stationary 1.8 MHz DIDSON	20 h	10 h	Fish abundance and 100 mm length classes; size-guild analysis; community composition	Habitat and annual or seasonal comparison, depth distribution; influence of diurnal patterns and in an estuary in Australia (NSW)	Manual; MeanN of 5 random 3-min intervals 30-min period^{-1} ($n = 40$); sub-sampling; no ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Becker *et al.* (2011a)	Stationary 1.8 MHz DIDSON	64 h	32 h	Fish abundance and 100 mm length classes; school size, frequency, and milling activity; fast or slow individuals, fast or slow schools, and feeding classes; size-guild analysis; community composition	Habitat comparison and spatial distribution; influence of turbidity in an estuary in South Africa	Manual; MeanN of 10 random 3-min intervals 60-min period^{-1} ($n = 64$); sub-sampling; net ground truth
Becker *et al.* (2011b)	Stationary 1.8 MHz DIDSON	120 h	60 h max counts; 36 h mean counts	Fish abundance and 100 mm length classes; school size, frequency and milling activity; fast or slow individuals, fast or slow schools, and feeding classes; size-guild analysis; community composition	Habitat comparison and predation; influence of diel cycles and diurnal patterns in an estuary in South Africa	Manual; MaxN of the first 30 min interval 60-min segment^{-1}; MeanN of the first 6, 3-min intervals 60-min period^{-1} ($n = 120$); sub-sampling; net ground truth
Becker *et al.* (2013a)	Stationary 1.8 MHz DIDSON	110 h	44 h	Fish abundances and 100 mm length classes; slow-meandering (milling), stationary, and rapid swimming classes; size-guild analysis; community composition	Influence of light at a dockside restaurant in an estuary in South Africa	Manual; MeanN of 8 random 3-min intervals 60-min period^{-1} ($n = 110$); sub-sampling; no ground truth
Becker *et al.* (2013b)	Stationary 1.8 MHz DIDSON	13 h 20 min	2 h 24 min	Fish abundance and 100 mm length classes; size-guild analysis; community composition	Threat avoidance; influence of short-term (within 20 min) and long-term (10-h day period) boat traffic disturbance in an estuary in South Africa	Manual; MeanN from 3 random 1-min intervals 20-min period^{-1} ($n = 40$); MeanN of 6 random 1-min intervals 30-min period^{-1} ($n = 27$); sub-sampling; no ground truth
Becker *et al.* (2016a)	Stationary 1.1 MHz DIDSON	60 h	All	Fish abundance and length classes; school frequency; movement into or out of the estuary;	Inlet passage; influence of diurnal patterns and incoming and outgoing flood and ebb tides at an estuary in Australia (NSW)	Manual; all occurrences 180-min deployment^{-1} ($n = 20$); no ground truth
Becker *et al.* (2016b)	Stationary 1.1 MHz DIDSON	20 h	All	Fish abundance and length; school frequency; swim direction	Inlet passage and depth distribution; influence of tide in an estuary in South Africa	Manual; all occurrences 60-min period^{-1} ($n = 20$); no ground truth
Becker *et al.* (2017)	Mobile 1.8 MHz DIDSON	6 h 6 min	All	Fish abundance and length; position in estuary; size-guild analysis; community composition	Spatial and depth distribution in an estuary in South Africa	Manual counts; MeanN of 3 upstream and 3 downstream 100-m distance intervals transect^{-1} ($n = 33$); no ground truth
Bennett *et al.* (2021)	Stationary 1.8 MHz DIDSON	37 h	All	Fish abundance and length	River passage; influence of diurnal patterns and tide in inland Australia (NSW)	Manual; all occurrences 180-min period^{-1} ($n = 16$); trapping and trawl ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Bevelhimer *et al.* (2017)	Stationary 1.8 MHz DIDSON	202 h + 1 h 52 min	All	Abundance and length; swim speed, direction, vertical distribution, change in range, body angle, tortuosity; community composition	Threat avoidance; influence of three turbine operation classes, ebb and flood tide, 3 current velocity classes, and comparison of manual and automated analyses at a tide-power turbine in an estuary in the USA (NY)	Manual and automated; all occurrences 60-min period^{-1} ($n = 202$) and normalized to the total per operating mode; no ground truth
Bilotta *et al.* (2011)	Stationary 1.8 MHz DIDSON	~3 672 h	All night data (~1836 h)	Nighttime European eel abundance and length	Spawning passage and interannual or seasonal comparison in a river in the UK (England)	Manual and semi-automated; all occurrences night^{-1} ($n = 152$); no ground truth
Bolland *et al.* (2019)	Stationary ARIS	353 h	345 h 18 min	European eel abundance; tactile and non-tactile responses, and retreat or passage through small- and large-diameter pump stations	Spawning passage and threat avoidance; influence of lunar phase and diurnal patterns and diel cycles at a power pump station in a river in the UK (England)	Manual; all occurrences day^{-1} ($n = 73$); fyke net, entrainment, and acoustic telemetry ground truth
Bolton *et al.* (2017)	Stationary 1.8 MHz DIDSON	241 h 30 min	All	Fish abundance and 200 mm length classes; community composition	Predation; influence of light, diel cycles, diurnal patterns, and atmospheric conditions at a wharf in an estuary in Australia (NSW)	Manual; MaxN counts 15-min period^{-1} ($n = 21$); video ground truth
Boswell *et al.* (2008)	Stationary 1.8 MHz DIDSON	12 h	6 h	Leatherjackets, ludernick, red morwong, wrasses, and yellowfin bream abundance and length; size-guild analysis;	Habitat comparison in an estuary, river, and water control structure in the USA (AL, AK, and LA, respectively)	Manual and semi-automated; MeanN of 4 evenly- distributed 30-min intervals 240 -min period^{-1} (60); manual and automated processing comparison and influence of sonar range on length measurement; sub-sampling; no ground truth
Boswell *et al.* (2019)	Stationary 1.8 MHz DIDSON	74 h	1 480 and 170 000 frames (~3 min 5 s and 5 h 54 min 10 s)	Fish density and ≥ (predator) or < 250 mm (prey) size classes; distance from sonar; community composition	Inlet passage, habitat comparison (channel and edge habitat), and spatial distribution; influence of diurnal patterns, tide, and water chemistry in an estuary in the USA (SC)	Manual and automated; MaxN of 10 random frames 15-min interval^{-1} 30 min period^{-1} ($n = 148$); sub-sampling; no ground truth
Boys *et al.* (2013)	Stationary 1.8 MHz DIDSON	3 h 40 min	22 min	Fish abundance and length; 5 rheotaxis classes; size-guild analysis; community composition	Threat avoidance (contact with irrigation pump screen at 2 operational speeds and 4 screen meshes); influence of current in a river in Australia (NSW)	Manual; all occurrences in 1-min intervals 10-min period^{-1} ($n = 22$); sub-sampling; electrofishing, seine, and entrainment ground truth
Braga *et al.* (2022)	Stationary 1.8 MHz DIDSON	420 h	15 h 36 min	Fish abundance	Influence of diel cycles, in a river in Brazil (MG)	Manual; all occurrences 3-min period^{-1} ($n = 8$ 400); analysis evaluation; sub-sampling; no ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Brien *et al.* (2021)	Stationary 0.72 MHz Gemini	2 h	All	Saltwater crocodile abundance; swimming direction and milling activity	Gear evaluation assessing video detection of submerged saltwater crocodiles in Australia (QL)	Manual; all occurrences deployment^{-1} ($n = 28$ events); video ground truth
Budnik and Miner (2017)	Stationary 1.8 MHz DIDSON	2 208 h	All	Stocked juvenile steelhead salmon abundance and length; swimming direction	River passage (emigration); influence of diurnal patterns, and photoperiod in a river in the USA (PA)	Manual; all occurrences 60-min period^{-1} ($n = 2$ 208); electrofishing ground truth
Capoccioni *et al.* (2019)	Stationary 0.9 MHz BlueView	413 h	383 h	Nighttime fish abundance and length; small and large school (5–9 and $\geq$ 10 fish) frequencies	Inlet passage and interannual or seasonal comparison; influence of tide and water chemistry in an estuary in Italy	Automatic; all occurrences 60-min period^{-1} ($n = 383$); no ground truth
Chang *et al.* (2017)	Stationary 1.8 MHz ARIS	180 h	All	Chinese sturgeon abundance and length; pairing, and distance among individuals; vertical distribution	Spawning passage, interannual or seasonal comparison and depth distribution; influence of diurnal patterns, current, discharge and water chemistry in a river in China (HE)	Manual; all occurrences 60-min period^{-1} ($n = 180$); no ground truth
Cheng *et al.* (2022)	Stationary1.1 and 1.8 MHz DIDSON	100	All	Bull trout and sockeye salmon abundance and length; swim direction	Habitat comparison, threat avoidance, and predation; influence of diurnal patterns, threat avoidance, predation in a lake in the USA (WA)	Manual; all occurrences 30-min period^{-1} ($n = 200$); no ground truth
Crossman *et al.* (2011)	Stationary 1.1 MHz DIDSON	UNS	All	White sturgeon abundance and length; swim direction and distance from sonar	Spawning passage and interannual or seasonal comparison; influence of discharge in a river in the Canada (BC)	Manual; all occurrences 60-min period^{-1} ($n =$ UNS); hooked gear ground truth
Cupp *et al.* (2018)	Stationary 3.0 MHz ARIS	96 h	All	Fish abundance; swim direction	Inlet passage and threat avoidance; Influence of discharge, water chemistry, and deterrence by CO^2 release in a river in the USA (IL)	Manual; all occurrences 60-min period^{-1} ($n = 96$); no ground truth
Davis *et al.* (2016)	Stationary 3.0 MHz ARIS	~25 min	5 frames (~1 s)	Marked golden shiner and bycatch abundance	River passage and threat avoidance; entrainment, retention, and transport of fish through electrical barrios within barge junction gaps in a river in the USA (IL)	Manual; MaxN of a single frame following cast net sampling ($n = 5$); net and mark-and-recapture ground truth
Doehring *et al.* (2011)	Stationary 1.8 MHz DIDSON	49 h	All	Juvenile whitebait abundance; swim direction	Spawning passage and movement at gated and ungated culverts; influence of lunar phases, diel cycles, and tide at a river mouth in New Zealand	Manual; all occurrences 5-min period^{-1} ($n = 588$); visual observation ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Dos Sanos *et al.* (2017)	Mobile 0.9 MHz BlueView	0.43 min	All	Fish abundance	River in Brazil (RS)	Manual and automated; all occurrences frame^{-1} ($n = 257$); analysis evaluation comparing manual and automated counts; no ground truth
Egg *et al.* (2017)	Stationary 1.8 MHz ARIS	157 h 45 min	All	European eel abundance; swim direction; community composition	Spawning passage and habitat comparison; influence of lunar phase, diurnal patterns, light, tide, current or flow, and opening width under a hydroelectric plant sluice gate in a river in Germany	Manual; mean of 4 independent counts; all occurrences 15-min period^{-1} ($n = 631$); no ground truth
Egg. *et al.* (2018)	Stationary 3.0 MHz ARIS	40 h 30 min	All	Fish abundance and length; swim direction; size-guild analysis; community composition	River passage and gear evaluation comparing stow nets and video to sonar in a river in Germany	Manual; all occurrences and all occurrences with visible tail-beat patterns 45-min period^{-1} ($n = 54$); stow net and video ground truth
Egg *et al.* (2019)	Stationary 1.8 MHz ARIS	9 h	All	Fish abundance and length; large deep-bodied, small deep-bodied, large streamlined, and small, streamlined fish body classes; swim direction; fish passage attempts and events; size-guild analysis; community composition	River passage and thread avoidance; deterrence effects of electricity at a dike pumping station in Germany	Semi-automated; all occurrences 15-min period^{-1} ($n = 36$); no ground truth
Eggleston *et al.* (2020)	Stationary 1.8 MHZ DIDSON	718	35	Fish abundance, swim direction, milling activity	River passage, analysis evaluation at a water control structure in the USA (OH)	Manual and automated; all occurrences 60-min period^{-1} ($n = 35$) and all occurrences 2-min interval^{-1} 6-min period^{-1} ($n = 136$); analysis evaluation comparing manual and automated counts; sub-sampling; no ground truth
Faulkner and Maxwell (2020)	Stationary0.7, 1.1, 1.2, and 1.8 MHz DIDSON	1107 h 7 min 12 s	184 h 31 min 12 s	Sockeye salmon abundance and length; swim direction	Spawning passage, habitat and interannual or seasonal comparison; influence of diel cycles and tide in a river in the USA (AK)	Manual; all occurrences in 10-min interval^{-1} 60-min period^{-1} ($n = 185$); sub-sampling; visual observation ground truth
Francisco *et al.* (2022)	Stationary 0.9 MHz BlueView	69 h 20 min	All	Fish, seal, and cetacean abundance and length; school size and frequency; swim speed, direction; community composition	Diurnal patterns, diel cycle, and predation at a nearshore wave-power station in Sweeden	Manual and automated; all occurrences deployment^{-1} ($n = 240$); analysis evaluation for automatic classification of broad taxonomic groups; no ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Frias-Torres and Luo (2009)	Stationary 1.8 MHz DIDSON	1 h 43 min 30 s	1 h 4 min 30 s	Atlantic goliath grouper abundance and length	Habitat comparison (coastal mangrove and overhanging habitats) and gear evaluation comparing video and imaging sonar; influence of turbidity along shorelines of the USA (FL)	Manual; all occurrences 5-min period^{-1} ($n = 14$); visual observation and video ground truth
Fujimori *et al.* (2018)	Stationary 1.1 and 1.8 MHz DIDSON	5 + 5 h	All	Nighttime Kuril harbor seal abundance and length; swim speed	Predation; gear evaluation of seal interactions with a set net in nearshore coastal waters of Japan	Manual; all occurrences 15-min period^{-1} ($n = 40$); video ground truth
Giorli and Au (2017a)	Stationary 1.8 MHz DIDSON	4 h	All	Sperm whale prey abundance and length; vertical distribution	Habitat comparison and depth distribution; sperm whale deep-sea scattering layer foraging and control sites; depth in water column in the open ocean; USA (HI)	Manual; all occurrences 20-min deployment^{-1} ($n = 12$); hydrophone ground truth
Giorli and Au (2017b)	Stationary 1.8 MHz DIDSON	10 h	All	Sperm whale prey abundance and length; vertical distribution	Habitat comparison, depth, and interannual or seasonal distribution; sperm whale deep-sea scattering layer foraging sites, depth in water column, and monthly temporal differences in the open ocean; USA (HI)	Manual; all occurrences 20-min deployment^{-1} ($n = 30$); hydrophone ground truth
Giorli *et al.* (2018)	Stationary 1.8 MHz DIDSON	25 h	All	Fish and invertebrate abundance and length	Habitat and interannual or seasonal comparison, and depth distribution (of deep-sea scattering layer); influence of diurnal patterns in the open ocean; USA (HI)	Semi-automated; all unidirectional occurrences 20-min deployment^{-1} ($n = 75$); no ground truth
Godinho *et al.* (2017)	Mobile 1.8 MHz DIDSON	40 min	All	Zulega abundance and length; school size and spacing; swim direction; community composition	Spawning and spatial distribution; impacts of discharge and water level in a river in Brazil (BA)	Manual; all occurrences 40-min survey^{-1}; hydrophone ground truth
Grabowski *et al.* (2012)	Mobile 1.8 MHz DIDSON	7 h 40 min + 1 min 59 s	All	Atlantic cod abundance and length; school size and spacing; swim speed, and vertical distribution	Habitat comparison and depth distribution of 3 Atlantic cod spawning aggregations on the continental shelf of Iceland	Manual; MaxN at each of 3 sites ($n = 3$); gill net and video ground truth
Grote *et al.* (2014)	Stationary 1.8 MHz DIDSON	1301 h	65 h	River herring, shad, and salmon abundance and length; movement patterns; community composition	Spawning passage and interannual or seasonal comparison; influence of diel cycle and water chemistry near a hydroelectric dam in a river in the USA (ME)	Manual; all occurrences 30-s interval^{-1} 10-min period^{-1} ($n = 7\,800$); sub-sampling; electrofishing and trap ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Grothues *et al.* (2016)	Mobile 1.8 MHz DIDSON	18 h 15 min	All	Small (< 250 mm) and large (> 250 mm) fish abundance and length; size-guild analysis; community composition	Habitat comparison; influence of diurnal patterns in an estuary in the USA (NY)	Manual; mean from 2 independent counts; all normalized occurrences transect^{-1} ($n = 219$); cast net, gill net, and hooked-gear ground truth
Gurney *et al.* (2014)	Stationary 1.8 MHz DIDSON	9 960 h	All	Atlantic salmon and brown trout abundance and length; swim direction; community composition	Spawning passage in a river in Ireland	Semi-automated; all occurrences moving upstream normalized for the study period; hooked-gear ground truth
Gutiérrez-Estrada *et al.* (2022)	Stationary 1.1 MHz LiveScope	6 h 30 min	All	Gilt-head seabream abundance and length	An aquaculture salt pond in Spain	Manual; MeanN 5-min-period^{-1} ($n = 78$); stocked pond ground truth
Han and Uye (2009)	Mobile 1.8 MHz DIDSON	40 min	All	Moon jellyfish medusae abundance and width	Spatial and depth distribution; influence of water chemistry in a brackish lake in Japan	Manual; MeanN of 6 10-s intervals 1-min period^{-1} ($n = 40$); towed net ground truth
Han *et al.* (2009a)	Stationary 1.8 MHz DIDSON	40 min	All	Japanese amberjack abundance and length	An aquaculture net pen in Japan	Manual and automated; all occurrences deployment^{-1} ($n = 4$); analysis evaluation comparing manual and automated counts; video ground truth
Han *et al.* (2009b)	Stationary 1.8 MHz DIDSON	10 min	All	Ayu abundance and length	Spawning passage in a river in Japan	Automated; all occurrences 1-min interval^{-1} ($n = 10$); video ground truth
Handegard and Williams (2008)	Mobile 1.1 and 1.8 MHz DIDSON	184 frames (31 s) + 174 frames (22 s) + 409 frames (58 s)	All	Gulf menhaden and spotted seatrout abundance and length; school size, frequency, and spacing; swim speed, direction, reaction speed and direction, vertical distribution, body angle, tortuosity	Threat avoidance; gear evaluation of movement within a trawl on the continental shelf of the USA (AK)	Manual and automated; all occurrences dataset^{-1} ($n = 3$); analysis evaluation comparing manual and automated counts; trawl ground truth
Handegard *et al.* (2012)	Stationary 1.8 MHz DIDSON	2 h	All	Gulf menhaden and spotted seatrout abundance and length; school size, frequency, and school spacing; swim speed, direction, vertical distribution; information transfer, and collective response within Gulf menhaden schools to spotted seatrout predation; spotted seatrout spacing and orientation relative to Gulf menhaden prey schools	Threat avoidance and predation; influence of decreasing school size and reduced information transfer on predation risk within an estuary in the USA (LA)	Manual and semi-automated; manual identification of all schools and individuals deployment^{-1}; automated optical flow school velocities; seine and fyke net ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Handegard *et al.* (2017a)	Stationary 1.8 MHz ARIS	32 min	24 min	Atlantic mackerel school size and spacing; swim speed, direction, and body angle; predator response classes (0–4)	Habitat comparison, threat avoidance and predation; influence of water chemistry; gear evaluation assessing density and decreased dissolved oxygen effects and response to a predator model within a purse seine in an estuary in Norway	Manual and automated; MeanN of 4 10-s intervals 1-min period^{-1} ($n = 36$); 3 independent manual response classes; automated optical flow school velocities; net pen ground truth
Hayes *et al.* (2015)	Mobile 1.1 MHz DIDSON	75 h	All	Brown trout abundance and length; swim direction	Spawning passage and threat avoidance to vessel traffic; Gear evaluation comparing video and diver survey counts to sonar counts in a river in New Zealand	Mean from 2–3 independent manual counts; all occurrences 60-min period^{-1} ($n = 75$); drift dive ground truth
Helminen and Linnansaari (2021)	Stationary 1.1 MHz ARIS	48 h	All	Atlantic salmon abundance and length; swim speed, direction, reaction speed or direction, milling activity and tortuosity	River passage in Canada (NB)	Manual and automated; all occurrences 15-min period^{-1} ($n = 192$); analysis evaluation comparing manual and automated counts; no ground truth
Helminen *et al.* (2021)	Stationary 1.8 MHz DIDSON	UNS	All events	American shad, Atlantic salmon, and striped bass abundance; reaction speed or direction, and tortuosity	An experimental pond in Canada (NB)	Manual and automated; all occurrences transect^{-1} ($n = 150$); analysis evaluation comparing manual and automated length measurements and species identification using tail-beat patterns
Hightower *et al.* (2013)	Stationary 1.8 MHz DIDSON	10 min 39 s	All	Atlantic sturgeon, channel catfish, striped bass, and white perch abundance and length; community composition	An aquaculture pond in the USA (DE)	Manual and automated; all occurrences deployment^{-1}; analysis evaluation comparing manual and automated length measurement; net pen ground truth
Holmes *et al.* (2006)	Stationary 1.8 MHz DIDSON	12 and 240 h	All	Sockeye salmon abundance; swim direction	Spawning passage; methods evaluation comparing visual field- and imaging-sonar-based counts at unconstrained and constrained observation points in a river in Canada (BC)	Manual; all occurrences 30-min period^{-1} ($n = 480$); visual observation ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Hughes and Hightower (2015)	Stationary 1.8 MHz DIDSON	1 268 h	All	Alewife, American shad, blueback herring, hickory shad, striped bass, white perch abundance and length; community composition	Spawning passage and interannual or seasonal comparison in a river in the USA (NC)	Manual and automated; all occurrences 5-min period^{-1} ($n = 15\ 216$); analysis evaluation comparing manual and automated counts; electrofishing and gill net ground truth
Hwang *et al.* (2017)	Stationary 1.1 and 1.8 MHz DIDSON	3 h	All	Nighttime hairtail abundance and length; swim direction, body angle, and tortuosity	Gear evaluation assessing the effect of hairtail length and swimming angle on echosounder target strength on the continental shelf of South Korea	Manual; all occurrences deployment^{-1}; no ground truth
Izzo *et al.* (2022)	Stationary 1.1 MHz DIDSON	2046 h	All	Lake sturgeon abundance and length; swim direction	Spawning passage, interannual or seasonal comparison; influence of discharge, analysis evaluation in a river in the USA (VT)	Manual; all occurrences day^{-1} ($n = 85$); analysis evaluation; acoustic telemetry ground truth
Jiang *et al.* (2012)	Mobile 1.8 MHz DIDSON	36 h	All	Chinese sturgeon abundance	Spawning passage and interannual or seasonal comparison; influence of water chemistry and effect of dam impoundment in a river in China (HE)	Manual; all occurrences year^{-1} ($n = 3$); gill net and hooked gear ground truth
Jing *et al.* (2017)	Mobile 1.8 MHz DIDSON	206 107 frames (~8 h 10 min 44 s)	144 + 214 frames (~51 s)	Fish abundance	Spatial and depth distribution in a reservoir in China (SH)	Manual and automated; all occurrences transect^{-1} ($n = 32$); analysis evaluation comparing manual and automated counts; sub-sampling; no ground truth
Jing *et al.* (2018a)	Mobile 1.8 MHz ARIS	8 h 10 min 48 s	0.01	Fish abundance; swim speed, direction, vertical distribution, body angle	Spatial and depth distribution in a reservoir in China (SH)	Manual and automated; all occurrences frames^{-1} ($n = 4\ 800$); analysis evaluation comparing manual and automated counts from a mobile platform; no ground truth
Jones *et al.* (2021)	Stationary 3.0 MHz ARIS	10 h	All	Common smooth-hound, European plaice, European seabass, European spiny lobster, small-spotted catshark, thick-lipped mullet, and thornback ray abundance and length; community composition	A bay in the UK (England)	Manual; all occurrences 60-min deployment^{-1} ($n = 10$); analysis evaluation of inter-annotator error; video ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Jones and Petreman (2015)	Stationary 0.7 and 1.2 MHz DIDSON	1644 h + 1644 h	264 h + 480 h	Salmonid abundance and length; swim speed, direction, and distance from sonar	Spawning passage and interannual or spatial comparison; influence of diurnal patterns, diel cycles, water chemistry, discharge, and current in a hydropeaking river in Canada (ON)	Automated; all occurrences 15-min period^{-1} ($n = 2$ 016); no ground truth
Jůza *et al.* (2013)	Mobile 1.8 MHz DIDSON	2 h	All	Nighttime fish abundance and length; swim direction; trawl attraction and avoidance behaviour	Threat avoidance; gear evaluation of electrified trawl selectivity for 3 electricity modes in a lake in Austria	Manual; all occurrences 1-min period^{-1} ($n = 120$); trawl ground truth
Kang (2011)	Stationary 1.8 MHz DIDSON	23 h 50 m 55 s	All	Quinnat salmon abundance and length; swim speed, direction, vertical distribution, and tail-beat frequency	River passage, habitat comparison, and depth distribution in New Zealand	Semi-automated; all occurrences normalized; analysis evaluation comparing manual and automated length measurement and behavioural classification; no ground truth
Kang *et al.* (2020)	Stationary 0.9 MHz BlueView	52 h	All	Fish abundance and length; swim direction, vertical distribution, body angle	Influence of diel cycle; gear evaluation of a set net in South Korea	Automated; all occurrences 60-min period^{-1} ($n = 52$); no ground truth
Keefer *et al.* (2017)	Stationary 1.8 MHz DIDSON	228 h	11 h 30 min	Pacific lamprey abundance; swim direction and milling activity; parasitic attachment events	River passage and movement either side of a dam powerhouse and fishways in a river in the USA (WA)	Manual from 6 reviewers; all occurrences 10-min period^{-1} ($n = 69$); analysis evaluation of inter-annotator error; sub-sampling; no ground truth
Kerschbaumer *et al.* (2020)	Mobile 1.1 MHz ARIS	9 h	All	Fish abundance and length; community composition	Habitat and seasonal comparison; influence of spatial distribution, and current; gear evaluation assessing the effectiveness of electrofishing in a river in Austria	Manual; all occurrences deployment^{-1} ($n = 1$); analysis evaluation; electrofishing ground truth
Kimball *et al.* (2010)	Stationary 1.8 MHz DIDSON	31 h	2 h	Fish abundance and length; milling activity	Inlet passage and interannual or seasonal comparison; influence of diel cycle, tide, and slot width on fish movement through, and behaviour around, an estuary water control structure in the USA (LA)	Semi-automated; all occurrences in 4 random intervals 5-min period^{-1} for each of 6 tide stages ($n = 24$); sub-sampling; cast net and gill net ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Kimball *et al.* (2015)	Stationary 1.8 MHz DIDSON	48 h	12 h	Fish abundance and length; swim direction and milling activity	Inlet passage and habitat comparison; influence of diurnal patterns, water chemistry and current at an estuary water control structure in the USA (LA)	Manual; all occurrences 5-min random interval^{-1} ($n = 216$); sub-sampling; cast net and gill net ground truth
Kirk *et al.* (2015)	Stationary 1.8 MHz DIDSON	528 h 54 min	178 h 42 min	Pacific lamprey and white sturgeon abundance and length; swim speed, direction, reaction speed or direction, vertical distribution, tortuosity, tail-beat frequency	River passage, habitat and, interannual or seasonal comparison, and predation; depth distribution, predation at a river dam fishway in the USA (WA)	Manual; all occurrences 10-min random interval^{-1} ($n = 1\,072$); sub-sampling; no ground truth
Kruusmaa *et al.* (2016)	Stationary 3.0 MHz ARIS	12 min 30 s	12 min 30 s	Atlantic mackerel swim direction and reaction speed or direction	Threat avoidance and predation; response to size, speed, and tail-beat activity of a robotic fish in an aquaculture net pen in an estuary in Norway	Manual; all occurrences trial^{-1} ($n = 10$); net pen ground truth
Lagarde *et al.* (2020)	Stationary 1.8 MHz ARIS	2 833 h	14 h 30 min	European eel abundance and length; swim direction	Inlet passage in an estuary in France	Manual; all occurrences 15-min random interval^{-1} ($n = 58$); analysis evaluation of inter-annotator error; sub-sampling; net ground truth
Lagarde *et al.* (2021)	Stationary 1.8 MHz ARIS	12 552 h	3 408 h	European eel abundance and length; swim direction	Spawning passage and interannual or seasonal comparison; diurnal patterns, diel cycle, discharge, current, water chemistry, and atmospheric conditions in an estuary inlet in France	Manual; all occurrences 360-mini random interval^{-1} ($n = 508$); net ground truth
Langkau *et al.* (2016)	Stationary 1.1 and 1.8 MHz DIDSON	12 h	All	Allis shad abundance	Spawning behaviour in a river in France	Manual; all occurrences 30-min period^{-1} ($n = 24$); hydrophone ground truth
Lankowicz *et al.* (2020)	Mobile 1.8 and 3.0 MHz ARIS	32 h	All	Forage fish abundance and length; community composition	Habitat (creek and river channel) and interannual or seasonal comparison, spatial and depth distribution (2-m depth strata from < 2 to >22 m) in an estuary in the USA (MD)	Manual: MeanN 7.5-m distance interval^{-1} ($n = 115\,200$); no ground truth
Lenihan *et al.* (2019)	Stationary 1.1 MHz DIDSON	672 h	All	Nighttime European eel abundance and length; swim speed, direction, tortuosity	Spawning passage; influence of discharge and current in a river in Ireland	Manual; all occurrences 60-min period^{-1} ($n = 672$); set net ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
LeRoy *et al.* (2019)	Stationary 1.1 MHz DIDSON	79 transects at 1.5 m s^{-1}	All	Fish abundance; swim direction	River passage, habitat and interannual comparison, and threat avoidance; influence of large vessel and discharge on an electric fish-passage barrier in the USA (IL)	Manual; mean from 3 manual counts; all occurrences transect^{-1} ($n = 79$); electrofishing ground truth
Lilja *et al.* (2008)	Stationary 1.8 MHz DIDSON	104 h	All	Sockeye salmon abundance; swim direction	Spawning passage and minimum sampling effort required to measure escapement in a river in Canada (BC)	Manual: all occurrences 10-min period^{-1} for the first 20 min h^{-1} ($n = 208$); analysis evaluation of optimal sampling rate; visual observer ground truth
Lin *et al.* (2016)	Stationary 0.7 MHz DIDSON	24 h	All	Fish abundance and length; distance from sonar, swim speed, direction, distance from sonar, body angle, and tortuosity	Influence of diel cycle; gear evaluation comparing EY60 echosounder measurements in a river in China (SC)	Manual; all occurrences deployment^{-1} ($n = 1$); gill net ground truth
MacNamara and McCarthy (2014)	Stationary 1.1 MHz DIDSON	224 h	74 h 40 min	Nighttime European eel abundance and length; swim direction	Spawning passage and interannual or seasonal comparison in a river in Ireland	Manual; all occurrences 20-min interval^{-1} 60-min period^{-1} ($n = 224$); sub-sampling; net and mark and recapture ground truth
Magowan *et al.* (2012)	Stationary 1.8 MHz DIDSON	42 h	All	American eel, river herring, and other fish abundance and length; swim direction	River spawning passage; diurnal patterns, and diel cycle in a river in Ireland	Manual and automated; all occurrences 10-min period^{-1} ($n = 252$); analysis evaluation comparing manual and automated counts; visual observation ground truth
Makabe *et al.* (2012)	Mobile 1.8 MHz DIDSON	417 000 frames (~12 h 52 min 12 s)	4 170 frames (~7 min 43 s)	Moon jellyfish medusae abundance and diameter; vertical distribution	Interannual or seasonal comparison, spatial, and depth distribution; influence of water chemistry in a brackish lake in Japan	Manual; MaxN 1-frame^{-1} 100-frame period^{-1} ($n = 4$ 212); assessment of detection capability; sub-sampling; plankton net ground truth
Marras *et al.* (2015)	Mobile 1.1 and 1.8 MHz DIDSON	108	All	Sailfish and round sardinella abundance and length; swim speed and tailbeat frequency	Predation in continental shelf waters of Mexico	Manual; all occurrences 360-min period^{-1} ($n = 18$); visual observation and video ground truth
Martignac *et al.* (2021)	Stationary 1.8 MHz DIDSON	8 h	All	Fish abundance and length; swim speed, direction, milling activity, and body angle	River passage in France	Manual and automated; all occurrences 30-min period^{-1} ($n = 16$); analysis evaluation evaluating Sonar5Pro automated processing; no ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Maxwell and Gove (2007)	Stationary 1.8 MHz DIDSON	10 h	All	Sockeye salmon abundance; school size, frequency, spacing; swim direction	Spawning passage; influence of turbidity; gear and methods evaluation of echosounder, video, and visual observation in rivers of the USA (AK, WA)	Manual; all occurrences 15-min period^{-1} ($n = 40$); visual observation and video ground truth
Maxwell *et al.* (2019)	Stationary 1.1 and 1.8 MHz DIDSON	UNS	17%	Chinook salmon abundance and length; swim direction and vertical distribution	Spawning passage, and comparison, and depth distribution in a river in the USA (AK)	Manual; all occurrences 10-min interval^{-1} 60-min period^{-1} ($n =$ UNS); sub-sampling; gillnet and acoustic telemetry ground truth
McCarthy *et al.* (2014)	Stationary 1.1 MHz DIDSON	560 h	280 h	Nighttime European eel abundance; swim direction	Spawning passage, habitat, and interannual or seasonal comparison; influence of discharge; escapement from 2 hydro-electric power stations and net fishing with trap-and-transport assistance; gear evaluation of capture efficiency at a fishing weir, in a river in Ireland	Manual; all occurrences alternating 10-min interval^{-1} ($n = 1\,680$); sub-sampling; various nets, trap, and acoustic telemetry ground truth
McCauley *et al.* (2014)	Stationary 1.8 MHz DIDSON	443 h	All	Manta ray abundance and length; swim direction	Inlet passage; influence of diurnal patterns, diel cycle, and tide in a coastal lagoon in the USA (Palmyra Atoll)	Manual; all occurrences 60-min period^{-1} ($n = 443$); video ground truth
McCauley *et al.* (2016)	Stationary 1.8 MHz DIDSON	443 h	All	Shark abundance and length; swim direction	Inlet passage; diurnal patterns, diel cycle, and tide in a coastal lagoon in the USA (Palmyra Atoll)	Manual; all occurrences 60-min period^{-1} ($n = 443$); no ground truth
Mizuno *et al.* (2013)	Mobile 1.8 MHz DIDSON	1 h 31 min 12 s	All	Whooping swan predation marks on sacred lotus	Depth distribution and predation in a pond in Japan	Manual; all occurrences survey^{-1} ($n = 1$); visual observation and video ground truth
Mizuno *et al.* (2016)	Stationary 1.8 MHz DIDSON	20 h	All	Crayfish and Japanese mysterysnail abundance; movement speed, foraging activity	Habitat comparison (planted vs. natural area), spatial distribution, and predation; influence of diel cycle in a pond in Japan	Semi-automated; all occurrences 60-min period^{-1} ($n = 20$); no ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Mora *et al.* (2015)	Mobile 1.1 MHz DIDSON	18 h 30 min	All	Green sturgeon abundance	Spawning passage and spatial distribution in a river in the USA (OR)	Mean of 3 manual counts; all occurrences 30 min period^{-1} ($n = 40$); gill net, PIT tag, and mark-and-recapture ground truth
Mora *et al.* (2018)	Mobile 1.1 MHz DIDSON	750 UNS transects	All	Green sturgeon abundance	Spawning passage and interannual or seasonal comparison in a river in the USA (CA)	Manual: all occurrences transect^{-1} ($n = 750$); video and acoustic telemetry ground truth
Mueller *et al.* (2008)	Stationary 1.8 MHz DIDSON	23 h	All	Nighttime American eel and floating debris abundance; swim direction	Spawning passage past a hydroelectric power station intake canal in a river in the USA (ME)	Manual and automated; all occurrences dataset^{-1} ($n = 187$ events); analysis evaluation comparing manual and automated counts; no ground truth
Mueller *et al.* (2010)	Stationary 1.2 and 1.8 MHz DIDSON	UNS	All	Chinook salmon, sockeye salmon and American eel abundance and length; swim speed, direction, reaction speed or direction, tortuosity, and tail-beat frequency; community composition	Spawning passage; influence of tide in 2 rivers in the USA (AK)	Manual; all occurrences dataset^{-1} ($n = 97$ events); analysis evaluation of tail-beat frequency; species-level identification using length, schooling behaviour, and tail-beat frequency; fish wheel catch ground truth
Munroe *et al.* (2020)	Stationary and mobile UNS DIDSON	11 h 36 min + 13 min 30 s	All	Single and amplexus (mating) horseshoe crab abundance and width; swim speed, direction, body angle, and tortuosity	Spawning behaviour and habitat comparison (at and inshore of an oyster farm) in an estuary in the USA (DE)	Manual; all occurrences 10-min period^{-1} ($n = 709$); visual observation ground truth
Nelson *et al.* (2021	Stationary 3.0 MHz ARIS	128 h	All	Fish abundance	Depth distribution; influence of diurnal patterns, light, and predation in a river in the USA (CA)	Automated; all occurrences 10-min period^{-1} ($n = 1$ 056); hooked-gear and tether ground truth
Nelson *et al.* (2022)	Stationary 3.0 MHz ARIS	176 h	All	Rainbow trout abundance and length	Habitat comparison; influence of diurnal patterns, diel cycle, light, current, predation in an estuary in the USA (CA)	Automated; all occurrences 30-min period^{-1} ($n = 256$); hooked-gear, visual observation video, and tethering ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Nichols *et al.* (2014)	Stationary 1.8 MHz DIDSON	24 + 48 h	32 h	Bluefish, gray seal, and longfin inshore squid abundance	Influence of diurnal patterns, diel cycle, light, current, and predation in a fishing weir in nearshore continental shelf waters of the USA (MA)	Manual: all occurrences 5-min interval^{-1} 30-min period^{-1} ($n = 144$); sub-sampling; video ground truth
Nyqvist *et al.* (2017)	Stationary 1.0 MHz Simsonar	336 h	All	Atlantic salmon abundance and length; swim direction and vertical distribution	Spawning passage and interannual or seasonal patterns; influence of diurnal patterns and threat avoidance at a turbine at a river in Sweeden	Manual; all occurrences ($n = 430$ events); net and acoustic telemetry ground truth
O'Connell *et al.* (2014)	Stationary 1.8 MHz ARIS	6 h	All	Bull shark, nurse shark, great barracuda, lemon shark, and yellow stingray abundance and length; swim direction and distance from sonar	Inlet passage, habitat comparison, threat avoidance, and predation; influence of light; methods evaluation assessing visual observer counts of deterrence events at magnetic barrier and effects of high and low light intensity at a coastal pier in the Bahamas	Manual; mean of 3 counts; all occurrences 30-min trial^{-1} ($n = 12$); video and visual observation ground truth
Ogburn *et al.* (2017)	Stationary 1.8 MHz DIDSON	344 h	All	Alewife and blueback herring abundance and length; swim direction	Spawning passage and interannual or seasonal comparison; influence of diel cycle, discharge and water chemistry in a coastal stream in the USA (MD)	Manual: all occurrences random 10-min interval^{-1} 60—min period^{-1} ($n = 344$); electrofishing and trap ground truth
Parker *et al.* (2015)	Mobile 1.8 MHz DIDSON	4 h 19 min	All	Gizzard shad incapacitation; swim direction	Inlet passage, habitat, and interannual or seasonal comparison; influence of water chemistry; distance into electric barrier system and season in a ship canal in the USA (IL)	Manual; mean of 2 counts; all occurrences trial^{-1} ($n = 10$); net, video, and caged fish ground truth
Parker *et al.* (2016)	Stationary 1.8 MHz DIDSON	53 h 20 min + 53 h 20 min	All	Fish abundance and length; school frequency and mean length; swim speed, direction, reaction speed or direction, and 4 activity classes (including milling)	Inlet passage, habitat and interannual or seasonal comparison, spatial distribution, and threat avoidance; distribution within an electric dispersal barrier in a ship canal in the USA (IL)	Manual; mean of 2 counts; all occurrences 10-min period^{-1} (n = 640); electrofishing ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Patrick *et al.* (2014)	Stationary 1.8 MHz DIDSON	1 152 h	51 h	Alewife and large predator abundance and length classes; swim direction, and reaction speed or direction classes; community composition	Habitat and interannual or seasonal comparison, threat avoidance and predation; influence of diurnal patterns Responses inside and outside of fish diversion system at a nuclear generation station intake in a lake in Canada (ON)	Manual; all observations 60-min interval^{-1} day^{-1} ($n = 51$); sub-sampling; entrainment, gill net and video ground truth
Patrick *et al.* (2015)	Stationary 1.1 MHz DIDSON	Sampled for 3 d	Qualitative	Fish swim direction and qualitative interactions	Interannual or seasonal comparison and threat avoidance; qualified observations at an electric cooling water intake in a lake in the USA (OH)	Manual; qualified observations; entrainment and net ground truth
Pavlov *et al.* (2009)	Stationary 0.7 and Mobile 1.2 MHz DIDSON	672 h + 15 h	All	Kamchatka steelhead abundance and length; swim direction	Spawning passage, habitat, and interannual or seasonal comparison and spatial distribution; influence of diel cycle in a river in Russia (KT)	Manual; all occurrences 60-min period^{-1} (stationary) ($n = 697$) or 1-km^{-1} (mobile); seine net ground truth
Petreman *et al.* (2014)	Stationary 0.7 and 1.2 MHz DIDSON	2 988 h + 2 988 h	2 h + UNS 3–24 h	Salmonid abundance and length; swim speed, and direction	Spawning passage, interannual or seasonal comparison in a river in Canada (ON)	Manual and automated; all occurrences 15-min period^{-1} ($n = 104$); analysis evaluation comparing manual and automated counts; comparing random, systematic, and automation-assisted sub-sampling; no ground truth
Pipal *et al.* (2012)	Stationary 1.8 MHz DIDSON	3 672 h	All	Steelhead abundance and length; school frequency, spacing; swim direction and milling activity; pairing and distinctive swimming patterns	Spawning passage and interannual or seasonal comparison; methods evaluation assessing visual observer counts in a creek in the USA (CA)	Semi-automated; all occurrences day period^{-1} ($n = 153$); net, visual observation and mark-and-recapture ground truth
Piper *et al.* (2018)	Stationary 1.8 MHz ARIS	2 h 40 min	All	Nighttime European eel abundance and length; swim direction, reaction speed or direction, milling activity; bank or turbine approaches (4 response classes)	Spawning passage, habitat, and interannual or seasonal comparison and threat avoidance; operation of an Archimedes-screw hydropower station in a river in the UK (England)	Manual; all occurrences min period^{-1} ($n = 300$); fyke net, visual observation, acoustic, and PIT tag ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Plumlee *et al.* (2020)	Mobile 1.8 MHz ARIS	3 h 15 min	3 min 54 s	Fish abundance	Habitat and interannual or seasonal comparison at concrete, oil platform, and shipwreck artificial reefs on the continental shelf of the USA (TX)	Manual: MeanN of 50 frames 5-min transect^{-1} ($n = 39$); sub-sampling; hooked gear and trap ground truth
Pratt *et al.* (2021)	Stationary 1.8 MHz ARIS	264	All	American eel abundance	River passage; gear evaluation assessing echosounder target estimates at a hydroelectric dam in a river in the USA (NY)	Automated; all occurrences ($n = 2$ events); analysis evaluation developing CNN automated classification distinguishing eels from sticks; no ground truth
Price *et al.* (2013)	Stationary 1.8 MHz DIDSON	3 h 12 min	All	Predator and prey fish abundance and length; swim direction and reaction speed or direction; predator attacks, prey responses, and duration of events; size-guild analysis; community composition	Threat avoidance and predation; predator-prey interactions on the continental shelf of the US (GA)	Manual; all occurrences 12-min period^{-1} ($n = 16$); video ground truth
Purser *et al.* (2022)	Mobile 0.9 MHz BlueView	UNS	All	Notothenioid icefish nest abundance	Nest distribution at a spawning ground in the British Antarctic territory of the UK	Manual; all occurrences transect^{-1} ($n = 21$); video and side-scan sonar ground truth
Rakowitz *et al.* (2012)	Mobile 1.1 MHz DIDSON	20 h 36 min 4 s	1 h	Bleak, common bream, and silver carp abundance and length; swim speed, direction, distance from trawl, body angle, and tortuosity; first avoidance track, total avoidance track, angle at first avoidance track, total avoidance tracks, and 11 trawl-avoidance behaviours; community composition	Threat avoidance; diurnal patterns and light; gear evaluation assessing species-specific avoidance reactions and capture success of a trawl in a reservoir in the Czech Republic	Manual; all occurrences 30-min period^{-1} ($n = 2$); cluster analysis for estimating community composition; sub-sampling; trawl ground truth
Rakowitz *et al.* (2014)	Stationary 1.1 MHZ DIDSON	196 h	All	Fish abundance and length; size-guild analysis; community composition	Habitat and interannual comparison, and depth distribution; influence of diel cycle, discharge and water chemistry at overfall or groin-head pools in a river in Austria	Manual; all occurrences 60-min period^{-1} ($n = 196$); longline ground truth
Rand and Fukushima (2014)	Stationary 1.8 MHz DIDSON and 3.0 MHz ARIS	519 h 45 min + 543 h 22 min 30 s	All	Sakhalin taimen abundance and length; swim direction	Spawning passage and interannual or seasonal comparison; influence of light and water chemistry in a river in Japan	Manual; all occurrences 30-min period^{-1} ($n = 2$ 126); video ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Rieucau *et al.* (2015)	Stationary 3.0 MHz ARIS	49 920 frames (1 h 44 min)	80 frames (10 s)	Fish abundance and length; school size, frequency, and spacing	Influence of diurnal patterns and tide in an estuary in the USA (SC)	Manual; MeanN of 10 random frames 13-min period^{-1} ($n = 8$); sub-sampling; seine net ground truth
Rieucau *et al.* (2016)	Stationary 1.8 MHz DIDSON	32 min	1 min 44 s	Atlantic herring school spacing; swim speed, direction, reaction speed or direction, vertical distribution, milling activity, body angle, tortuosity, integrated correlation strength, rotational order parameter and behavioural wave-propagation speed	Habitat comparison, threat avoidance and predation; collective response to a predator model and effect of brown and white net contrast in a net pen in an estuary in Norway	Semi-automated; 32 × 32-pixel particle image velocimetry school velocities from 4-s intervals trial^{-1} ($n = 26$); sub-sampling; stocked net pen ground truth
Rillahan *et al.* (2021)	Stationary 1.8 MHz ARIS	145 h	All	Alewife, American eel, blueback herring, and striped bass abundance and length; swim direction and milling activity; community composition	Inlet passage, diel cycle, tide, current, water chemistry in estuary culverts in the USA (MA)	Manual; all occurrences; hooked gear and net ground truth
Rodriguez-Pinto *et al.* (2020)	Stationary 1.8 MHz DIDSON	105 h	All	Gulf menhaden school spacing; swim speed, direction, reaction speed or direction, distance from sonar, tortuosity	Habitat comparison, threat avoidance and predation in an estuary in the USA (LA)	Manual; all occurrences; net ground truth
Rodriguez-Pinto *et al.* (2022)	Stationary 1.8 MHz DIDSON	48 h	All	Gulf menhaden abundance and length; school size and spacing; swim speed, direction, reaction speed or direction, distance from sonar, and tortuosity	Habitat comparison, threat avoidance, predation in an estuary in the USA (LA)	Manual; all occurrences; net ground truth
Rose *et al.* (2005)	Stationary 1.8 MHz DIDSON	24 h + 4 h + 7 h 30 min	All	Sablefish and Pacific halibut abundance and length; swim direction; time to first appearance to first pot entry or hook interaction around pot and longline gears and a baited rotating sonar	Habitat comparison; gear evaluation assessing the performance of standard vs. modified baited traps and hooks and influence of soak time in the deep ocean; USA (OR)	Manual; all occurrences 15-min period^{-1} ($n = 14$); trap, hooked gear, and video ground truth
Schmidt *et al.* (2018)	Stationary 1.8 MHz DIDSON and ARIS	179 h	51 h 30 min	Fish abundance and length; number of contacts with a hydropower trash rack	River passage, habitat comparison, spatial and depth distribution, and threat avoidance; Influence of diurnal patterns and flow on vertical and horizontal position along a hydroelectric trash rack in Austria	Manual; all occurrences 15-min interval^{-1} 60-min period^{-1} ($n = 51$); sub-sampling; electrofishing video ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Shahrestani *et al.* (2017)	Stationary 3.0 MHz ARIS	637 200 frames (59 h)	42 480 frames (3 h 56 min)	Small and large fish abundance size-guild analysis	Influence of diurnal patterns, tide, and water chemistry during a storm at a pier in an estuary in the USA (MD)	Manual and automated; MeanN of 60 frames (20 s) from 5-s intervals 5-min period^{-1} ($n = 47$); sub-sampling; analysis evaluation comparing manual and automated counts; no ground truth
Shahrestani *et al.* (2020)	Mobile 3.0 MHz ARIS	24 h	All	Sea nettle abundance; school size and frequency; vertical distribution	Inlet passage, habitat and interannual or seasonal comparison, spatial and depth distribution; influence of water chemistry within an estuary in an estuary in the USA (MD)	Manual; all occurrences 5-m distance-interval^{-1} ($n = 51$); no ground truth
Shen *et al.* (2013)	Mobile 1.1 MHz DIDSON	16 h	All	Fish abundance and length	Spatial distribution in a reservoir in China (SH)	Manual: all occurrences transect^{-1} ($n = 1$); net ground truth
Smith *et al.* (2021a)	Stationary 1.8 MHz DIDSON	1 h	~36 s	Fish abundance and length	Habitat comparison; influence of diurnal patterns; gear evaluation assessing traps at a marsh bulkhead in the USA (NC)	Manual; MeanN of 25 frames random 5-min interval^{-1} ($n = 12$); sub-sampling; trap ground truth
Smith *et al.* (2021b)	Stationary 1.8 MHz ARIS	816 h	All	Salmonid abundance and length; swim direction	River passage and predation; influence of diurnal patterns, discharge, current, and turbidity in the USA (OR)	Automated; all occurrences 60-min period^{-1} ($n = 816$); no ground truth
Staines *et al.* (2020)	Mobile 1.8 MHz DIDSON	384 h	All	Fish, porpoise, and shark abundance and length; reaction speed or direction	Habitat and interannual or seasonal comparison; influence of diurnal patterns, tide, and current on the continental shelf off the USA (ME)	Manual; all occurrences 60-min period^{-1} ($n = 384$); no ground truth
Staines *et al.* (2022)	Stationary 1.8 MHz ARIS	15 h 15 min	All	Fish abundance and length	Threat avoidance in a river in the USA (NH)	Manual; all occurrences 10-min period^{-1} ($n = 92$); net ground truth
Stott and Miner (2022)	Stationary 1.8 MHz DIDSON	1601 h	All	Bowfin, common carp, longnose gar, and northern pike abundance and length; swim direction; community composition	Spawning passage and interannual or seasonal comparison; influence of diel cycle, discharge, and water chemistry at a lake inlet in the USA (OH)	Manual; all occurrences; discriminant analysis for estimating community composition; no ground truth
Stuart *et al.* (2008)	Stationary 1.1 MHz DIDSON	UNS	Qualitative	Silver perch abundance and length; qualitative reaction speed or direction	River passage; qualitative gear evaluation assessing cage shyness at a water management structure in Australia (NS)	Manual; qualified observations; electrofishing and hydrophone ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Swanson *et al.* (2021)	Stationary 1.8 MHz DIDSON	1 700 h	51 h	Fish abundance and length; size-guild analysis; community composition	Stream passage and interannual or seasonal comparison; influence of diurnal patterns, discharge, water chemistry, community composition in a lake in the USA (MI)	Manual: all occurrences 2-min interval^{-1} 360-min period^{-1} ($n = 153\ 000$); sub-sampling; electrofishing and PIT tag ground truth
Terayama *et al.* (2019)	Stationary 1.8 MHz ARIS	10 min	All	Fish image sharpness, resolution, and colour conversion	Influence of light and turbidity; Paired video and imaging sonar to develop a sonar-to-video image translation in an aquaculture system in Japan	Automated; all occurrences in 8-min training data, 2-min test data; video ground truth
Tiffan *et al.* (2004)	Mobile 1.8 MHz DIDSON	2 019 m among 4 transects	All	Chinook salmon abundance; vertical distribution	Spawning passage, depth and spatial distribution and vessel traffic; gear evaluation of video-based counts in a river in the USA (OR)	Manual: all occurrences transect^{-1} ($n = 4$); visual observation and video ground truth
Tiffan *et al.* (2010)	Stationary 1.8 MHz DIDSON	72 h	All	Chum salmon spawning pair abundance; swim speed, direction, and tail-beat frequency; spawning events and digging activity	Spawning passage; influence of current or flow in a river in the USA (OR)	Manual; all occurrences 15-min period^{-1} ($n = 288$); seine and acoustic telemetry ground truth
van Hal *et al.* (2017)	Mobile 1.1 MHz DIDSON	29 h 30 min	All	Fish and marine mammal abundance and length; school size and frequency; vertical distribution	Habitat and interannual or seasonal comparison, and spatial, and depth distribution; Fish schooling classes among open water, transition zone, and protection revetment habitats at a wind farm on the continental shelf of the Netherlands	Manual; all occurrences 10-s (~10 m) period^{-1} ($n = 177$); gillnet ground truth
van Keeken *et al.* (2020)	Stationary 1.1 and 1.8 MHz DIDSON	42 h 50 min 24 s	All	Nighttime European eel abundance and length; swim direction, reaction speed or direction, vertical distribution, milling activity, body angle and tortuosity; rheotaxis classes and avoidance classes	Spawning passage, habitat comparison, and threat avoidance; influence of current near a pumping station with trash rack in a river in the Netherlands	Manual; mean of 2–3 counts; all occurrences; no ground truth
Veinott *et al.* (2018)	Stationary 1.1 and 1.8 MHz DIDSON	UNS	All	Atlantic salmon abundance; swim direction	Spawning passage, interannual or seasonal comparison, and spatial distribution; and catch per unit effort under different management policies in a river in Canada (NL)	Manual; all occurrences year period^{-1} ($n = 5$); visual observation and video ground truth

Table 2. Continued

Study	Sonar	Data	Processed	Information extracted	Effects and environments	Methods
Velez (2015)	Stationary 1.8 MHz DIDSON	12 h	All	American shad abundance; school size and frequency; swim speed, direction, and reaction speed or direction	Threat avoidance; gear evaluation of responses to 120 200, and 420 kHz echosounders in a river in the USA (MA)	Manual; all occurrences ~80 min deployment^{-1}; $n = 9$); no ground truth
Viehman and Zydlewski (2015)	Stationary 1.8 MHz DIDSON	22 h	All	Fish abundance and length; school frequency; swim speed, direction, reaction speed or direction, and milling activity; distance from a tidal energy turbine; 7 fish and school reaction classes to a tidal energy turbine size-guild analysis	Threat avoidance; influence of diurnal patterns, diel cycle, and tide; probability of entering, avoiding, or passing, rotating vs. not rotating tidal energy turbine in an estuary in the USA (ME)	Manual; all occurrences 30-min period^{-1} ($n = 44$); no ground truth
Williams *et al.* (2013)	Mobile 1.8 MHz DIDSON	1 h 8 min 37 s	All	Fish abundance; swim speed, direction, and reaction speed or direction; distance to trawl panel within a trawl; escaping, herding, and undetermined behavioural classes	Habitat comparison and threat avoidance; influence of diurnal patterns and light; gear evaluation of trawl selectivity and comparing video and imaging sonar behavioural information in the deep ocean of waters of the USA (AK)	Automated; all occurrences 11-min haul^{-1} ($n = 6$); trawl, pocket net, and video ground truth
Xie and Martens (2014)	Stationary 1.1, 1.2, and 1.8 MHz DIDSON	132 h	All	Sockeye salmon abundance; swim direction	Spawning passage in a river in Canada (BC)	Manual; all occurrences 5-min period^{-1} ($n = 1\,584$); analysis evaluation of sub-sampling time intervals and random vs. systematic selection; sub-sampling; no ground truth
Xie *et al.* (2008)	Stationary 1.1 MHz DIDSON	33 h	14 h	Pink salmon and sockeye salmon abundance; school size and frequency; swim speed, direction, and distance from sonar	Spawning passage and threat avoidance; influence of vessel traffic in a river in Canada (BC)	Manual; all occurrences 10-min random interval^{-1} ($n = 90$); sub-sampling; no ground truth
Zhang *et al.* (2014)	Stationary 1.2 MHz DIDSON	12 h	All	Nighttime Chinese sturgeon abundance and length; swim speed, direction, body angle, tortuosity, and tail-beat patterns	Nighttime patterns in an aquaculture net pen in a reservoir in China (HE)	Semi-automated; all occurrences 120-min period^{-1} ($n = 6$); net-pen ground truth
Zhang *et al.* (2020)	Stationary 1.8 MHz DIDSON	204 h	55 h	Fish abundance and length; swim direction	Spawning passage and interannual or seasonal comparison; influence of discharge and water chemistry in a river in China (SH)	Automated; all occurrences 60-min period^{-1} ($n = 55$); analysis evaluation comparing manual and automated counts; sub-sampling; stocked fish ground truth

only makes imaging sonars excellent counting and measurement tools for abundance quantification, but also provides the necessary detail for fine-scale behavioural studies by increasing the probability of observing subtle movements. Abundance estimates of migrating diadromous spawners have benefited from improved accuracy provided by imaging sonar that allowed collection of continuous data over long durations irrespective of underwater light conditions (e.g. through night and day) or water quality (e.g. turbidity) (see Table 2 for specific studies). In addition, the behavioural information availed by imaging sonar can improve understanding of ecosystem connectivity and inform management based on how aquatic organisms move and interact with each other or react to natural or anthropogenic environmental stimuli or disturbances. Species-level, size-guild, or community-wide comparisons have been made to study inter- or intra-species interactions undetectable by other gears such as predator-prey engagements and collective reactions (Handegard *et al*., 2012; Price *et al*., 2013; Marras *et al*., 2015; Kruusmaa *et al*., 2016; Rieucau *et al*., 2016; Cheng *et al*., 2022; Francisco *et al*., 2022), shifts in predation response across habitats (Rodriguez-Pinto *et al*., 2020, 2022), or environmental conditions (Nelson *et al*., 2021, 2022), Pacific lamprey parasitic attachment events (Kirk *et al*., 2015; Keefer *et al*., 2017), spawning-related digging activity and spawning events (Tiffan *et al*., 2010; Langkau *et al*., 2016), spawning school structure (Godinho *et al*., 2017), spawner habitat associations (Grabowski *et al*., 2012), environmental effects on behaviour on spawning grounds (Crossman *et al*., 2011; Jiang *et al*., 2012; Chang *et al*., 2017), environmental variables affecting juvenile emigration (Budnik and Miner, 2017), and monitoring fish in aquaculture or aquarium systems (Han *et al*., 2009b; Hightower *et al*., 2013; Zhang *et al*., 2014; Terayama *et al*., 2019; Jones *et al*., 2021; Gutiérrez-Estrada *et al*., 2022).

A particularly complex property of animal aggregations like fish schools is the ability to execute highly coordinated movements in unison when confronted with environmental perturbations or predators. Recent research in the field of collective animal behaviour in general, and fish schooling in particular, has shifted focus from the importance of global properties (i.e. group size and frequency of occurrence) to local properties (e.g. individual spacing, speed, angle, displacement, and so on) as well as considering rules of interactions among individuals to give a mechanistic basis for how groups are formed, move, and react as a unit in the face of biotic (i.e. predators) and abiotic factors (i.e. hydrodynamic properties of the environment) (Handegard *et al*., 2012; Strandburg-Peshkin *et al*., 2013; Tunstrøm *et al*., 2013; Rosenthal *et al*., 2015). Despite the growing interest to ascertain the mechanisms that underlie the capability of aggregations to perform coordinated collective reactions and the hydrodynamic benefit of swimming in schools, knowledge of these processes has been impaired by the methodological approaches available to quantify fine-scale swimming dynamics in natural settings. Imaging sonar has provided researchers with an effective means to observe and explore dynamic behaviours of individuals and collective patterns of schooling fish in various ecological contexts (e.g. antipredator responses and social attraction) without disturbing the focal organisms. The ability of imaging sonar technology to collect high-resolution data describing fine-scale swimming kinematics, and group or school topology and organization under natural conditions will, therefore, advance research underlying how aquatic organisms interact within their environments and reach the energetic and safety benefits of group organization.

Studying complex and sensitive habitats

Habitat complexity is important for many species but adds sampling challenges to the study of fish associated with a lot of productive aquatic habitats. For instance, high rugosity or interstitial spaces among submerged timber or aquatic vegetation in ponds, lakes, or reservoirs (Mizuno *et al*., 2013; Jing *et al*., 2017; Brien *et al*., 2021), marsh grasses (Rodriguez-Pinto *et al*., 2020), seagrass (Olson *et al*., 2023), mangrove forests (Frias-Torres and Luo, 2009; Olson *et al*., 2023), or rocky outcroppings and reefs (Grabowski *et al*., 2012; Auster *et al*., 2013; Artero *et al*., 2021; Dunn *et al*., 2023; Olson *et al*., 2023), provide abundant sources of gear snags and places for fish to hide undetected but can be studied using imaging sonar. While resolution of organisms at similar distances to objects or debris can be obscured, imaging sonar provides one of the best tools for conducting studies in these environments. Small, shallow-water marsh or intertidal pools (Handegard *et al*., 2012; Rieucau *et al*., 2015; Rodriguez-Pinto *et al*., 2020, 2022), tributaries (Becker *et al*., 2011a; Magowan *et al*., 2012; Lankowicz *et al*., 2020; Shahrestani *et al*., 2020; Swanson *et al*., 2021), inlets (Becker *et al*., 2016a, b; Lagarde *et al*., 2020, 2021) or coastal lagoons (McCauley *et al*., 2014, 2016; Capoccioni *et al*., 2019) are difficult to survey due to depth restrictions and large ranges in tidal and current amplitude and direction but can also support high densities of fish and are a highly understudied ecosystem component where imaging sonar is well suited for use (Lankowicz *et al*., 2020). Many imaging sonars can also resist high pressure and have been deployed to the seafloor off the continental shelf (Rose *et al*., 2005; Purser *et al*., 2022). Including the examples listed above, imaging sonar has thus far been used in no fewer than 46 studies within complex natural habitats, most of which have been steep-banked rivers with rapid depth transitions (Table 2; "Effects and Environment" column, providing the study location and environment). At least 33 studies have incorporated natural habitat comparisons, and 18 have incorporated one or more complex natural habitats. To our knowledge, Auster *et al*. (2013), Dunn *et al*. (2023), and Olson *et al*. (2023) are the only studies to have utilized the non-interactive aspect of imaging sonar to study fish associations with, or map delicate and slow-growing live-bottom habitats, including a subtropical ledge (Auster *et al*., 2013), polychaetae reefs (Griffin *et al*., 2020), fringing oyster reefs (Dunn *et al*., 2023; Olson *et al*., 2023), coral reefs (Olson *et al*., 2023), and seagrass beds (Olson *et al*., 2023). These and other biogenic reefs can be damaged by extractive sampling gears, representing another area of field research that imaging sonar is well suited to expand.

Anthropogenic features pose similar sampling challenges to complex natural habitats. Incidental or planned artificial reefs (Baumann *et al*., 2016; van Hal *et al*., 2017; Zeng *et al*., 2018; Plumlee *et al*., 2020; Sibley *et al*., 2023b), urbanized shorelines (Able *et al*., 2013; Becker *et al*., 2013a, 2014; Accola *et al*., 2022a, b), industrial-cooling, hydrocarbon, hydroelectric, wave, tidal, or wind energy stations (Viehman and Zydlewski, 2015; Egg *et al*., 2017; van Hal *et al*., 2017; Francisco and Sundberg, 2019; Zhang *et al*., 2020; Braga *et al*., 2022; Francisco *et al*., 2022; Staines *et al*., 2022; Bender *et al*., 2023; Cotter and Staines, 2023), water control structures (Kimball *et al.*, 2010; Bilotta *et al.*, 2011; Doehring *et al.*, 2011, 2015; Bennett *et al.*, 2021; Rillahan *et al.*, 2021; Rodriguez-Pinto *et al.*, 2022), and an assortment of other man-made features are widely distributed throughout aquatic environments. These features often provide substrate for different assemblages of organisms relative to their natural surroundings, stand as obstacles for fish attempting passage (O'Connell *et al.*, 2014; Cupp *et al.*, 2018; Egg *et al.*, 2019), alter natural responses to current flow (Jones and Petreman, 2015) or pose a threat to unwary individuals that may become impinged or entrained (Boys *et al.*, 2013; Patrick *et al.*, 2015; Viehman and Zydlewaski *et al.*, 2015; Bevelhimer *et al.*, 2017, Bolland *et al.*, 2019; Piper *et al.*, 2018; Egg *et al.*, 2019; van Keeken *et al.*, 2020; Staines *et al.*, 2022). Imaging sonar has been used to study biotic associations with complex anthropogenic habitats in at least 69 studies. At least 34 studies have used imaging sonar to classify situational avoidance behaviours related to fish passage barriers, or industrial water intake impingement or entrainment. Future studies using imaging sonar around complex anthropogenic features would benefit from incorporation of nearby natural habitats to take advantage of the ability to sample consistently across large changes in benthic complexity to provide insight into microhabitat partitioning, ontological (life stage) differences, and other ways in which communities share resources throughout the environment. At the time of this review, at least 51 studies have incorporated a habitat comparison, including 29 comparing one or more anthropogenic habitats, and 12 studies that have directly compared natural and anthropogenic habitats.

Low-visibility environments

In many ecological contexts, video-based and other visual methods are not viable. The most obvious cause of reduced visibility is low light availability. Little or no natural lighting occurs in deep waters (Giorli and Au, 2017a, b; Giorli *et al.*, 2018), overhanging environments such as piers (Able *et al.*, 2013; Becker *et al.*, 2013a, 2014; Grothues *et al.*, 2016; Shahrestani *et al.*, 2017), undercuts (Frias-Torres and Luo, 2009), caves, below ice (Mueller *et al.*, 2006), under stratified surface blooms, during periods of high cloud cover, and of course, at night (Becker *et al.*, 2011a; Rakowitz *et al.*, 2012; Able *et al.*, 2013; Rieucau *et al.*, 2015). Turbidity is another factor that mediates visibility, caused by the suspension of sediments in the body of water, such as occurs in surf zones, river mouths, benthic nepheloid layers, shallow environments during storms (Shahrestani *et al.*, 2017), by phytoplankton blooms, and in the presence of high tannins, or other leached solutions. While artificial lighting can be used when turbidity is not limiting, fish behaviour is likely to be altered (Nelson *et al.*, 2021, 2022). Imaging sonar offers an efficient means to overcome the limitations of surveying aquatic organisms under restricted visibility conditions by using sound- rather than light-refraction to produce imagery. This is true not only for *in situ* studies, but additionally applies to controlled laboratory experiments (Amaral *et al.*, 2015), leading to a large data deficiency in visibility-restricted settings that can now be studied.

The ability of imaging sonars to produce video-like pictures under visibility-restricted conditions was certainly a top incentive for its development and has been touted as a primary advantage over other sampling gears used to study aquatic organisms. While suspension of high-density sediments like sand can still obscure imagery due to reverberation, imaging sonar presents the best option for sampling in most turbid environments. Imaging sonar has since been used in at least 92 studies in turbid environments, and 90 studies that incorporated nighttime sampling that would preclude the use of optical methods (53 with both high turbidity and night sampling). Of these studies, we identified 50 that used imaging sonars to compare diurnal patterns or assess abundance trends throughout entire diel cycles. The effects of anthropogenic light were evaluated in 12 studies, and just five studies reviewed here (Maxwell and Gove, 2007; Frias-Torres and Luo, 2009; Becker *et al.*, 2011a; Terayama *et al.*, 2019; Smith *et al.*, 2021b) have employed this technology to directly evaluate the effects of turbidity. Visibility effects are undoubtably highly influential to many species or life-history stages. Many fish species greatly depend upon their vision to forage or hunt effectively (Utne-Palm, 2002). Conversely, many predatory aquatic animals rely on other sensory modalities to exploit their prey in low-visibility conditions (Dehnhardt *et al.*, 2001). This factor may be one major contributor of the diel species-distribution cycles that are ubiquitous to nearly every aquatic environment. This additionally contributes to refuge-seeking behaviours observed by juveniles of some species associated with high turbidity (Blabber and Blabber, 1980). Imaging sonar permits the investigator to examine behaviours of aquatic organisms when effects of turbidity would render other remotely-sensed sampling gear ineffective.

Evaluation of traditional fishing gears

In addition to enabling many new research opportunities, imaging sonar offers an effective means for evaluating the performance of traditional sampling methods. We reviewed 26 behavioural studies that have used imaging sonar to evaluate the efficiency of various fishing gears or survey techniques. In particular, imaging sonars have been employed to assess species interactions with, and escapement from, hooked gear and trapping surveys (Rose *et al.*, 2005; Stuart *et al.*, 2008; Smith *et al.*, 2021a), trawls (Handegard and Williams, 2008; Rakowitz *et al.*, 2012; Jůza *et al.*, 2013; Williams *et al.*, 2013), purse seines (Handegard *et al.*, 2017a), set nets (McCarthy *et al.*, 2014; Nichols *et al.*, 2014; Egg *et al.*, 2018; Fujimori *et al.*, 2018; Kang *et al.*, 2020; Helminen and Linnansaari, 2023), video arrays (Tiffan *et al.*, 2004; Maxwell and Gove, 2007; Frias-Torres and Luo, 2009; Hays *et al.*, 2015; Egg *et al.*, 2018; Brien *et al.*, 2021; Sibley *et al.*, 2023b), trained observers (Holmes *et al.*, 2006; Maxwell and Gove, 2007; Tong *et al.*, 2009; Pipal *et al.*, 2012; O'Connell *et al.*, 2014; Hayes *et al.*, 2015), and electrofishing (Kerschbaumer *et al.*, 2020). In addition, this technology has been used to assess sampling bias and accuracy of echosounder hydroacoustic equipment, including effects of low-frequency sound avoidance (Maxwell and Gove, 2007; Velez, 2015), target detection (Pratt *et al.*, 2021), length measurements (Lin et. al., 2016), and variation in species-specific target strength at different swim angles (Hwang *et al.*, 2017).

Additional fishing effects such as invasion of set nets by seals (Nichols *et al.*, 2014; Fujimori *et al.*, 2018) and stress and injury levels induced by crowding during purse seine fishing (Handegard *et al.*, 2017a) have also been studied using imaging sonars. In total, six other studies relied on the utilization of imaging sonar to assess avoidance responses of fish to survey vessels (Xie *et al.*, 2008; Tiffan *et al.*, 2010; Becker *et al.*, 2013b; Hayes *et al.*, 2015; Davis *et al.*, 2016; LeRoy *et al.*, 2019), with ecological implications for high vessel traffic areas, as well as providing useful information for mobile surveys. Imaging sonar is also useful for making qualitative observations supporting and helping to explain results from other methods, such as passive integrated transponder (PIT) tags (Stuart *et al.*, 2008), trapping of entrained individuals (Patrick *et al.*, 2015), and side-scan sonar surveys (Purser *et al.*, 2022). The versatility of this non-intrusive gear has recently been used to compare multiple methods of fish herding techniques (Ridgway *et al.*, 2023). Finally, imaging sonar has been employed to assess non-biological gear interactions, such as general bottom mapping (Maxwell and Smith, 2007; van Middlesworth *et al.*, 2015; Pyo *et al.*, 2017), trawl interactions with benthic environments (Lomeli *et al.*, 2019), object detection (Cho *et al.*, 2015), detection of submerged aquatic vegetation (Mizuno *et al.*, 2013), and as a robust visual ground truth option for side-scan sonar observations (Griffin *et al.*, 2020). The particularly high-performance of imaging sonar in river and stream passage applications has led to its supplementation or replacement of existing monitoring strategies, such as visual observation (Maxwell and Gove, 2007; Magowan *et al.*, 2012), capture (Lenihan *et al.*, 2019), or tag and recapture (MacNamara and McCarthy 2014; Mora *et al.*, 2015), although the expense of the equipment and the processing effort required has prevented a wider adoption (Faulkner and Maxwell, 2020).

Data processing and analytical approaches

Taxonomic resolution of imaging sonar data

Species-level taxonomic resolution remains one of the prominent challenges when using imaging sonar due to an overall lower resolution than optical methods and an inability to reproduce pigments. Interpreting sonar imagery, therefore, largely relies upon the researcher's knowledge of the study environment or system in which the imaging sonar is being used. Despite this, imaging sonar has been used to study the behaviours of at least 89 species, belonging to 40 orders, and 11 classes of aquatic organisms *in situ* (Figure 2) (Table 2; "Information Extracted" column, providing the taxonomic resolution). This includes studies of at least 15 protected species. Qualified differences in body size, shape, and swim style make separations of major functional groups apparent and can help to effectively discriminate between distinct homogenous species groups (Grote *et al.*, 2014; Ogburn *et al.*, 2017), as has been used in 144, 83, and 65 studies (Figure 2) (Able *et al.*, 2014; Becker and Suthers, 2014; Egg *et al.*, 2017; Giorli *et al.*, 2018). Related to the visual signatures of the echogram, acoustic shadows provide additional morphometric information for relatively robust organisms within the middle to lower portions of the ensonified area (Langkau *et al.*, 2012; Parsons *et al.*, 2014; Connolly *et al.*, 2022). Using this approach, the orientation of the sonar relative to the target organisms is critical to providing resolution on key morphometric characteristics needed to identify species or separate guilds (Martignac *et al.*, 2015). This is substantiated by the non-intuitive way that imaging sonar depicts objects. The 2-dimensional imagery produced along the X and Z polar planes renders more of a downward, overhead viewpoint for objects appearing straight in front of the beam (Brahim *et al.*, 2010; Eggleston *et al.*, 2020). Visually discerning morphometrics is both easier and more consistent for larger animals, making

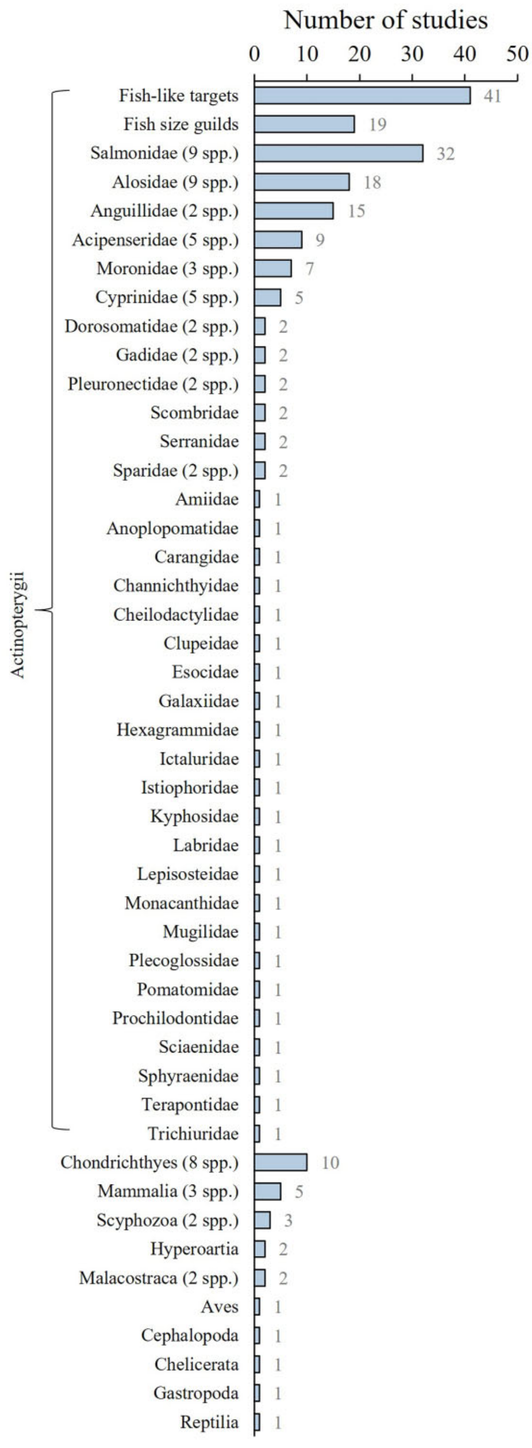

Figure 2. The taxonomic resolution of studies using imaging sonar. A total of 41 studies identified ensonified targets as "fish" or "animals", 19 studies separated the fish assemblages by size guilds to identify separate functional groups, seven studies identified organisms to genus, and 88 studies have identified organisms to the species level. Organisms identified to species level are grouped by Class (or sub-phylum), and family. Note that several studies involved more than one species-level identification. A total of 89 animals have been identified to species level using imaging sonar.

this technology particularly well-suited for species-level identification of distinct organisms greater than 0.5 m in length (Francisco and Sundberg, 2019; Staines *et al*., 2020; Francisco *et al*., 2022).

Behavioural patterns, such as schooling tendencies, habitat use, and known cyclical events that separate taxa of interest (e.g. diurnal, tidal, or seasonal migrations) (Figure 3) can also help to refine identifications to lower taxonomic levels. This approach has been relied upon in at least 20 studies. However, in most cases, ground-truthing remains necessary for species-level assessments. One or more ground-truthing methods have been used in 103 previous studies reviewed here (Table 2; "Methods" column, keyword: "ground truth"). Among those methods, traditional direct-capture techniques using nets have been the most commonly used means to relate to imaging sonar observations (43 studies). Other ground truth methods used include: video or trained observer observations (29 and 20 studies, respectively), hooked gear (12 studies), acoustic telemetry (seven studies), electrofishing (11 studies), traps (eight studies), stocking or tethering (eight studies), hydrophone recordings (five studies), trawling (five studies), mark-and-recapture, T-bar, and PIT tags (five studies), and turbine or water intake-pump entrainment (four studies).

The higher image resolution produced by imaging sonars when compared with echosounders comes at a compromise of techniques available to refine taxonomic resolution with echosounders. The higher echo frequencies used by imaging sonars, where the wavelengths are typically much smaller than the target organisms, have non-Rayleigh scattering properties, making them more reflective than echosounder signals and, therefore, less reliant upon highly reflective tissues such as swim bladders. A drawback to using higher frequencies is a high sensitivity to the angle of ensonification, rendering traditional echo integration approaches less feasible, although this is offset by the increased resolution and the ability to count the individual targets as opposed to echo integration. Another tradeoff is the inability to use multi-frequency comparisons of backscatter (through decibel differencing or broadband scattering), or swim bladder target strength values used to refine taxonomic resolution with echosounders. Mueller *et al.* (2010) showed that tail-beat frequency patterns can be distinguishable using imaging sonar and used this to discriminate between two salmonid species with similar body shapes, independent of size; a technique that has also been developed using split-beam echosounders (Handegard *et al*., 2009). However, some limitations emerge from this technique, such as the challenge to resolve tail-beat frequencies of smaller fish, or that the recording frame rate must be at least twice the tail-beat frequency to avoid signal distortion by aliasing (Mueller *et al*., 2010). Despite these shortcomings, there are situations where this technique could be applied to refine taxonomic classifications, or to study bioenergetics (Tiffan *et al*., 2010). For example, eels have been identified in 15 studies using imaging sonar largely based on their distinct movement patterns (Table 2). Also, Helminen *et al.* (2021) were able to separate Atlantic salmon, striped bass, and American shad using both manual and automated approaches. To date, the studies using this method have employed DIDSON sonars recording at 1.1–1.8 MHz. The current availability of ARIS, BlueView, and Oculus imaging sonars, which use a greater number of beams and are capable of operating at 2.1–3.0 MHz, might make species identification using tail-beat patterns all the more viable. For instance, a Myliobatoid ray (cownose ray, *Rhinoptera bonasus*) recorded by a vessel-mounted 1.8-MHz ARIS (Rieucau and Munnelly, unpublished data), demonstrates that the distinctive pectoral fin motion of these animals can help to refine taxonomic resolution as tail beats can, even when recorded from a mobile platform (Figure 4).

Despite the limitations of taxonomic resolution of imaging sonar used to observe diverse aquatic communities, community composition has been assessed in no fewer than 34 studies. In addition to using discernable morphometrics, behaviours themselves can be used to enhance taxonomic resolution. As with other sonar data, species-specific biomass can be approximated by dividing the number of sonar targets by relative species abundances sampled with another survey gear (Kerschbaumer *et al*., 2020; Helminen and Linnansaari, 2023). Finer resolution can be obtained by using size guilds separated based on length frequency (Becker *et al*., 2011a, b; Becker and Suthers, 2014; Gurney *et al*., 2014; Veinott *et al*., 2018; Swanson *et al*., 2021; Francisco *et al*., 2022) and aspect–ratio distributions (Francisco and Sundberg, 2019; Francisco *et al*., 2022) that are compared with those obtained through direct capture or stereo-video ground truthing, as has been done in at least 19 studies. Transiting versus milling behaviour, position in the water column, school size or organization, and other behavioural metrics can be used in multivariate analyses to probabilistically determine likely assemblage species compositions. Examples of this include Rakowitz *et al.* (2012), Able *et al.* (2014), Bevelhimer *et al.* (2017), and Stott and Miner (2022) who used cluster analysis, principal components analysis, and canonical discriminant analysis to separate taxa and compare species distributions and interactions around anthropogenic features.

Abundance estimates: metrics, autocorrelation, and sub-sampling

Several approaches currently exist to calculate abundance estimates (e.g. fish counts) or to measure other metrics of interest. Counting all occurrences through an entire time series or survey transect is the most basic method. However, this method can be labour intensive, risks the potential to count the same animals repeatedly, and results in high autocorrelation between successive intervals (Lilja *et al*., 2008; Petreman *et al*., 2014; Rand and Fukushima, 2014). This can limit the possible interpretations of the data unless there is something inherent about the study site or subject that reduces the likelihood of this occurring, or the goals of the study are focused on the number of interactions occurring at the site itself such as foraging or predation events (Mizuno *et al*., 2016; Bolton *et al*., 2017; Nelson *et al*., 2021, 2022), the number of approaches to barrier systems (O'Connell *et al*., 2014) or designed passage-restricting methods (Parker *et al*., 2015, 2016), or incapacitation due to incidental entrainment (Boys *et al*., 2013; Hightower *et al*., 2013; Patrich *et al*., 2014, 2015, Bolland *et al*. 2019), and other circumstances of interest. In addition, due to the narrow beam width of imaging sonar, this method can provide overly conservative estimates of small fish due to reduced detection of fish moving parallel to the sonar beam (Tušer *et al*., 2014), and the aforementioned 2-dimensional imagery can impair resolution of individuals within high-density aggregations in the Z polar plane (Capoccioni *et al*., 2019). Interpretation of the imagery can be subjective, and comparisons of inter-reviewer error have been variable (Able *et al*.,

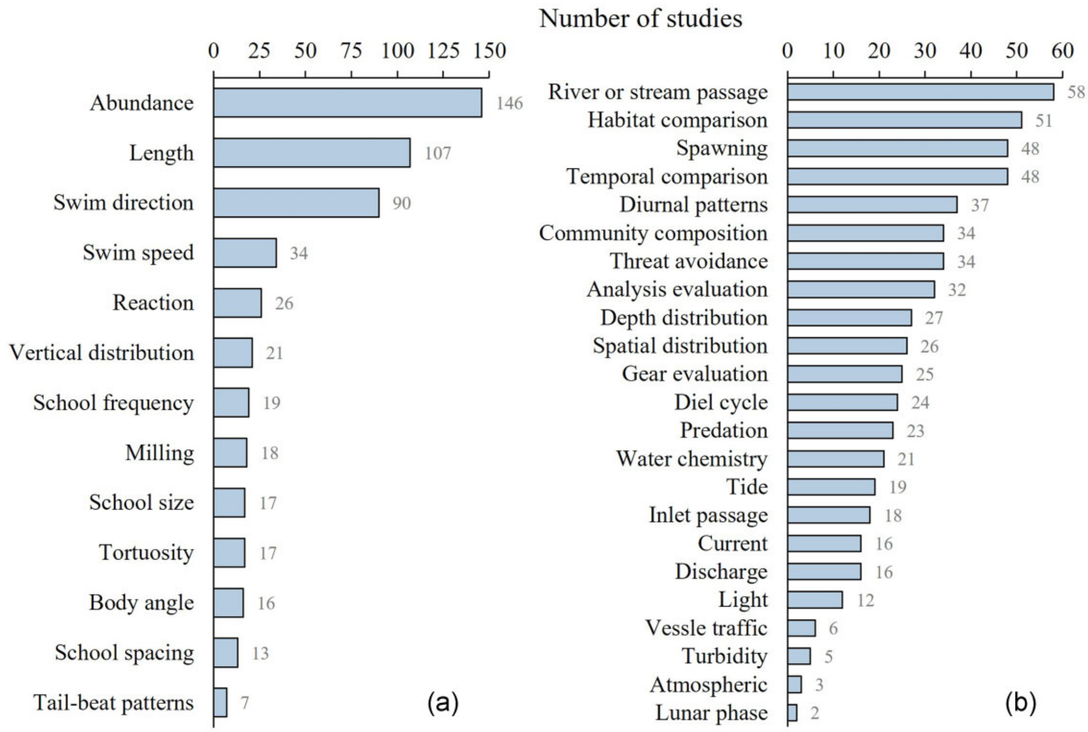

Figure 3. The number of studies that have extracted abundance, length–frequency, or behavioural information from imaging sonar recordings (a) and the number of studies using behavioural information quantified using imaging sonar to study ecological topics (b). Note that several studies extracted more than one abundance, length–frequency, or behavioural metric, and tested more than one effect.

2014; Petreman *et al.*, 2014; Keefer *et al.*, 2017), and the numbers and the variance are rarely reported. Despite these issues, abundance estimates using imaging sonar are often higher than those obtained using other methodologies, representing a standard for comparison (Sibley *et al.*, 2023a).

Migratory events where organisms are passing a sonar at a fixed location are an ideal application of imaging sonar for estimating abundance (Martignac *et al.*, 2015). Tracking the net number of events in one direction removes counts from individuals repeatedly moving upstream and downstream. This strategy has been used extensively to study diadromous Salmonids, Clupeids, Anguillids, and Acipenserids in rivers and streams where narrow, high-flow passage bottlenecks are used to a sampling advantage as has been used in 58 studies in rivers and streams and 18 studies in inlets, including 42 studies of spawning passage (Figure 3b). Surveys from mobile platforms can also overcome this issue, especially for low-mobility organisms like jellyfish (Han and Uye, 2009; Makabe *et al.*, 2012; Shahrestani *et al.*, 2020) or horseshoe crabs (Munroe *et al.*, 2020), however, moving vessels can disrupt the routine behaviour of many nektonic species. A direct approach to account for repeated detections of individuals can also be incorporated into imaging sonar surveys through use of acoustic telemetry, which is particularly useful in unconstrained environments (Tiffan *et al.*, 2010; Nyqvist *et al.*, 2017; Mora *et al.*, 2018; Maxwell *et al.*, 2019; Izzo *et al.*, 2022).

Autocorrelation is a relationship between a signal and a copy of itself as a function of delay, which violates the assumption of independence common to many statistical models (Bartlett, 1946). All imaging sonar data inherently contain some temporal or spatial autocorrelation. Imagery collected from a stationary point will be temporally autocorrelated, the extent of which depends on the speed of the ensonified organisms moving through the beam array, sampling rate, and the time scale of the analysis (Lilja *et al.*, 2008). Additionally, temporal autocorrelation can follow rapid (Thompson and Page 1989) or slow (Downton and Miller 1998) time-scales, which should be treated differently depending on the goals of the analysis. Rapid time scale autocorrelation can be removed through data sub-sampling, or statistical correction techniques. Removal of autocorrelation through pre-whitening or first-differencing methods that assume a unique correlation structure is important for preserving the assumption of independence between samples for rapid time scales, when a parametric statistical analysis is to be used, but might result in an increased Type 2 error rate (i.e. failure to detect a significant relationship) when the primary source of autocorrelation is from slow time scales (Pyper and Peterman, 1998). In this case, a smoothing approach that accounts for autocorrelation (Pyper and Peterman, 1998; Rieucau *et al.*, 2016) or geostatistical approach (Pavlov *et al.*, 2009; Shen *et al.*, 2013) is more appropriate. Imagery collected from a mobile platform will be spatially autocorrelated, which is additionally influenced by the speed that the sonar is moving through the water column (Lankowicz *et al.*, 2020). This spatial autocorrelation can be reduced by averaging information over a large enough interval (Parker-Stetter *et al.*, 2009), but is important to retain in data when using geostatistical analyses (Rivoirard *et al.*, 2008).

Counting the peak abundance that occurs within a single frame across a time or spatial interval (MaxN) has the advantage of not risking double counting and having reduced autocorrelation among successive intervals (Ellis and DeMartini, 1995). This peak abundance does not, however, reflect

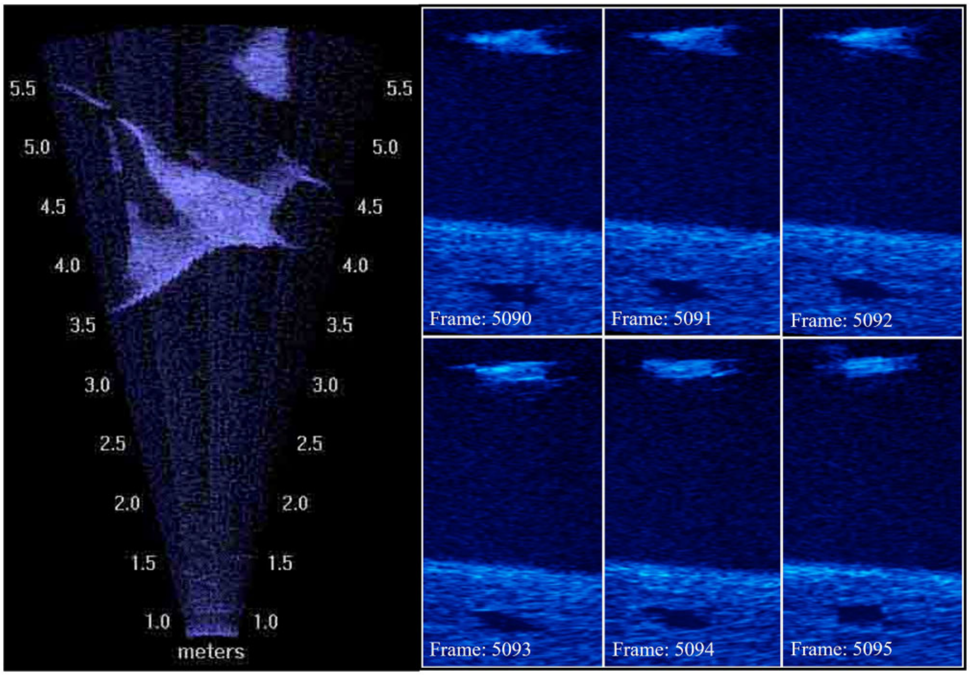

Figure 4. The leftmost panel shows an image of a Myliobatoid ray (Manta alfredi) recorded by McCauley *et al.* (2014) using a stationary 1.8 MHz DIDSON. The series of panels to the right recorded by Rieucau and Munnelly (unpublished data) represent ~1 s of sonar imagery recorded at 5.5 frames s^{-1}, showing another Myliobatoid ray (*R. bonasus*) recorded at 1.8 MHz. The image was recorded with a vessel-mounted ARIS moving at 1 m s^{-1}. The rhomboid shape of the acoustic shadow on the seafloor helps to confirm the body shape produced by the signal return in the water column. Note that the pectoral fin-beat pattern is discernible from the imagery. When viewed as a video, swimming patterns and morphometrics become much more pronounced.

the number of individuals expected to occupy a given time or spatial point within the chosen interval where large schools periodically pass. Means of multiple peak abundance counts within intervals (MeanN) more accurately represent the abundance over the data collection period (Schobernd *et al.*, 2014), but are also the most labour-intensive method. Mean peak abundance counts are most effective when derived from sub-sampled intervals that reduce the amount of autocorrelation with the added benefit of reducing processing effort (Petreman *et al.*, 2014). Despite the wide application of these metrics for analyzing optical data, MaxN and MeanN methods have only been used in 6 and 17 studies, respectively (Table 2; "Methods" column, keywords: "all occurrences", "MaxN", and "MeanN"). Among the studies using MeanN counts, the number of samples, and independence between samples has varied considerably, with between 2 and 60 samples, and no independence in seven studies, randomized independence in six studies, and sampling at set intervals of 5–42 min in five studies.

The spatial correlation present in many fish distributions makes sub-sampling a viable strategy to increase data processing efficiency without reducing precision in estimates of abundance, length frequency, or behavioural metrics quantified (Levine and De Roberts, 2019). Systematic sub-sampling is more consistent relative to the existing spatial correlation, but often provides similar precision to random sub-sampling and both can be a logistical solution when sampling over long time series (Lilja, 2008; Petreman *et al.*, 2014; Xie and Martens, 2014; Boswell *et al.*, 2019). Sub-sampling routines can be optimized to represent a series by increasing the sample frequency rather than the length of time of each sub-sample (Xie and Martens, 2014). Using this strategy, hourly time intervals can be accurately represented by sub-sampling one-sixth to one-third of the total. Despite the practicality of this approach, only 37 studies (less than one-quarter of those using imaging sonar reviewed) have sub-sampled from the dataset (Table 2; "Methods" column, keyword: "sub-sampling"). Of these studies, random- and fixed-interval sub-sampling have been used to process < 1–50% of the dataset in 16 and 21 studies, respectively with 3 s to 12 h of independence between successive samples (Table 2; "Data" and "Processed" columns, providing the amount of data processed relative to that collected). Truly random sub-sampling is another option that generally performs well when compared with systematic sub-sampling (Petreman *et al.*, 2014), and has been used in at least four studies. In order to assess how researchers have scaled sub-sampling intervals to meet their research objectives, we compared the relative frequency of the total proportion of the data processed and the systematic sub-sample intervals used to process imaging sonar data among these studies (Figure 5a and b). Most of the studies using this strategy used intervals within a 60-min period, and so we constrained our analysis accordingly, although it is important to point out that daily, or larger sub-sampling intervals can be appropriate for many analyses and have also been used (Petreman *et al.*, 2014). This analysis showed a positive correlation (Figure 5c), indicating that the sub-sampling interval increases as the overall proportion of the data processed increases. Sub-sampling strategies that are carefully adapted to a specific dataset in the context of the study environment and research objectives can be highly effective at efficiently representing the metrics of interest (e.g. Boswell *et al.*, 2019). While flexibility in determining the interval and sampling intensity of metrics of interest is advantageous and diversifies the scope and scale of studies that can be

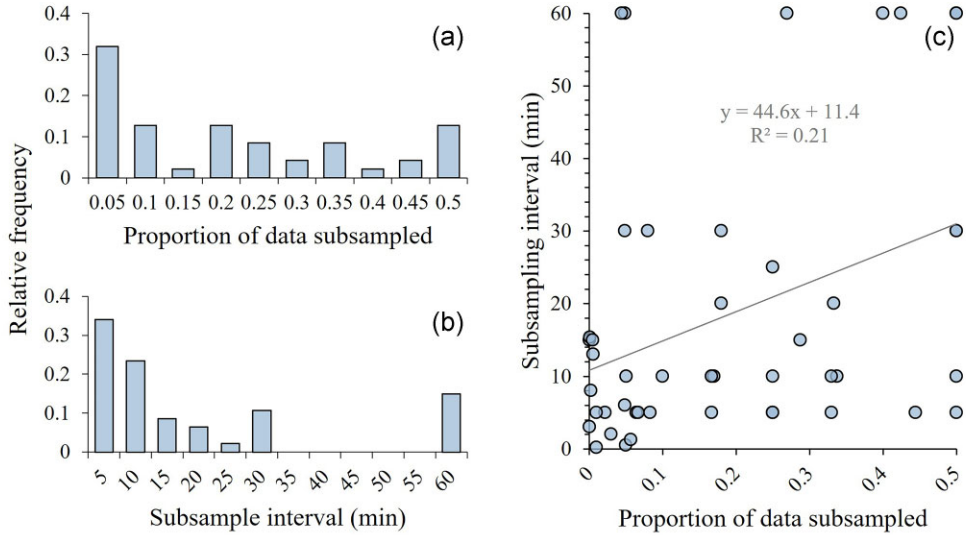

Figure 5. The proportion of data sub-sampled (a), the sub-sampling interval used (b), and a regression of the sub-sampling interval by the proportion of data sampled (c), for the 37 studies that sub-sampled data during post processing.

done, there has so far been little consistency among analytical methods, as identified by Schmidt *et al.* (2018), who rightly stated that standardization of certain sonar output metrics is a critical next step for cross-referencing results from studies.

Behavioural metrics: from an individual's reactions to collective patterns

Fish tracking methods using imaging sonar enable direct measurement of behavioural metrics at the individual or shoal level, including: swimming speed, swimming direction, reaction speed or direction, milling (large groups moving in no particular direction), position in the water column, body angle or alignment, tortuosity (a measure of the number of changes in direction, or path efficiency), and tail-beat patterns (frequency or motion), and at the school-level, including: school frequency, school size, and spacing among individuals (Figure 3a) (Table 2; "Information extracted" column, keywords: listed above). One or more of these variables have been measured using imaging sonar in at least 108 studies. The remaining 47 studies have measured abundances and lengths only, which themselves have been extracted in 146 and 107 studies, respectively.

Besides abundance and length, swimming speed and direction are the most straightforward metrics to measure by tracking a fish across its passage through the imaging sonar FOV and have been recorded in 34 and 90 and of the studies reviewed, respectively. Changes in swimming speed or direction in reaction to stimuli of interest are a particularly useful application that have been used in 26 studies. Swimming direction becomes more difficult to assess where milling activity occurs and can inflate abundance estimates. It is, therefore, commonly acknowledged that milling individuals were excluded from analysis and milling behaviour has only been incorporated into the analysis of 18 studies. Individual swimming depths or depth ranges of schools are also straightforward to extract using the distance from the bottom reported and the angle of the sonar unit when it is oriented vertically, or rotated horizontally (Able *et al.*, 2014). Vertical distributions can reflect important physico-chemical relationships when analyzed alongside environmental data (Munnelly *et al.*, 2019) and have been measured in 18 imaging-sonar studies. Variables such as tortuosity, body angle, and tail-beat patterns, are among the more subtle and labour-intensive metrics that can be extracted from imaging sonar recordings, useful for helping to identify subsets of groups engaged in unique behaviours (Egg *et al.*, 2019), separating species of similar body size and shape (Mueller *et al.*, 2010) or representing stress responses and energy expenditure (Tiffan *et al.*, 2010; Kirk *et al.*, 2015). These behaviours have been documented in 17, 16, and 7 studies, respectively (Figure 3a). For example, Tiffan *et al.* (2010) evaluated the energetic expenditure of chum salmon, *Oncorhynchus keta*, required to maintain position when spawning using tail-beat frequency.

In addition to the information these metrics can provide at the individual level, they may also be applied to schooling dynamics that result from collective group responses. Schooling is generally considered as a strategy that enhances fish safety (Pitcher and Parrish, 1993; Rieucau *et al.*, 2015), facilitates foraging and navigation (Quinn and Fresh, 1984; Makris *et al.*, 2009), or improves energetic and hydrodynamic efficiency (Domenici, 2001, 2010; Hemelrijk *et al.*, 2015). Variation in schooling tendency and school topology in marine fish species is commonly observed in response to environmental variation, predation risk, and anthropogenic disturbance (Fernö *et al.*, 1998; Soria *et al.*, 2003; Makris *et al.*, 2009; Paramo *et al.*, 2010), involving acute and rapid adjustments at the level of their collective structure (e.g. swimming faster and being more aligned with their school mates). These reactions support the idea that fish schools can display a high degree of behavioural and structural plasticity involving collective responsiveness that improve competence to cope with environmental stimuli (Makris *et al.*, 2009; Paramo *et al.*, 2010; Rieucau *et al.*, 2015).

A broad range of metrics have been used to quantify the behavioural state of schools using optical survey techniques (Delcourt and Poncin, 2012). For instance, these metrics include the school's cross-sectional area (Partridge *et al.*, 1980), swimming speed (Berdahl *et al.*, 2013; Kent *et al.*, 2019), individual's polarization (Viscido *et al.*, 2004; Cavagna *et al.*, 2008), angular velocity (Tunstrøm *et al.*, 2013), and rotational order and correlation strength providing a measure of information transfer rate between neighbouring fish (Handegard *et al*., 2012). Mainly, these metrics have been employed to characterize internal schooling states (Tunstrøm *et al*., 2013), quantify the behavioural responses to predator attacks (Rieucau *et al*., 2016), and information propagation rate (Strandburg-Peshkin *et al*., 2013; Rosenthal *et al*., 2015). Although the collective behaviour of aggregated fish has been well-studied in both simulation and laboratory settings, at both the individual and group levels (for instance see Gautrais *et al*., 2012), remote observations in the field under natural conditions remain challenging and are required to provide a suitable representation of the underlying mechanisms in schooling fish (Handegard *et al*., 2012; Rieucau *et al*., 2016).

In the study of schooling behaviour and dynamics, imaging sonar has been used to extract group-level metrics to describe dynamic fish schooling states influenced by several environmental or biotic factors. To this end, 19 studies have tracked school frequency and 17 have assessed school size. Distances of fish to one another can be time consuming to measure but provide fine-scale information on school structure and density (Handegard *et al*., 2012; Rieucau *et al*., 2015; Kruusmaa *et al*., 2016; Rodriguez-Pinto *et al*., 2020, 2022) and have been measured in 13 studies. In general, indirect methods for measuring many behavioural metrics are available for studying high densities of fish (schooling or not) where individual target tracking becomes impractical or impossible. Optical flow or particle image velocimetry (PIV) (Handegard *et al*., 2012; Rieucau *et al*., 2016, 2017b) can be used to measure swim velocity within a group or a subset within the group, to ascertain group polarization, rotational order, or correlation strength by assessing the net fluid-dynamic flow properties within the imagery. By allowing quantification of changes in swimming velocities within a school, the PIV technique has enabled the measurement of information transfer, or wave of agitation within a school (Handegard *et al*., 2012; Rieucau *et al*., 2016). School-level modifications are thought to reflect changes in the way that fish in groups balance fitness tradeoffs (e.g. feeding, survival, or reproduction). In an aggregation, such as a fish school, each individual responds to its local environment as well as to the behaviour of its neighbours; a process which can elicit emergent collective responses (Couzin *et al*., 2006; Herbert-Read *et al*., 2015). Changes in group state over time are thought to reflect how aggregated individuals in a group balance the trade-offs between the benefits and costs of being in a group (Pitcher and Parrish, 1993). Collecting high-resolution data about school topology, organization, as well as fine-scale swimming mechanisms (like tail-beat frequency) *in situ* will provide critical information underlying how schooling fish organize to extend their sensory ability and reach the energetic benefits of moving in groups under natural conditions.

The high-precision metrics extractable from imaging sonar recordings at the individual, shoal, or school-level have been used to examine several environmental or biological processes in addition to those already mentioned (Figure 3b) (Table 2; "Information Extracted" column, keyword: "community composition"; Table 2; "Effects and Environments" column, keywords: "passage", "habitat comparison", "spawning", "inter-annual or seasonal comparison", "diurnal patterns", "threat avoidance", "depth distribution", "spatial distribution", "gear evaluation", "diel cycle", "predation", "water chemistry", "tide", "current", "discharge", "light", "vessel traffic", "turbidity", "atmospheric conditions", "lunar phase"; and Table 2; "Methods" column, keyword: "analysis evaluation"). Unfortunately, manually tracking objects directly and extracting movement information is labour intensive, time consuming, and subjective (Braga *et al*., 2022). This is among the most prohibitive aspects of using imaging sonar to study fine-scale animal behaviours, requiring automated processing procedures for reasonable efficiency.

Automated quantification approaches

Automated or semi-automated approaches are objective strategies requiring less training and which save processing time. Automating at least part of the data processing procedure can be necessary to extract behavioural metrics with reasonable efficiency. Key steps involved in automating data processing include background removal of all stationary objects, threshold filtering of objects greater than a desired size, and object tracking through the sonar FOV (Neupane and Seok, 2020). Depending on the research objective, automated processing can increase or reduce precision. For example, metrics related to movement benefit from increased precision. Direct comparisons of automated and manual count methods have been included in 21 *in situ* studies (Figure 6). Success of automated fish detections has been variable, even among similar techniques that are applied across different study environments (Boswell *et al*., 2008). Generally, automated methods tend to underestimate counts in high-density settings and overestimate counts in low-density settings and can vastly overestimate counts when milling activity is common (Figure 6) (Hughes and Hightower, 2015). While automated procedures can be used to obtain length measurements, manual length measurements are currently preferred to ensure that fish alignment is perpendicular to the beams and to assure consistency in length metrics (i.e. standard or total length). This is because the caudal fin is often not fully defined throughout the recording, especially for smaller fish, for which the imagery is usually more similar to the standard length than the total length (Boswell *et al*., 2008; Burwen *et al*., 2010; Tušer *et al*., 2014; Cook *et al*., 2019).

Despite the advantages of automated approaches, 113 studies have used a manual processing strategy, while just 42 have used an automated or semi-automated processing procedure (Table 2; "Methods" column, keywords: "manual", "automated"). The various imaging sonars available have specific characteristics among manufacturers and so lack a common data format allowing standardized access to the information. This limitation has important implications that make it difficult to use the sonar information from external software other than those provided by the manufacturers. Although the imagery can be exported to still frames or video files for analysis external to manufacturer-specific software, the format in which the data is exported is usually pre-processed rather than raw, which can lead to a loss of data accuracy. This forces developers to look for unofficial solutions to interpret the raw data files, access the raw files captured by the sonar manually, analyze the information at a low level, or try to parse it to avoid loss of information, and many of these solutions are specific to individual sonar models (Cotter and Polagye, 2020a) and complicated to integrate with other sensors (Cotter *et al*., 2017; Polagye *et al*., 2020). The data models manufacturers use are often unavailable to the public, so manual access to the data may also be incomplete.

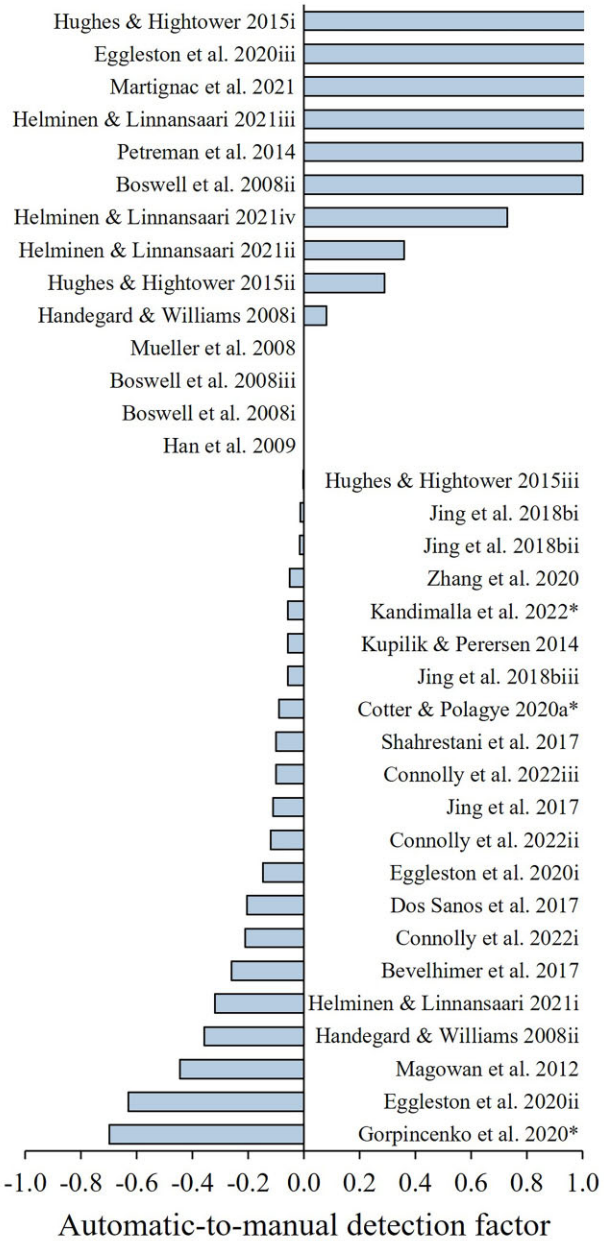

Figure 6. The automatic-to-manual detection factor for the 21 studies that directly compared manual and automated or semi-automated post-processing strategies, showing the proportional underestimation or over-estimation of automated or semi-automated counts, relative to manual counts. Multiple comparisons within individual studies are presented separately. Studies that used automated approaches to separate taxonomic groups are marked with asterisks. Cotter and Polagye (2020a) compared several approaches among many taxonomic groups, so we have limited our comparison to their best result for quantifying fish abundance.

Also for consideration is that the applications allowed by manufacturers are usually related to analyzing the information offline rather than working in real-time. It is difficult to access real-time imaging sonar data from external applications. Using drivers developed by the community outside the manufacturers, it is still challenging to access the data files once the acquisition is finished. This problem is partially mitigated by the fact that some manufacturers allow their devices to be connected via standard protocols, such as Ethernet (Polagye *et al.*, 2020), but this relies upon the transmission of a video feed provided by the sonar rather than the raw data. This major limitation has prevented the widespread analysis and detection applications that can use real-time information, although some promising progress to this end has been made (Cotter and Polagye, 2020a, b).

Software used to implement automated or semi-automated data processing include: Echoview, DIDSON, ARIS Fish, Sonar5-Pro, and MetaMorph, (20, 5, 2, 1, and 1 study, respectively), while programming environments such as C++, Matlab, and Python have been used to develop specific automated applications in 11 studies. All of these software and programming environments allow background removal and threshold filtering options. The DIDSON and ARIS Fish software enable the removal of footage of empty water from recordings using the "convolved samples over threshold" tool. This option can condense data collected over long time periods, focus subsequent manual processing efforts, and reduce the amount of storage space required. DIDSON, ARIS Fish, and MetaMorph all allow background removal and adjustments to threshold and intensity settings, however, these software are only useful for tracking individuals manually. Li *et al.* (2017) developed a similar tool that additionally output images for the purpose of training machine-learning programs. Sonar5-Pro additionally allows tracking of individuals, although the results need to be manually supervised to avoid over-counting (Martignac *et al.*, 2021). Of these methods, only Echoview, Matlab, and Python have been used to automate tracking individuals through successive frames. This key utility for fully automating the extraction of abundances and behavioural metrics also greatly simplifies successive manual reviewing steps in a semi-automated approach. Unfortunately, the license costs for these programs are high, which presents a barrier for researchers. Additionally, the coding and algorithm development required to automate object tracking in Matlab and Python has traditionally reduced accessibility, although artificial intelligence interfaces such as the Chat Generated Pre-trained Transformer (ChatGPT) are beginning to enable more researchers to develop or diversify their use of these and other programming environments. More accessible options for automating object tracking through the FOV are, therefore, anticipated to greatly progress the use of imaging sonar for tracking abundance and fine-scale behaviours.

Background removal of stationary objects within the sonar FOV becomes more complicated when imagery is surveyed from a mobile platform (see Figure 4 for an example of a Myliobatoid ray recorded by McCauley *et al.* (2014) using a stationary 1.8 MHz DIDSON and another recorded by Rieucau and Munnelly (unpublished data) using a mobile, vessel-mounted 1.8 MHz ARIS). Of the 36 studies using imaging sonar mounted to mobile platforms (Table 2; "Sonar" column, keywords: "mobile", and "stationary"), only six have used an automated data processing approach (Handegard and Williams, 2008; Mizuno *et al.*, 2013; Williams *et al.*, 2013; Dos Sanos *et al.*, 2017; Jing *et al.*, 2017; Jing, 2018a). Of these, only Dos Sanos *et al.* (2017) and Jing *et al.* (2017) have resolved targets against a changing seafloor. These studies used an edge-detection algorithm available in Echoview to separate fish from the bottom based on contrast. Jing *et al.* (2017) showed that abundance estimates obtained using this method in a sand-bottomed reservoir closely tracked manual counts. Automation of data processing from imaging sonar data collected from mobile platforms greatly increases the utility of this technology and is important to continue to develop and evaluate in other study environments. The main drawback associated with acquiring data from a moving platform is that sonar information must be aligned between frames in order to allow automated processing. In this sense, exploring the use of stabilization devices, such as gimbals, can bring benefits to underwater sensor data processing. These devices have been recently used in other related scenarios, such as aerial observation of marine species (Durban *et al.*, 2022) or for the monitoring of water resources (Rangel *et al.*, 2019). In addition, sonars can be coupled to other sensors capable of measuring the changes in pose (position and orientation) in real time. Inertial sensors, such as accelerometers or gyroscopes, have been used in underwater vehicle navigation tasks and are able to sense unintentional movements (Shakuat, 2021; Xu *et al.*, 2022). Some of the principles integrated in these navigation systems could be applied to compensating the movement of sonar devices. As mentioned previously, the other limitation for mobile surveys are motion artefacts. Objects can appear fragmented or disappear entirely due to aliasing when the object is moving faster than the image is created within the beam array, which will be a function of the ping rate, the platform speed, and the object velocity relative to the platform.

Several methods have been used to automate object detection and classification from imaging sonar recordings. Kalman filter automatic classification procedures are a common method when tracking individuals moving in a linear path (Han *et al.*, 2009a, b), which can be adapted to more complex scenarios by incorporating discriminant function, neural network, or nearest-neighbour analyses, to help distinguish fish from floating debris based on differences in patterns of motion (Mueller *et al.*, 2008; Tong *et al.*, 2009). Hungarian, DeepSORT, and Multiple Model Joint Probabilistic Data Association (IMMJPDA) algorithms are other similar options (Jing *et al.*, 2018a; Shen *et al.*, 2023). These techniques have also been used to automate length measurements (Kupilik and Petersen, 2014) and have been adapted to acquire comparable results between ARIS and BlueView sonars across different study sites (Le Quinio *et al.*, 2023).

Recent studies propose the use of machine learning techniques for fish detection and classification. Most of these techniques have been adapted from traditional object detection approaches for underwater surveying or navigational aids for other survey equipment outside the scope of this review (Cho *et al.*, 2015), but may offer additional advancements applicable to surveys of aquatic organisms, particularly from mobile platforms. Some of these approaches have been customized to recognize fish species using morphometric features (Bothmann *et al.*, 2016; Le Quinio *et al.*, 2023) and behavioural patterns such as body alignment and tail-beat patterns (Kang *et al.*, 2011; Helminen *et al.*, 2021), and acoustic shadows (Connolly *et al.*, 2022). In this regard, the work of Jalal *et al.* (2020) used a deep learning-based method complemented with temporal information combined in a hybrid solution that uses optical flow with Gaussian Mixture Models (GMM) and the "You Only Look Once" (YOLO) technique (Redmon and Farhadi, 2018), a neural network developed originally for object detection, to detect and classify fish in unconstrained underwater videos that is also useful for processing imaging sonar footage. This approach has been used by Kandimalla *et al.* (2022) and Fernandez-Garcia *et al.* (2023) to automatically detect and classify fish to species level. Cui *et al.* (2020) developed an autonomous underwater vehicle, and address the challenge of perceiving the environmental information acquired from its sensors using a convolutional neural network (CNN) based method to detect and count fish. CNNs have also been used to track and count fish in stationary settings where milling activity is high (Feng *et al.*, 2023), and to identify eels (Yin *et al.*, 2020; Pratt *et al.*, 2021; Zang *et al.*, 2021) and jellyfish (Gorpincenko *et al.*, 2020). Schneider and Zhuang (2020) and Christensen *et al.* (2020) developed approaches for calculating fish abundance using deep learning able to calculate estimates from sonar images acquired from the back of a trolling boat, and remote-operated vehicle, respectively. The video-like imagery is amenable to optical flow techniques developed for video image processing (Perivolioti *et al.*, 2021). Another recent study described an image generation system that used sonar and camera images to allow nighttime monitoring through an approach that used conditional generative adversarial networks (cGAN), which learned the image-to-image translation between sonar and optical images (Terayama *et al.*, 2019). As these and other techniques continue to be refined, it is important that researchers make them available as tools for the rest of the scientific community (Handegard and Williams, 2008).

Conclusion

Imaging sonar offers many unique properties compared to traditional extractive or remote sampling gears. The ability to non-intrusively survey complex habitats and obtain detailed behavioural information, even where visibility is limited, make imaging sonar suitable for addressing many research questions that have been difficult or impossible to study otherwise. These features additionally make imaging sonar an effective tool for evaluating the performance of other sampling gears, and are best used in conjunction with other gears. Integration with optical systems is particularly useful for improving the versatility of remote underwater video surveys. The amount of information that can be derived from the sonar imagery and the options to process the data can make sonar data overwhelming. There is no "one size fits all" method when processing imaging sonar data. An efficient processing strategy appropriate to addressing the research question at hand must be developed which takes into consideration the auto-correlative nature of the data, sub-sampling intervals, and environmental or behavioural aspects that might impact the results. When bounded by a carefully framed research question, even datasets over large time periods, spanning high spatial coverage, or those with high densities of targets can be processed efficiently. As imaging sonar becomes increasingly available to researchers, and automated processing procedures continue to develop, this technology will play an increasing role in demonstrating interconnectivity among organisms and habitats in the aquatic sciences.

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Conflict of interest

The authors have no conflict of interest to declare.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

Authors' contributions

RM: conceptualization, investigation, data curation, formal analysis, visualization, and writing. JC: conceptualization, writing, review, and editing. NOH: writing, review, and editing. MK: investigation, writing, review, and editing. KB: writing, review, and editing. GR: conceptualization, writing, review, and editing.

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