



REVIEW

The capacity of imaging sonar for quantifying the abundance, species richness, and size of reef fish assemblages

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ABSTRACT: Reef fish assemblages across tropical and temperate latitudes are increasingly threatened by human impacts and climate change. Accurate and efficient survey methods are essential for quantifying these communities to inform management strategies. Imaging sonars (ISs) are high-frequency acoustic devices that produce camera-like images of objects. Unlike optical instruments, IS functions effectively in turbid and dark water and has proven valuable in detecting fishes in poor visibility and at night. Abundance, species richness, and fish size are desirable metrics in most reef fish surveys. This review investigates previous attempts to quantify these metrics using IS across different habitats. These metrics are often quantified in comparison with alternative methods (e.g. cameras, extractive techniques). This review examines the causes of agreement or incongruence between estimates from IS and estimates from these alternatives. Any instrument employed to quantify reef fishes should be able to operate in structurally complex habitats, and thus the ability of IS to function in these circumstances is also reviewed. Finally, 5 notable limitations of IS are described and solutions discussed. Overall, this review underlines the net value of IS for surveying reef fishes but advises using alternative methods to complement IS estimates of abundance, species richness, and fish size.

KEY WORDS: Acoustics · Survey methods · Artificial reefs · Structural complexity · Data processing

1. INTRODUCTION

Degradation and overexploitation of the ocean over the past several decades have caused a major decline in marine biodiversity (Jackson 2008, Butchart et al. 2010, Duarte et al. 2020). This includes the depletion of numerous fisheries around the world (Fernandes & Cook 2013, Vasilakopoulos et al. 2014, Warren & Steenbergen 2021), and the capacity of fish stocks to recover remains very uncertain (Worm et al. 2009, Memarzadeh et al. 2019, Britten et al. 2021).

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Reef fish assemblages across both tropical and temperate latitudes are subjected to intense fishing pressure due to increasing demand from a growing human population (Cramer & Kittinger 2021), rapid urban development in coastal areas that has polluted and homogenised reef ecosystems (Gibson et al. 2007, Sandin et al. 2008), and the multifaceted effects of climate change (Hoey et al. 2016, Holland et al. 2020, Worm & Lotze 2021). The recovery of reef fish assemblages hinges on effective conservation and management strategies (McClanahan et al. 2011,

[§]Corrections were made after publication. For details see www.int-res.com/abstracts/meps/v717/c_p157-179/
This corrected version: December 7, 2023

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Publisher: Inter-Research · www.int-res.com

MacNeil et al. 2015). In turn, these strategies are informed and supported by accurate quantification of metrics of reef fish richness, including abundance, biomass, and species diversity, achieved using effective and efficient survey methods.

Reef fish sampling methods can be broadly characterised as extractive or non-extractive. Extractive methods, such as netting (e.g. Hickford & Schiel 2008, Lin et al. 2022) and use of ichthyocides (Ackerman & Bellwood 2002, Bellwood et al. 2006), are used for directly estimating fish size and species diversity, but result in the stress or mortality of sampled fishes. Non-extractive methods, including optical and acoustic techniques, are valuable for enumerating fishes whilst minimising impact on the target assemblage. Optical survey methods, including human-conducted underwater visual censuses (UVCs) and high-definition (HD) cameras, describe fish assemblages through visual detection. Optics are often considered the best means of directly observing fish behaviour, distribution, and community structure (Stoner et al. 2008, Dunlop et al. 2015), and are widely used in fish surveys as a result (Bicknell et al. 2016). However, optics are entirely dependent on light and, in order to be used at night or in deep water, need the addition of artificial light that can induce variable attraction and avoidance behaviours in fishes (Fitzpatrick et al. 2013, McIntyre et al. 2015). Optics are largely inhibited in highly turbid habitats, such as estuaries.

Acoustic methods use sound to detect aquatic life. Active acoustics propagate sound waves across the water column (a process termed ensonification) and detect the echoes that are produced when the sound waves intercept a physical target. Properties of these

echoes can then be quantified and displayed. Critically, acoustics function independently of light, so can be applied in turbid habitats (Frias-Torres & Luo 2009, Jůza et al. 2013, Egg et al. 2017, Griffin et al. 2020, Artero et al. 2021; Fig. 1), at night (Able et al. 2013, Viehman & Zydlewski 2015, Egg et al. 2017, Cotter & Polagye 2020a), and in deep water (Rose et al. 2005, Giorli & Au 2017, Giorli et al. 2018), often providing greater spatial coverage than optics in these circumstances.

However, acoustics are not without limitations. The range resolution (hereafter simply termed 'resolution') of acoustics is markedly lower than that of optics. Consequently, characteristics of fishes that can be visually detected, most notably colour and pattern, cannot be detected by acoustics. The simultaneous collection of alternative evidence, often using optical survey methods (e.g. Holmes et al. 2006, Maxwell & Gove 2007, Faulkner & Maxwell 2020), that provides information on taxonomic composition is essential to determine the species diversity of the ensonified fish assemblage (a process sometimes referred to as 'ground truthing'; McClatchie et al. 2000).

The resolution of acoustic devices can be augmented by increasing the frequency of the propagated sound waves. Imaging sonar (IS), alternatively termed 'acoustic cameras', propagates sound in an array of multiple simultaneous beams between 0.7 and 3 MHz. In common with other multibeam sonars, IS uses beamforming to process echoes in multiple adjacent, simultaneously transmitted, narrow beams. These sonars can distinguish multiple echoes from various parts of large targets relative to the beam width. However, the higher frequency of IS affords resolution

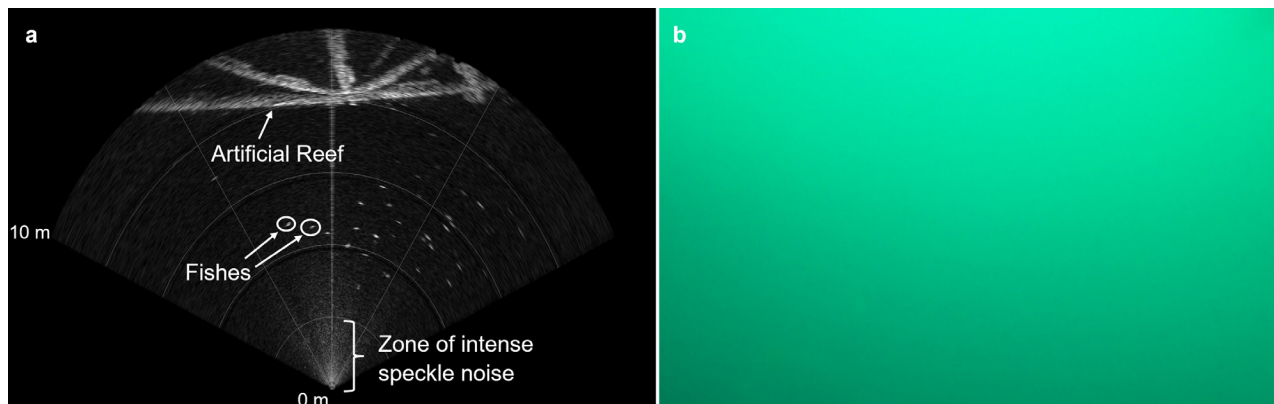


Fig. 1. Simultaneous frames captured by (a) a Blueprint Subsea Oculus Imaging Sonar (IS) operating at 1.2 MHz and (b) a high-definition optical camera around an artificial reef (a reeved oil and gas platform jacket) in the western Gulf of Thailand. The high turbidity in the region prevents fishes from being observed on the camera, yet the IS display reveals the true presence of fishes, which appear as white dashes set against a black backdrop of empty water. The structure of the artificial reef is clearly visible on the IS display, starting at approximately 8 m range. The first 2 m of the IS display contains significant amounts of 'speckle noise', in this case caused by the echoes produced by suspended sediment or organic matter in the water column

sufficient to produce camera image-like quality of individual fishes. This differs from the potential target detection of wider, single-beam echosounders which, in the case of split-beam, can ascertain the location of a target within the wider beam, but do not provide this location as a standard output on an echogram, only its range (see Simmonds & MacLennan 2005 for information on split-beam echosounders). Higher-frequency ISs work equally well in freshwater and saltwater because there is a negligible difference in sound absorption beyond 1 MHz (Moursund et al. 2003). Furthermore, the high resolution and high frame rate of IS permit real-time target visualisation (Moursund et al. 2003). Lower-frequency acoustics are favoured for surveying pelagic fish assemblages due to the higher spatial coverage afforded, ensonifying vast expanses of featureless water (Simmonds & MacLennan 2005, Irigoien et al. 2014). However, coastal waters are often more shallow and structurally complex, necessitating higher-frequency-higher-resolution devices that can more effectively discriminate between fishes, benthic biota, and physical habitat, albeit in much smaller sampling volumes.

ISs are efficient, versatile, and portable acoustic instruments that have been used to survey fish assemblages in various habitats. Following the introduction of the dual-frequency identification sonar (DIDSON) in the early 21st century (Belcher et al. 2001), later succeeded by the adaptive resolution imaging sonar (ARIS) series, several IS models have been developed, encompassing a range of frequencies and specifications (Table 1). However, the capacity of IS to describe and quantify reef fishes remains unresolved. Although tropical shallow-water reefs are typically characterised by clear water that permits the use of optical methods for fish surveys (e.g. UVCs, Samoilys & Carlos 2000), instances of high turbidity exist. For example, reefs adjacent to high riverine outflow (e.g. in the northern Gulf of Mexico) are often challenging to survey using optics due to poor visibility (Fig. 1). Moreover, the waters of many subtropical and temperate reefs often have reduced visibility due to greater quantities of suspended organic matter, algal blooms, and high densities of plankton (Lønborg et al. 2021). Therefore, visibility for optical surveys of fishes is generally lower on temperate reefs than on tropical reefs (Fabricius & De'ath 2000, Unsworth et al. 2014). Regardless of latitude, the absence of natural light at night means optical instruments require artificial lighting for surveying fishes during nocturnal periods, which may affect fish behaviour and subsequently bias estimations of density and species richness (Harvey et al. 2012, Fitzpatrick et al. 2013).

IS has predominantly been used to monitor fishes in freshwater or brackish habitats, and applications of IS to study marine fish assemblages are relatively scarce. Reef fish assemblages comprise a substantial proportion of fish abundance and diversity across the oceans. Coral reefs are estimated to support more than 25 % of all fish species, despite covering less than 0.1 % of the ocean floor (Fisher et al. 2015, Hoegh-Guldberg et al. 2017). Reef fish communities are also of substantial socio-economic significance, affording food to hundreds of millions of people and generating substantial tourism revenue (Munday et al. 2008). These factors motivate the dedicated quantification and monitoring of reef fishes, particularly given the uncertain future of reef ecosystems. In this review, the potential of IS for reef fish surveillance is explored, analysing previous studies of fishes across a range of habitats to determine how effectively 3 fish metrics can be quantified: (1) fish abundance, (2) species richness, and (3) fish size. These metrics are key for the accurate quantification of reef fish populations for the purpose of stock and habitat management, as outlined in a short background that precedes each subsection. This review also assesses how effectively IS can operate in habitats of high structural complexity, a requisite for any method of surveying reef fishes. Finally, the limitations of IS that can impact its use for reef fish surveys are also described.

2. QUANTIFYING FISH ABUNDANCE

2.1. Background

The abundance of different reef fish taxa and functional groups can reflect ecosystem health and the viability of fish populations for human exploitation. Both relative and absolute estimates of abundance are combined with species-specific measures of fish size to generate community-level estimates of biomass, a fundamental metric used in reef fish stock assessments (Nash et al. 2016). However, estimating abundance can prove problematic, particularly using visual methods, due to instances of multi-counting (Brehmer et al. 2006) and challenges in discriminating cryptic fishes from the background substrate (Willis 2001, Pelletier et al. 2011, Holmes et al. 2013).

2.2. IS application

Fish abundance is the most basic metric that can be quantified using IS. Comparisons of IS abundance

Table 1. Examples of imaging sonar (IS) models used to survey fish assemblages, spanning the typical range of specifications of ISs. H (V): horizontal (vertical) beam angle; NS: not specified. For cost, ***US \$50–80k, **\$25–50k, *\$<25k

Manufacturer	Series	Model	Frequency (MHz)	Beamwidth (H° × V°)	Number of beams	Horizontal field of view (°)	Resolution (mm)	Max. range (m)	Cost category
Sound Metrics	DIDSON	SV 300 m	1.1	0.4 × 14	48	29	NS	30	Out of prod.
			1.8	0.3 × 14	96	29	NS	NS	
		Diver Held 100 m	1.1	0.4 × 14	96	28	NS	35	Out of prod.
			1.8	0.3 × 14	96	28	NS	15	
	ARIS	Voyager 3000	1.8	0.3 × 15	64 or 128	30	3–19	15	***
			3	0.2 × 15	64 or 128	30	3–19	5	
		Defender 3000	1.8	0.3 × 15	128	30	3–19	15	***
			3	0.2 × 15	128	30	3–19	5	
		Defender 1800	1.1	0.5 × 14	96	28	3–23	35	***
			1.8	0.3 × 14	96	28	3–23	15	
		Explorer 3000	1.8	0.3 × 15	64 or 128	30	3–19	15	***
			3	0.2 × 15	64 or 128	30	3–19	5	
		Explorer 1800	1.1	0.5 × 14	48 or 96	28	3–23	35	***
			1.8	0.3 × 14	48 or 96	28	3–23	15	
		Explorer 1200	0.7	0.8 × 14	48	28	3–29	80	***
			1.2	0.6 × 14	48	28	3–29	35	
Tritech	Gemini	1200ik	0.72	1 × 20	512	120	4	120	**
			1.2	0.6 × 12	1024	120	2.4	50	
	Micron		0.72	2.34 × 20	128	90	8	50	*
Teledyne Marine	Blueview	M900-2250	0.9	1 × 12	768	130	13	100	**
			2.25	1 × 20	256	45	6	10	
Kongsberg	Flexview		0.7	1 × 30	NS	140	10	70	**
			0.95	0.8 × 27	NS	140	10	70	
			1.2	0.65 × 21	NS	75	10	70	
			1.4	0.55 × 18	NS	45	10	70	
Blueprint Subsea	Oculus	M750d	0.75	1 × 20	512	130	4	120	*
			1.2	0.6 × 20	512	130	2.5	40	
		M1200d	1.2	0.6 × 20	512	130	2.5	40	*
			2.1	0.4 × 12	512	60	2.5	10	
		M3000d	1.2	0.6 × 20	512	130	2.5	30	*
			3	0.4 × 20	512	40	2	5	

estimates with those from alternative methods (e.g. optic studies) are essential to determine the accuracy and precision of IS in quantifying reef fish populations. The distance gradings on many IS displays (Fig. 1), which enable calculations of sampling volume, can facilitate calculations of density. However, many studies have incorrectly assumed rudimentary beam shapes, most commonly rectangular-based pyramids (Shahrestani et al. 2017, Lankowicz et al. 2020), such that resulting density estimates are erroneous due to inaccurate calculations of sampling volume. IS beams are instead conical, defined by vertical and horizontal apertures of known size at the apex, with a curved base (Sibley et al. 2023).

Numerous studies have reported correlations between abundances quantified by IS and estimates from alternative methods, including mark–recapture sampling (Pipal et al. 2012), extractive methods (Rakowitz et al. 2012, Faulkner & Maxwell 2020, Kerschbaumer et al. 2020, Smith et al. 2021, Gutiérrez-Estrada et al. 2022), visual counting (Holmes et al. 2006, Maxwell & Gove 2007, Faulkner & Maxwell 2020), and lower-frequency acoustics (Maxwell & Gove 2007). Silver-phase European eels *Anguilla anguilla* have been a focal species for abundance quantification with IS to inform migratory patterns and management techniques, with several studies reporting correlations between IS abundance estimates and

both historic and contemporaneous catch data (Bilotta et al. 2011, Lenihan et al. 2019). The efficiency of IS in quantifying fish abundance (even accounting for data postprocessing) has been reported to be higher than several extractive techniques that have been historically favoured for abundance estimation (Mora et al. 2015, Kerschbaumer et al. 2020, Artero et al. 2021, Staines et al. 2022). IS abundance estimates have been shown to correlate with alternative methods of various size selectivity, from minnow traps (Smith et al. 2021) to targeted fishing of large demersal species (Artero et al. 2021), indicating that IS abundance estimates are applicable across a range of fish sizes.

Nevertheless, some studies have reported discrepancies between IS abundance estimates and alternative methods. Several reports of higher IS abundance estimates compared to assorted alternative methods include: higher detection rates of potadromous fishes than an HD camera, relative to stow-netting abundance estimates, in a shallow river (Egg et al. 2018); densities from a deep-sea scattering layer (400–800 m deep), thought to be squid, that were several orders of magnitude higher than previous trawling estimates (Giorli et al. 2018); higher detection rates of Chinese sturgeon *Acipenser sinensis* in their deep riverine spawning ground than a long-range echosounder (Chang et al. 2017); IS abundance estimates of juvenile salmonids twice those of snorkelling UVCs along a constructed seawall (Accola et al. 2022); and fish densities recorded by ISs operating at 4 different frequencies to be on average 3 times greater than those quantified using a simultaneous HD camera at artificial reefs off Western Australia (Sibley et al. 2023). Abundance estimates were also demonstrated to have greater accuracy and precision than mark–recapture estimates of salmonids in Holmes et al. (2006).

Conversely, some studies have reported higher abundance estimates from alternative methods when compared to IS. Hayes et al. (2015) compared counts of brown trout *Salmo trutta* from a raft-mounted IS with visual estimates from drift diving UVCs. IS estimates were markedly lower (only ~22% of dive estimates) and less precise. IS surveys were also estimated to be 34% more costly in terms of effort than the UVCs, though this is likely balanced by fewer health and safety concerns. Mora et al. (2015) reported higher abundance estimates of green sturgeon *Acipenser medirostris* using mark–recapture compared to IS estimates, although the latter were markedly less variable. Regarding extractive techniques, Smith et al. (2021) reported higher fyke net abundance estimates than IS across assorted shoreline habitats. All 3 studies used a DIDSON operating at either 1.1 or 1.8 MHz.

The differences in abundance estimates between IS and alternative methods can be attributed to several factors. Foremost, sampling volume has been identified as a highly influential variable. Holmes et al. (2006) compared IS (DIDSON, 1.8 MHz) counts of sockeye salmon *Oncorhynchus nerka* with human counts over different sampling volumes in a shallow river. When salmon were forced through an enumeration fence, generating high fish density, there was strong agreement in the estimates from both methods. However, when sampling volume was unconstrained, differences arose; the study identified the angle at which the IS was deployed to underpin differences between the 2 methods. Specifically, orientating the IS towards the riverbed meant IS estimates were greater than visual counts. This was because fishes near the riverbed could be ensonified that were otherwise obscured from visual detection from the surface due to water turbulence and sun glare. Orientating the IS at higher angles generated markedly lower IS estimates compared to visual counts, suggesting that visual enumeration outperforms IS in open water. Precision of IS estimates was markedly higher at greater fish densities, indicating that IS should be employed for quantifying abundance when the number of fishes per unit volume is high. In Maxwell & Gove (2007), IS accurately counted fishes even at passage rates of up to 6000 fish h⁻¹, whereas lower-resolution acoustic instruments struggled. In contrast to Holmes et al. (2006), Faulkner & Maxwell (2020) reported that error in IS counts relative to human and gill-net counts occurred at high fish density. Overestimation of fishes by IS was caused by multipathing, where echoes reflect off the surface or seabed prior to intercepting the transducer. This can cause targets to appear segmented, as can geometric scattering, whereby IS beams scatter irregularly from body parts of variable density, such as bones, muscle tissue, and swimbladders (Foote 1980, Sibley et al. 2023). Nevertheless, instances of multipathing and geometric scattering can be identified using continuous footage to discern the true appearance of affected targets (Fig. 2). For fishes that form dense aggregations, the limited resolution of IS relative to optics means that discrimination of these individuals has proved very challenging, such that categorical estimates are used as opposed to discrete counting (Becker et al. 2013). Alternatively, provided that individual fishes can be distinguished from one another, IS can detect fishes that are camouflaged against the background habitat structure where optical instruments fail to do so (Sibley et al. 2023).

A major factor causing challenges to IS abundance estimates is multipassing, which occurs when the

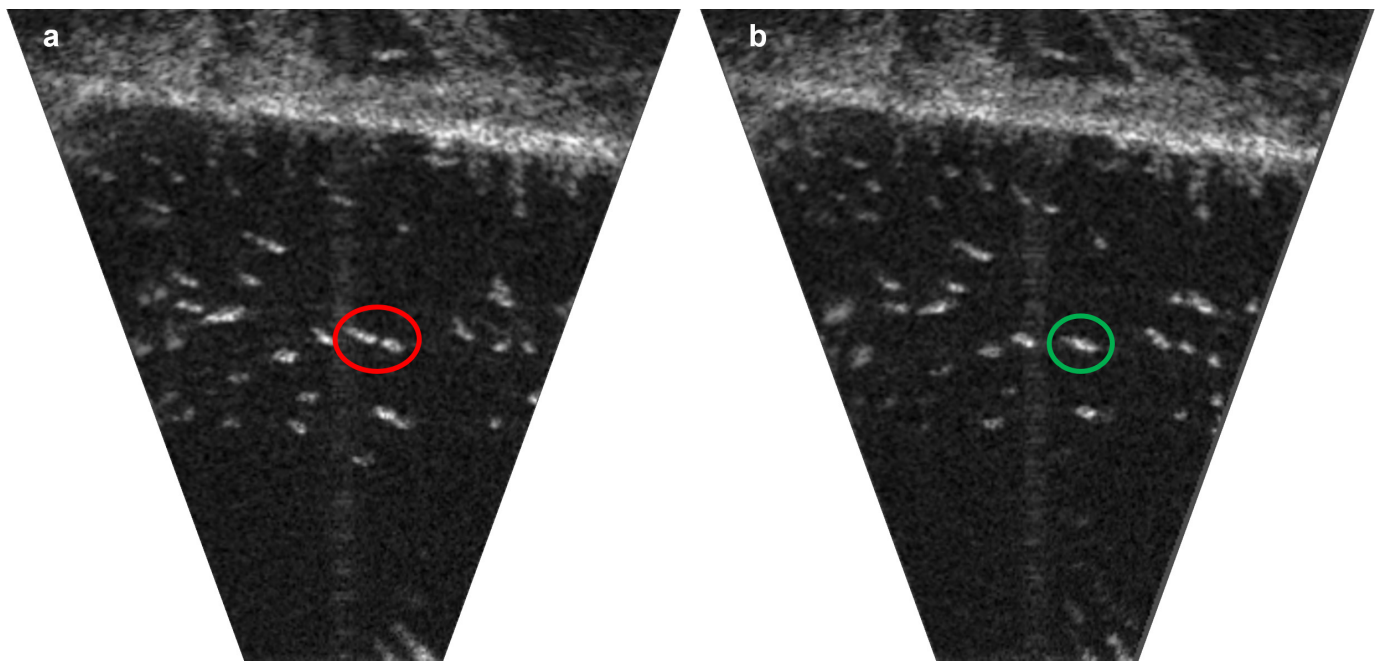


Fig. 2. Consecutive still frames from a Blueprint Subsea Oculus Imaging Sonar (IS) operating at 3 MHz at an artificial reef, the north Rottneest fish tower, off the coast of Perth, Western Australia. (a) The 2 targets circled in red appear as 2 distinct fishes of similar size to the other objects in the frame. However, in (b), these 2 objects appear as 1 fish, circled in green. This is attributable to either multipathing, whereby echoes from fishes reverberate off dense physical structures (e.g. the seabed or background reef habitat) before reaching the transducer, or geometric scattering, whereby IS beams scatter differently upon encountering body parts of varying density (e.g. muscle tissue, bones, swimbladders). Adjacent frames or continuous sequences of footage are needed to identify instances of geometric scattering and multipathing that can otherwise result in overestimation of fish abundance. The soft benthic growth (likely members of the subclass Octocorallia) on the upper crossbeams of the fish tower can also be visualised at this frequency

same individual exits and re-enters the field of view (FOV) of the IS and is counted multiple times. The limited resolution of IS makes it harder to track these individuals, whereas optical characteristics may help to distinguish recurring individuals in video footage. Multipassing can generate overestimations of fish abundance and is particularly apparent for fishes that mill in the FOV (Magowan et al. 2012, Grote et al. 2014, Petreman et al. 2014, Viehman & Zydlewski 2015, Eggleston et al. 2020), and taxa that are highly mobile and transient (e.g. reef sharks, McCauley et al. 2016). The risk of multipassing was considered by Wei et al. (2022) to be why most fish abundance estimation work using IS has focused on migrating fishes that are only moving in one direction, thus negating the impact of multipassing. More knowledge of species-specific milling tendencies would be valuable for mitigating potential overestimations (Wei et al. 2022). Lenihan et al. (2019) recommend that IS abundance estimates be compared against estimates from alternative methods prior to each survey; to mitigate double counting caused by multipassing, relative abundance was calculated as the maximum

number of individuals present in the FOV at the same time. In contrast, underestimation by IS can occur if fishes are demersal and sedentary, as it is harder to discriminate them from the underlying substrate without conspicuous movements (Frias-Torres & Luo 2009, Artero et al. 2021). Critically, multipassing can also be an issue for optical surveys. Implementation of conservative abundance estimates, such as MaxN (the maximum number of an individual species observed in any one frame of the video; Ellis & DeMartini 1995, Willis et al. 2000), can mitigate overcounting from multipassing by providing a conservative estimate of abundance. However, these estimates are often non-linear to true abundance (Schobernd et al. 2014), especially over smaller sampling volumes (Campbell et al. 2015), and are limited for counting individuals in large aggregations (Munnely et al. 2019). Instead, they may provide estimates of relative abundance in these circumstances.

Variable abundance estimations are not solely attributable to characteristics of the target fish community. Bathymetry has been demonstrated to influence the precision of IS abundance estimates (rela-

tive to visual counts), with the greatest IS precision achieved in deeper and more homogeneous channels of water (Holmes et al. 2006, Hayes et al. 2015). Limitations associated with the alternative methods used to estimate abundance must also be considered. For example, Smith et al. (2021) conjectured visual gear avoidance to underpin lower diurnal abundance estimates from netting techniques compared to IS. For non-invasive methods, behavioural responses of fishes to the platforms upon which instruments are mounted have also been widely reported. For example, the presence of both SCUBA divers (Lindfield et al. 2014, Reynolds et al. 2018) and remotely operated vehicles (Stoner et al. 2008, Ryer et al. 2009, Laidig et al. 2013) can elicit both attraction and avoidance in many fish taxa, resulting in over- and underestimations of abundance, respectively (Wetz et al. 2020).

3. QUANTIFYING SPECIES RICHNESS

3.1. Background

Reef fish communities are incredibly diverse, representing some of the most speciose assemblages on the planet (Fisher et al. 2015, Hoegh-Guldberg et al. 2017). Accurate and consistent species identification underpins quantification of ecosystem function and stability, allowing for changes to reef ecosystems to be monitored at relevant taxonomic scales. Identification is particularly critical for calculations of biomass by informing the correct selection of taxon-specific length–weight relationships. Overall, understanding reef fish composition helps ascribe the value of reef fishes to humans, be that through recreational or commercial activities (Mazzoldi et al. 2019, Tribot et al. 2019).

3.2. IS application

Species identification is the principal limitation of acoustics. Any taxonomic inferences to be made from acoustic data require expert understanding of the behaviour, ecology, and morphology of the target fish assemblage (Brehmer et al. 2006, Parsons et al. 2014, Schmidt et al. 2018). However, this becomes increasingly difficult with more diverse and complex assemblages such as reef fishes. Alternative evidence in IS studies of fish assemblages to infer species composition has been collected using various methods, including extractive techniques such as gillnetting (Patrick et al. 2014, Hughes & Hightower

2015, Lin et al. 2016, van Hal et al. 2017), seine netting (Becker et al. 2011b, Rieucan et al. 2015), electrofishing (Hughes & Hightower 2015, Ogburn et al. 2017, Henderson et al. 2023), trawling (Rakowitz et al. 2012), optics (e.g. human observations at the surface: Schmidt et al. 2018, Lankowicz et al. 2020; cameras: Cotter & Polagye 2020b; Fig. 3), and telemetry (Mora et al. 2018). Alternative evidence can be collected alongside IS data to provide simultaneous information on species composition, or collected independently, sometimes several weeks, months, or years before deployment of the IS (Becker et al. 2013, Grote et al. 2014, Lankowicz et al. 2020). Long-term monitoring programmes that encompass several different survey techniques have also provided alternative evidence in IS fish studies (Becker et al. 2011b).

Alternative evidence provides the basis for taxonomic interpretation of IS data that can drastically improve our insight into the surveyed fish community. For example, the assemblages observed by Becker et al. (2011a) were dominated by small schooling fishes. A fortnight of seine netting prior to the study, alongside the findings of a 15 yr long monitoring programme of the regional fish population, evidenced these highly abundant fishes to comprise only 2 species, a clupeid and an atherinid. In Capoccioni et al. (2019), alternative evidence from catch data indicated that large schools in a lagoon were typically monospecific, consistent with prior knowledge of species-specific distributions in the study region. Average fish size was also greater in larger schools; alternative evidence combined with IS can provide morphological and behavioural insight at a high taxonomic level. Species-specific length distributions acquired from previous surveys have been used to identify IS fishes (Becker & Suthers 2014, Grote et al. 2014, Lankowicz et al. 2020), enabled by the length measurement functions available on most IS post-processing software. In lieu of direct species identification, fishes detected using IS may alternatively be aggregated into size-based classes, defined by the known fish community composition of the region from alternative evidence (Becker et al. 2013). However, application of methods for gathering alternative evidence is contingent on the limitations of those methods. For example, Mago-wan et al. (2012) detected fish movement with IS to be greatest at night, though failed to provide species inference using an optical system due to the absence of light. Where light is not entirely absent, or can be appropriately supplemented, alternative optical methods may still function to provide taxonomic inference by identifying fishes that swim at very close ranges (see Bolser et al. 2020).

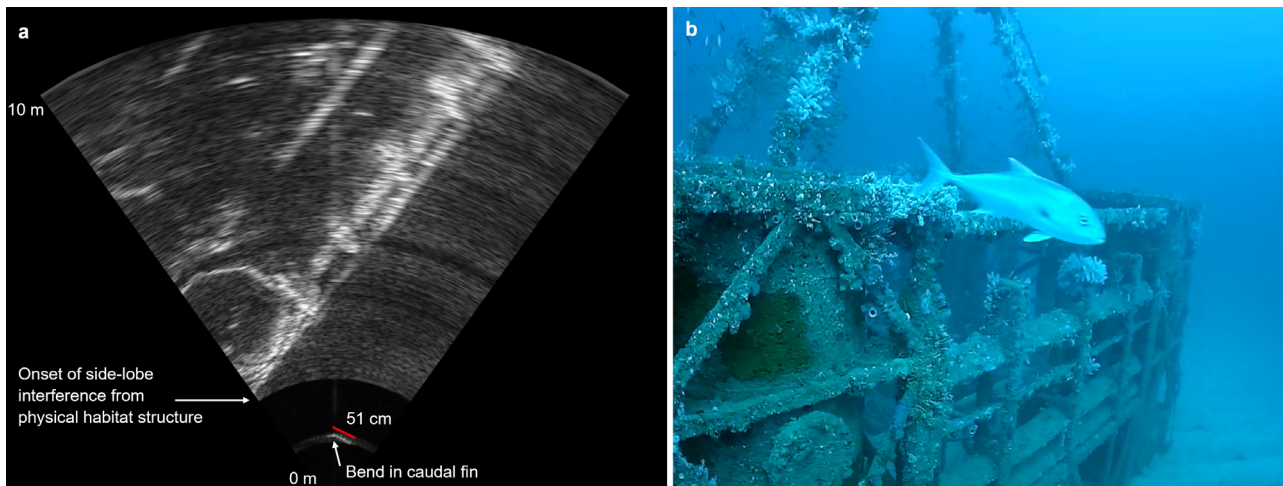


Fig. 3. (a) Still frame from a Blueprint Subsea Oculus Imaging Sonar (IS) operating at 0.75 MHz at the north Rottneest fish tower. The corresponding measurement tool in the Oculus Viewpoint software (www.blueprintsubsea.com/oculus/support) enables the sizing of objects on the IS display. (b) Simultaneous high-definition video footage reveals this target to be a greater amberjack *Seriola dumerili*. Note that the bend in the caudal fin in the IS display prevents the full linear measurement of the fish to be taken. Note the strong interference in the IS frame starting at approximately 2 m, caused by the simultaneous interception of the dense physical structure of the fish tower by adjacent beams in the IS beam array, resulting in noise in those adjacent beams at range (known as 'side-lobe interference' or 'crosstalk'). This can obscure targets near the structure, and altogether prevents detection of fishes occupying the interstitial spaces of the tower

Numerous studies have developed classification protocols based on traits detectable using IS alone. The success of species identification using IS particularly depends on marked morphological variation between the ensonified species (the likelihood of which is reduced if species richness is high, such as on coral reefs; Grote et al. 2014, Jones et al. 2021, Accola et al. 2022). Larger, more distinct species are easier to identify. Jones et al. (2021) used an ARIS Explorer 3000 (3 MHz) to distinguish finfish and elasmobranch species based on morphological and behavioural traits. Elasmobranchs were characterised by distinct fin shapes (especially the caudal fin), body shapes, and locomotion (see www.soundmetrics.com/Image-Gallery/Fisheries/Habitat-Observations/Nurse-Shark-captured-during-Aquarius-expedition as an example). By contrast, fin shape alone was not generally reliable for finfish identification. For finfishes in particular, family-level identification was deemed more appropriate when inter-specific differences were not obvious, with swimming motion proving especially challenging to distinguish between finfish species due to overlap in tail beat frequency and general locomotion. Application of concurrent video provided alternative evidence to classify individual finfish species. Likewise, a known species composition proved necessary in Becker et al. (2017) and Shahrestani et al. (2017) to confirm IS species identification based on discrete morphological and behavioural features. Able et al.

(2014) utilised various netting techniques to supplement the multivariate analysis of various fish traits observable on IS (including size, schooling tendency, and zonation) by verifying the presence of certain fish species. The study identified 15 discrete fish species, yet multivariate discrimination of each species was undermined by high overlap in the quantified traits.

Several traits have been consistently used to make taxonomic inferences on fishes detected by IS, including body size and shape (Rose et al. 2005, Becker et al. 2011b, Grabowski et al. 2012, Magowan et al. 2012, Parsons et al. 2014, Boulêtreau et al. 2018, Artero et al. 2021), and discrete morphological features, without the need for alternative evidence. Examples of morphological features include the use of head shape and dorsal fin to discriminate European catfish *Silurus glanis* from Atlantic salmon *Salmo salar* in Boulêtreau et al. (2018), the distinctive head and fusiform body to discriminate invasive silver carp *Hypophthalmichthys molitrix* from native species in Ridgway et al. (2023), and the large head and rounded pectoral fins of goliath grouper *Epinephelus itajara* that discriminate it from other demersal fish species in Frias-Torres & Luo (2009). Locomotion has also been used as a distinguishing trait (Rose et al. 2005, Becker et al. 2011b, 2017, Parsons et al. 2014, 2017, Zhang et al. 2014, Artero et al. 2021), and is particularly useful for the identification of eels (Mueller et al. 2008, Doehring et al. 2011) and lam-

preys (Keefer et al. 2017) due to their characteristic sinusoidal swimming motion and anguilliform shape. Furthermore, the refined characterisation of tail beat patterns in large salmonids as revealed by Mueller et al. (2010), indicative of size, shape and swimming motion, led the authors to suggest that IS could prove valuable in future bioenergetic studies. This is further reinforced by Lenihan et al. (2019), who recorded eel swim speeds using IS that strongly agreed with previous dedicated bioenergetic studies.

A novel approach to IS species identification was proposed by Langkau et al. (2012) based on the acoustic shadows cast by ensonified fish targets. Acoustic shadows are generated because targets both absorb and reflect most of the propagated sound, such that non-ensonified regions behind the objects are formed that show the outlines of the ensonified objects. The study created templates of 4 freshwater species and described the shadows cast by each template when ensonified with a DIDSON (1.8 MHz) to distinguish between each species. Success was contingent on size, with templates <20 cm identified less successfully, as the defining traits of these templates were relatively small. Body compactness was particularly important; templates of taxa with more protruding features (e.g. cyprinids) formed more distinguishable shadows than templates of more compact taxa (e.g. salmonids). The study then classified the shadows of live fishes, achieving an 83.9% success rate. However, fishes only cast shadows in certain circumstances, depending on the position of the fish in the beam array, the tilt angle of the IS, and bottom topography. Reduced classification success for densely aggregating fishes was reported due to overlapping shadows. Success was also lower at greater ranges, likely due to decreased resolution (see also Parsons et al. 2014). Shadows also proved important in distinguishing goliath grouper from other large demersal fishes by Artero et al. (2021), particularly the morphologically similar cubera snapper *Lutjanus cyanopterus*.

Species identification of fishes by IS may be limited by specifications of ISs themselves. The lower resolution of IS compared to optics means that morphological and behavioural traits of smaller fishes are often less conspicuous (Artero et al. 2021). Cotter & Polagye (2020b) demonstrated that enhancing the resolution of IS by increasing frequency can improve classification success, especially for smaller targets. IS operating at lower frequencies can still make taxonomic inferences. Using a Tritech Gemini at 0.72 MHz, Parsons et al. (2017) managed to detect distinct swimming patterns even for targets <40 cm, as well

as describe the high morphological diversity of the ensonified assemblage. Classification was contingent on target orientation. Targets at lower incident angles relative to the IS reflected a greater proportion of the propagated sound, hence more of the target was observable on the IS display. As expanded on by Wei et al. (2022), conspecifics may appear very different on IS displays if they are ensonified at contrasting incident angles. Differences in the density of distinguishing morphological features that cannot be accounted for by IS are likewise vital for species discrimination (Parsons et al. 2017). Peripheral yet distinctive features, such as fins, are generally less dense than the homogeneous torso of the fish, so generate less backscatter and are therefore less conspicuous (Hwang et al. 2017, Wei et al. 2022).

So far, the characterisation of fishes for taxonomic identification has nearly exclusively involved manual processing and appraisal of IS footage. However, deep-learning (a division of machine learning) has been proposed as an automated alternative that mitigates the challenges of distinguishing, processing, and extracting morphological or behavioural features manually and consistently (summarised by Wei et al. 2022). Deep-learning uses fish-like targets that are manually labelled as distinct from other objects and background noise, then inputs them into a neural network for classification. Application of deep-learning is in the early stages of development (Zang et al. 2021), with classifying species of similar morphology necessitating a high level of *a priori* training (Kandimalla et al. 2022). Nevertheless, deep-learning holds potential for discriminating morphologically unique species and fishes from non-biological objects (Wei et al. 2022), and has already proved successful for classifying multi-species assemblages (Kandimalla et al. 2022). Analogously, automated approaches for quantifying fishes using optical instruments are progressing rapidly, accurately counting, measuring, and identifying fishes to streamline the post-processing of optical data (Shortis et al. 2016, Connolly et al. 2021, Li et al. 2021).

4. QUANTIFYING FISH SIZES

4.1. Background

The diversity of reef fishes is reflected by the range of sizes on display; reef fishes can vary markedly in size at both inter- and intraspecific levels (Froese & Pauly 2023). Accurate size measurements are a prerequisite of biomass calculations. Abundance at

length (and, by inference, age) can also be critical for fish stock assessments and to monitor the impacts of fishing on particular taxa and functional groups (Graham et al. 2005, Shin et al. 2005, Wilson et al. 2010).

4.2. IS application

The size of IS targets can be quantified using the measurement tools available in most post-processing software (Fig. 3), and the resolution afforded by IS is generally adequate for size measurements (most commonly the total length of the target) to be taken directly from the footage (Martignac et al. 2015). Targets as small as 1–2 cm have been measured with IS (Kimball et al. 2010, Dunn et al. 2023), as have targets several metres in length (Giorli et al. 2018). Notably, Egg et al. (2018) demonstrated the minimum size threshold (specifically, the threshold beneath which fishes of a given size become underestimated) detectable using an ARIS Explorer 3000 (3 MHz) to be 10 cm, smaller than the threshold of an HD optical camera (15 cm) used in the same study. Analogously, UVCs commonly impose a minimum size threshold when surveying fishes that is commensurate with their detectability at range. Small fishes (typically <5 cm) can often only be detected, counted, and identified in the immediate FOV, unlike larger fishes that are quantifiable at greater ranges (Prato et al. 2017).

As explored in Section 3, size quantification and categorisation can support inferences on species composition, as well as ontogeny and ecological groupings. For example, Becker et al. (2013) aggregated fishes into size categories based on IS measurements. Fishes >50 cm were labelled as large piscivores that were predating shoaling planktivores <10 cm. Similarly, Becker et al. (2011a) observed larger fishes >50 cm occupying the mouth of an estuary, where fishes <10 cm (annotated as 'baitfish' by Becker & Suthers 2014) were most abundant. Likewise, the bimodality of target sizes in Giorli & Au (2017), either side of a 50 cm threshold, was interpreted to signify larger predatory squid and smaller prey nekton, reinforced by the abundance of >50 cm targets being correlated with a high abundance of targets <50 cm.

Reef fish assemblages are typically dominated by relatively small species, and reef fishes are often allocated to very fine size groups in UVCs (e.g. Di Franco et al. 2009, Pinheiro et al. 2016). Relatively small errors in length estimates can scale up to marked inaccuracies in biomass calculations (St. John et al. 1990, Harvey et al. 2002), so apportioning fishes into

refined size groups is important when using a categorical approach to assess fish size. However, the lower resolution of IS relative to optical instruments means the fish size groups implemented in some IS surveys are often coarser than in optical surveys. Nevertheless, key size-based inferences on the ensonified fish assemblage can still be made. In Able et al. (2013), benthopelagic fishes were partitioned into small (<25 cm) and large (>25 cm) categories that were further refined by schooling tendency and aggregation size. Division of fishes into small and large categories by the same threshold in Grothues et al. (2016) was considered to represent functional differences related to length distribution, commensurate with the known species composition of the study site. Viehman & Zydlewski (2015) made ontogenetic inferences from IS data on a temperate pelagic fish assemblage by considering fishes <10 cm (at the smallest end of the size spectrum of ensonified targets) to be juveniles. Size-based ontogenetic inferences were also made for rainbow trout *Oncorhynchus mykiss* by Schmidt et al. (2018). Such inferences are facilitated by comparison of IS size estimates with known length-at-age data (Crossman et al. 2011) or growth models. Alternatively, Becker et al. (2016) detected no marked variation in the size of fish moving between habitats, in turn suggesting that all fishes were from the same cohort.

The accuracy of IS size measurements has been extensively quantified through comparison with other fish sizing methods. For example, Cook et al. (2019) implemented a 3-pronged approach to assessing the accuracy and precision of measurements using an ARIS 3000 (model unspecified) of smaller fishes (10–40 cm): (1) tank-based comparisons between the IS (3 MHz) and stereo-camera on 2 focal species and artificial targets; (2) measurements of 4 fish species at 3 MHz with different swimming modes; and (3) comparison of IS (1.8 MHz) and direct measurements of fishes caught in bait traps in field settings. The 3 trials revealed that IS measurements were of lower accuracy and precision than stereo-cameras but were generally comparable with direct measurements of trapped fishes. Overall, IS measurement error for 10–40 cm fishes ranged from 1 to 10%. This error is markedly smaller than the error recorded for larger fishes. Gutiérrez-Estrada et al. (2022) reported a ~19% error in IS measurements (Garmin Panoptix LiveScope, 1.1 MHz) for large (~45 cm) gilt-head seabream *Sparus aurata*, and Zhang et al. (2014) quantified mean length estimates of Chinese sturgeon using an IS (DIDSON 300 LR, 1.2 MHz) to be 35.6% shorter than manual estimates. Compara-

tively, for optical instruments, Harvey et al. (2002) reported a mean error of <1 cm for SCUBA diver estimates of fish size, relative to stereo-video length estimates, for fishes ranging from 18 to 59 cm. The accuracy of stereo-video length estimates was then investigated relative to direct measurements for southern bluefin tuna *Thunnus maccoyii* ranging from 83 to 141 cm by Harvey et al. (2003), calculating a mean error of 0.17 cm.

As with comparison of IS abundance estimates, Cook et al. (2019) exemplified the use of alternative methods to gather independent size estimates (see also Frias-Torres & Luo 2009, Crossman et al. 2011, Lin et al. 2016, Kerschbaumer et al. 2020, Artero et al. 2021, Bennett et al. 2021, Staines et al. 2022). IS size estimates have been validated by ensonifying fishes of known length (Burwen et al. 2010, Bilotta et al. 2011, Hightower et al. 2013, Tušer et al. 2014, Lagarde et al. 2020), most commonly captive fishes in aquaculture (Zhang et al. 2014) and aquaria (Daroux et al. 2019). Such studies have identified multiple factors that impact the accuracy and precision of IS size estimates (Table 2).

Despite the diversity of factors that undermine IS size estimates, the effects of some are less impactful than others. For example, although the range of the target from the IS influences size estimate accuracy, this seems to only occur at ranges greater than at least 10–20 m. Using a DIDSON at 1.8 MHz, Daroux et al. (2019) reported accurate estimates out to 10 m for silver carp ranging from 51 to 67 cm in length. Helminen et al. (2020) demonstrated no effect of range on length estimate accuracy of Atlantic salmon, ranging from 49 to 99 cm, out to 29 m range when using an ARIS Explorer 1800 at 1.1 MHz. However, the effect of range may be more relevant for smaller fishes. Giorli et al. (2018) reported that targets <4 cm long were hard to detect (let alone measure) at ranges beyond 5 m with a DIDSON at 1.8 MHz. This further demonstrates that, as with visual surveys, the maximum range at which a target is still detectable using IS is contingent on target size (Doehring et al. 2011).

A recurring theme across studies investigating IS measurement error is that the sizes of smaller fishes are generally overestimated, and larger fishes are generally underestimated (e.g. Hightower et al. 2013, Cook et al. 2019, Daroux et al. 2019, Helminen et al. 2020). However, the threshold of measurement error between small and large fishes is variable. For example, Cook et al. (2019) found overestimation to occur at lengths <40 cm, in contrast to Daroux et al. (2019), who reported overestimation below a 57 cm threshold.

However, this dichotomy is not ubiquitous. Lagarde et al. (2020) demonstrated fish on either side of a 45 cm threshold to be underestimated. A factor in addition to those in Table 2 that could drive the underestimation of size is the compression of the IS display from 3 (x, y, and z) to 2 dimensions (x and z; Price et al. 2013, Martignac et al. 2015), whereby predominantly y-dimensional features that elongate total body size (e.g. heterocercal caudal fins, Hightower et al. 2013) may not be ensonified completely. Dorsal and ventral surfaces are typically less reflective than pectoral surfaces for perpendicularly oriented targets, so measurements of object width are broadly less reliable than measurements of object length (Parsons et al. 2017). As described by Martignac et al. (2015, p. 496):

... uncertainties as a function of fish length can be explained by differences in receiver sensitivity between acoustic beams. Sub-beams far from the central axis are less sensitive than those close to it. Consequently, the length of large fish with part of their bodies outside the central axis will be underestimated.

Despite the extensive reporting of erroneous IS size estimates, several studies have found consistency between IS lengths and lengths quantified by alternative methods (Frias-Torres & Luo 2009, Burwen et al. 2010, Bilotta et al. 2011, Crossman et al. 2011, Kerschbaumer et al. 2020, Zhang et al. 2021, Bennett et al. 2021). Length estimates using a DIDSON 300 LR (0.7 MHz) were demonstrated by Lin et al. (2016) to be more accurate (relative to manual measurements) than estimates from a split-beam echosounder, which were highly affected by the choice of target strength–length equation (see also Martignac et al. 2015). Improvements in the accuracy of echosounder *in situ* target strengths using IS have been made that improve biomass estimates (Hwang et al. 2017). Ultimately, accurate reporting of size estimates quantified by IS necessitates error functions pertaining to the influential factors listed in Table 2 (Tušer et al. 2014). Such are the variable impacts on IS size estimates that Daroux et al. (2019) recommended taking the mean estimate from 3 to 5 measurements per target as a method to reduce the error that can arise from individual measurements. The need for such time-consuming replication would be assuaged by a standardised calibration process for IS target detection and size estimation, but this is currently absent (Martignac et al. 2015). Alternatively, implementing size classes in lieu of more erroneous continuous estimates would substantially reduce variation. The error in Atlantic salmon length estimates reported by Helminen et al. (2020), up to 22.8 cm, prompted the allocation of targets to binary size cat-

Table 2. Causes of error in imaging sonar (IS) fish measurements, identified from studies that quantified IS measurement error by providing alternative evidence of fish size (e.g. using fishes of known length or calibrated optic instruments)

Factor	Source of measurement error	Description	References
Locomotion	Swimming style	Different swimming styles influence the ensonified area of a target (e.g. sinusoidal swimming produces a smaller reflective cross section than more planar swimming styles); certain swimming styles are specific to certain taxa (e.g. sharks).	Burwen et al. (2010), Hightower et al. (2013), Zhang et al. (2014), Keefer et al. (2017), Egg et al. (2018), Cook et al. (2019)
	Swimming speed	Swim speed limits the time in which a target can be ensonified; movement of the fish in the time needed to generate the IS image could cause overestimation of size.	
	Swimming behaviour	Fishes that mill in the IS field of view are ensonified for longer than unidirectionally moving fishes, hence are likely measured with greater accuracy.	
Orientation	Target incident angle	Target angle relative to the IS beam array influences the ensonified area (e.g. lower reflective cross section at higher tilt angles).	Tušer et al. (2014), Egg et al. (2018), Cook et al. (2019)
	Target distance	Resolution decreases with increasing distance from the IS, and sound wave absorption increases at farther ranges. Both factors reduce the degree of ensonification of targets at range and thus reduce the intensity of backscatter.	Tušer et al. (2014), Giorli et al. (2018), Cook et al. (2019)
	Position in beam array	Targets at the edge of a beam array are only partially ensonified compared to targets in the centre of a beam array; thus, the total length of peripheral targets is not measured.	Tušer et al. (2014), Egg et al. (2018)
Inter- and intraspecific differences in morphology	Length	Larger fishes have a greater reflective cross section relative to the resolution of the IS, increasing measurement accuracy.	Burwen et al. (2010), Hightower et al. (2013), Cook et al. (2019),
	Body shape	Fusiform fishes have greater reflective cross sections than anguilliform fishes of equivalent size.	Daroux et al. (2019), Helminen et al. (2020),
	Focal body parts	Fish body parts vary in density (e.g. fins are less dense than the torso, thus are weaker reflectors of sound and more likely to be obscured by background noise that impacts size measurement). If fork length is used over total length, tail morphology can impact length estimates.	Lagarde et al. (2020)
	Girth	Target girth (typically highest around the torso of the fish) can shadow the rest of the body.	Tušer et al. (2014)
IS specifications	Beam width	For some IS models (e.g. DIDSON), the width of each beam that contains an echo is included in size calculations, even if the beam does not fully encompass all of the target (i.e. irrespective of the proportion of the beam width occupied by the target).	Hightower et al. (2013)
	Frequency	Lower frequencies afford greater range but decreased resolution, causing less accurate size estimates due to greater beam dispersion and reduced definition of targets.	No demonstrable studies, but discussed by Martignac et al. (2015) and Wei et al. (2022)
Data processing	Manual size estimates	Measurement accuracy and precision for manual estimates are contingent on the observer, based on experience and the incidence of human error.	Daroux et al. (2019), Helminen et al. (2020)
	Automated size estimates	Semi- or fully automated estimates depend on accurate discrimination of targets (e.g. being able to detect extremes, distinguish fishes from non-fish targets).	Helminen et al. (2020)

egories on either side of 63 cm. Subsequent allocation of fishes to each size category achieved up to an 83% success rate. Regardless, IS fish sizes, even if not consistent with true sizes, are still useful as relative (albeit not absolute) measures (Artero et al. 2021) and permit comparisons of size distributions across various ecosystems to inform inter-habitat differences in fish assemblages (Olson et al. 2023).

5. OPERATING EFFECTIVELY IN STRUCTURALLY COMPLEX HABITATS

5.1. Background

The abundance and richness of reef fish communities are underpinned by the provision of structurally complex habitat generated by the underlying substrate and associated benthic growth, providing vital resources including refuge and aggregation markers (DeMartini & Anderson 2007, Graham & Nash 2013). However, structural complexity can inhibit many survey techniques. Extractive methods like trawling and other netting techniques risk gear entanglement, prompting the use of destructive techniques like the use of ichthyocides, or non-invasive approaches such as eDNA sampling (e.g. West et al. 2020, Mathon et al. 2022). Moreover, the FOV of visual techniques is constrained by structural complexity, potentially obscuring reef-attached fishes from detection and making sampled volumes difficult to estimate.

5.2. IS application

IS has proved particularly popular for detecting fish assemblages associated with structurally complex artificial habitats that cannot be effectively surveyed with alternative methods like low-frequency echosounding (Moursund et al. 2003) and netting techniques (Able et al. 2013, Schmidt et al. 2018, Lenihan et al. 2019, Braga et al. 2022). Fish-habitat associations quantified with IS benefit from being able to resolve and focus on discrete structural features in the FOV (Viehman & Zydlewski 2015). Fishes around numerous artificial habitats of varying complexity have been surveyed using IS, including piers (Able et al. 2013, Grothues et al. 2016, Shahrestani et al. 2017); seawalls (Accola et al. 2022); wind turbine monopiles (van Hal et al. 2017); hydroelectric turbines (Viehman & Zydlewski 2015, Piper et al. 2018, Staines et al. 2022); levees (Eggleson et al. 2020); dams (Moursund et al. 2003, Grote et al. 2014, Braga et al. 2022); and

dedicated artificial reefs, including reefed oil and gas platforms (Fig. 1), fish towers (Sibley et al. 2023; Figs. 2 & 3), and shipwrecks (Plumlee et al. 2020). IS has also been applied in natural habitats where alternative methods are not viable. Shallow water, such as the creeks surveyed by Lankowicz et al. (2020) and the intertidal salt marsh pool of Rieucan et al. (2015), are inaccessible to seines and trawls, as are narrow bodies of water like the tidal channels surveyed by Cotter & Polagye (2020a,b).

Fishes associated with complex natural habitats have also been quantified using IS. Grabowski et al. (2012) deployed IS in habitats of varying complexity, from high-relief boulder and lava fields to low-relief sandy seabed. Artero et al. (2021) and Frias-Torres & Luo (2009) used IS to survey fishes at a rocky tropical reef and mangrove forest, respectively, both of which are structurally complex and challenging to survey. Dunn et al. (2023) used IS to estimate diversity associated with fringing oyster reefs, detecting a size-diverse community that showed minimal temporal variation in abundance. However, the complexity of the oyster reefs was considered to mask vulnerable site-attached fishes from detection, such that the smallest taxa were likely underestimated. Olson et al. (2023) deployed an IS to quantify fish size spectra in assorted nearshore habitats of varying structural complexity, including seagrass beds, coral reefs, and mangroves, evidencing differences across habitats that reflect variation in structural complexity. Again, however, fishes hiding within the physical habitat structure could not be detected, likely resulting in the underrepresentation of smaller, more vulnerable species.

In some instances, the architecture of natural habitats has been defined using IS, a practice that could enhance our understanding of reef fish-habitat associations by more effectively quantifying reef structural complexity. Griffin et al. (2020) used 2 ARIS Explorers (1800 and 3000), both at 1.8 MHz, to characterise the heterogeneity and extent of biogenic reefs formed by tube-dwelling polychaetes (*Sabellaria*). The authors were able to resolve the structure of individual colonies, including quantification and categorisation of *Sabellaria* coverage, patchiness, and vertical relief. Estimates of vertical relief were consistent with optic and side scan sonar. However, the IS struggled to discriminate low-relief colonies from the seabed, principally because these colonies did not generate the distinct acoustic shadows characteristic of taller colonies. In contrast, fine-scale heterogeneity was ensonified on a gravel riverbed by Maxwell & Gove (2007), in parallel to the discrimination of Chinook salmon

Oncorhynchus tshawytscha redds by Tiffan et al. (2004) that were characterised by conspicuous acoustic shadows. Likewise, the pockhole-like nests of Antarctic icefish *Neopagetopsis ionah* were visualised by Purser et al. (2022), with IS contributing to the discovery and mapping of a vast breeding colony. At larger scales, IS was even considered by Maxwell & Smith (2007) to be comparable to traditional methods of bathymetric profiling, particularly in distinguishing offshore slope gradients. The resolution of IS is even sufficient to depict soft benthic growth including soft corals of the order Alcyonacea (Figs. 2 & 4).

6. LIMITATIONS OF IS

IS has unquestionably provided vast insight into the abundance, richness, and size of fish communities across assorted marine and freshwater habitats that are often difficult to sample with alternative methods. However, several limitations of IS have been reported across multiple studies. Further investigation and, where possible, remediation of these limitations will be essential to optimise IS for fish surveys across a range of habitats, including reefs.

6.1. Resolution

Overarchingly, acoustics cannot detect different colours and patterns—a characteristic benefit of optics. Identifying discrete species and individuals that may vary in visual traits is therefore very challenging; despite attempts to make taxonomic inferences from IS data alone as described in Section 3, species identification using IS has proven unsuccessful in many cases (e.g. Becker et al. 2013, O'Connell et al. 2014, Egg et al. 2018). Instead, the detection and distinction of other fine-scale details, particularly morphological features, are contingent on resolution, in turn a function of frequency. However, morphometrics are not always quantified successfully. Van Hal et al. (2017) reported the length and shape of fishes to be less detailed than anticipated when using a DIDSON (1.1 MHz), resulting in a failure to identify the species present when comparing with alternative evidence. Likewise,

Hwang et al. (2017) experienced challenges in detecting the extremes of fishes at the frequencies used (1.1 and 1.8 MHz; DIDSON), resulting in underestimations of total length. IS resolution has also proven limiting in distinguishing fishes in dense schools (Able et al. 2013; Fig. 4), not least given the masking of individuals by the shadows cast by other fishes (Magowan et al. 2012) and is particularly apparent for fishes smaller than 10 cm (Becker et al. 2011b). Ensonified fishes in dense schools therefore may not be countable (Braga et al. 2022) or measurable (Becker et al. 2016). Ultimately, the highest possible resolution is desirable in such circumstances. However, acoustic pulses attenuate faster at higher frequencies, hence range is inversely proportional to frequency. Decreasing resolution with range means targets at greater distances from the IS are less accurately resolved (Able et al. 2013), which can particularly impact size estimates (Viehman & Zydlewski 2015, Staines et al. 2022). Nonetheless, as discussed in Section 4, this is typically not an issue at short to intermediate ranges and can be further mitigated by developing ISs with narrower and more numerous beams that are propagated at higher frequencies.

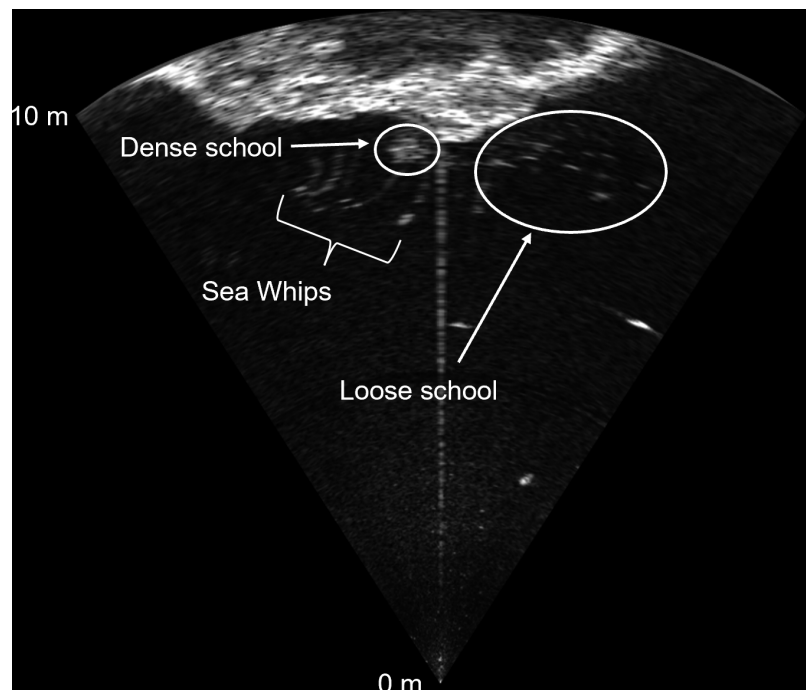


Fig. 4. Still frame from a Blueprint Subsea Oculus Imaging Sonar (IS) operating at 1.2 MHz at Hin Bai, a pinnacle coral reef in the western Gulf of Thailand. The resolution of the IS was sufficiently high to detect sea whips (order Alcyonacea), a type of soft coral protruding from the hard substrate of the reef. Two fish schools of low and high density were also captured, demonstrating the potential of IS to profile fish schooling dynamics. However, the resolution of the IS was not sufficient to discriminate individuals in the dense school

6.2. Noise

IS is also subjected to numerous sources of noise. Ensonification of background structures such as the seabed or benthic growth can mask echoes from both small (Dunn et al. 2023) and large (Parsons et al. 2014) fishes located between the structure and the IS (Rose et al. 2005, Magowan et al. 2012, Viehman & Zydlewski 2015, van Hal et al. 2017, Braga et al. 2022), examples of which are illustrated by Sibley et al. (2023). Entrained air in turbulent water can also reflect sound (Grote et al. 2014, Viehman & Zydlewski 2015, Cotter & Polagye 2020a,b). Entrained air echoes are particularly difficult to distinguish from small fish echoes (Holmes et al. 2006, Handegard & Williams 2008). Echoes from other non-fish objects, including debris, non-fish biota, and suspended organic matter (Holmes et al. 2006, van Hal et al. 2017, Staines et al. 2022), are also produced, reducing the signal-to-noise ratio (Maxwell & Gove 2007) and sometimes interfering with one another to produce 'speckle noises' that often appear similar to comparably sized fishes (Cho & Yu 2015, Staines et al. 2022, Wei et al. 2022; Fig. 1). Discriminating between fishes and speckle noises can prove particularly difficult if the fishes are not displaying active behaviour (Staines et al. 2022). When IS is deployed high in the water column, interference from the surface of the water may also conceal fish detections (Gutiérrez-Estrada et al. 2022, Staines et al. 2022). Side-lobe interference (also known as 'crosstalk') can impede fish detection and occurs when adjacent beams in the sonar array encounter the same dense object, generating noise in those adjacent beams at variable range (Cotter & Polagye 2020b, Sibley et al. 2023; Fig. 3). Fishes that are orientated perpendicular to the beam array at sufficiently close ranges may be detected in the centre of some beams and the side lobes of others (Hightower et al. 2013). Ultimately, most sources of noise generate echoes of lower intensity than fishes themselves. Therefore, implementing a conservative echo intensity threshold, as often practiced in lower-frequency echosounding (Korneilussen et al. 2008), may eliminate erroneous detections and interferences.

6.3. Display

IS is limited in the way echoes are displayed. IS compresses acoustic signals from detection in 3 dimensions to presentation in 2 dimensions, such that fishes in the same vertical plane cannot be distin-

guished from one another (Martignac et al. 2015, Egg et al. 2018). In instances of high fish density, this can cause underestimation of abundance and details of behaviours (e.g. predation) to be lost (Rakowitz et al. 2012, Price et al. 2013). One solution practiced by Holmes et al. (2006) is to rotate the sonar to provide information on vertical distributions having ensonified fishes in the horizontal dimension. 3-D modelling and reconstruction from 2-D IS imagery is also possible (Castellani et al. 2005, Jing et al. 2018), and the potential of true 3-D acoustic cameras continues to be explored (Lagudi et al. 2016).

6.4. Data processing

Ultimately, long-term deployments of IS generate vast amounts of data (Capoccioni et al. 2019, Cook et al. 2019). Processing IS data can be manually performed or semi- or fully-automated. Manual processing can take a long time (Schmidt et al. 2018, Wei et al. 2022), and vast datasets are typically analysed by multiple observers. However, inter-observer biases can arise, particularly based on differing interpretations of echoes as either fishes or non-fish objects (Keefer et al. 2017, Jones et al. 2021) and of different sources of noise (Petreman et al. 2014). Moreover, manual counting can be erroneous when fish density is high (Martignac et al. 2015) or fishes are milling in the FOV (Petreman et al. 2014) or multipassing (Brehmer et al. 2006). Differences in repeat counts can even arise within individual observers (Magowan et al. 2012).

Automated processing of IS data is increasingly used to improve the efficacy of analysing large datasets whilst reducing human error (Eggleston et al. 2020, Connolly et al. 2022, Wei et al. 2022). Automation incorporates refined and customisable fish detection, quantification, classification, measurement, and tracking algorithms (Mueller et al. 2008, Han et al. 2009, Hightower et al. 2013, Rieucan et al. 2015, Bothmann et al. 2016, Cotter & Polagye 2020a,b, Eggleston et al. 2020, Pratt et al. 2021, Feng et al. 2023, Fernandez Garcia et al. 2023, Le Quinio et al. 2023) that are essential for inferences of taxonomic richness and assessments of abundance, size, and behaviour (Kang 2011). Foremost, automated processing necessitates enhancing the images by subtracting background noise (Han et al. 2009, Viehman & Zydlewski 2015, Capoccioni et al. 2019, Eggleston et al. 2020, Helminen & Linnansaari 2021). This is typically achieved by excluding echoes attributable to non-target sources through comparison with refer-

ence images that contain no background noise, and then excluding echoes below a pre-determined intensity threshold (Staines et al. 2022, Wei et al. 2022). However, automatic partitioning of fish echoes from background noise and non-fish objects is not always successful (Cotter & Polagye 2020a). Different taxa may not be discriminated (Magowan et al. 2012), and multipassing fishes may not be tracked successfully, leading to autocorrelation in automated fish counts (Shahrestani et al. 2017). Moreover, most automated algorithms for IS data post-processing were developed for optic images, and algorithms tailored specifically to high-frequency acoustic data remain in the early stages of development (Wei et al. 2022). Also, automated processing can be highly costly given the necessary computer quality, prohibiting its widespread and routine use (Bilotta et al. 2011, Lenihan et al. 2019, Helminen & Linnansaari 2021).

Automated techniques have shown broad consistency with manual processing for the identification, quantification, tracking, and measurement of fishes (Boswell et al. 2008, Han et al. 2009, Eggleston et al. 2020, Helminen & Linnansaari 2021, Zang et al. 2021, Feng et al. 2023, Shen et al. 2023), though stark incongruity has also been reported (Handegard & Williams 2008, Mueller et al. 2008, Magowan et al. 2012, Helminen et al. 2020, Helminen & Linnansaari 2021, Le Quinio et al. 2023), particularly due to background noise influences (Helminen & Linnansaari 2021, Shen et al. 2023) and fragmentation of targets with sinusoidal swimming patterns (Le Quinio et al. 2023). Nonetheless, there are examples of full automation (e.g. Mueller et al. 2008), which has been reported to perform best for smaller, less dense targets that are similar in size and shape (Handegard & Williams 2008), although recent studies have proposed automated approaches that have achieved higher detection rates for larger targets than for smaller targets (Fernandez Garcia et al. 2023, Le Quinio et al. 2023, Shen et al. 2023). As introduced in Section 2, deep-learning algorithms hold promise for accurate automated quantification of fish abundance and diversity and are continuously improving (Tarlinton et al. 2022). Notably, Connolly et al. (2022) demonstrated that the success of deep-learning for abundance quantification can be increased when incorporating target shadows in detection algorithms, as opposed to solely relying on targets themselves. However, automated shadow detection is limited in instances of high fish density (e.g. milling fishes) where shadows may be obscured by other targets. Deep-learning success is underpinned by the correct labelling of data upon which the network is trained,

such that human error is still possible in automated processing (Kandimalla et al. 2022).

6.5. Range effects

Analogous to the contingency of optical FOV on light, the FOV of IS is dependent on the frequency used. At the highest frequencies around 3 MHz, IS range rarely exceeds 5 m, with narrower vertical and horizontal angles of ensonification than lower frequencies. A limited FOV has posed several challenges in IS fish surveys, including difficulty tracking individuals (Mueller et al. 2010, Viehman & Zydlewski 2015) and detecting behaviours (e.g. habitat associations) that occur at ranges exceeding IS range (Viehman & Zydlewski 2015). Additionally, the FOV of IS is also constrained at very short ranges. Here, the IS beam array is still forming, hence objects in the immediate vicinity of the sonar are not fully ensonified (Han & Uye 2009). This ‘near-field zone’ typically extends to a metre (Shahrestani et al. 2017); given that the FOV is already constrained at short ranges due to the tapered shape of the beam array, fishes (especially large fishes, Grote et al. 2014) at close ranges often go undetected (Mueller et al. 2006). To some extent, this can be mediated by deploying the IS on a mobile platform (Wei et al. 2022), like an ROV, to ensonify greater volumes of water, increasing the coverage of habitats and associated fish populations (Plumlee et al. 2020).

7. CONCLUSION

IS has already been demonstrated as a valuable tool for the description and quantification of fish assemblages in aquatic habitats, most notably in circumstances where alternative methods such as optical instruments are inadequate. Overall, this review has found that the effectiveness of ISs in profiling fish abundance, species richness, and size, as well as their ability to operate in structurally complex habitats, render them viable tools for surveying reef fish assemblages, both in conjunction with alternative methods (e.g. optical instruments) and independently. Nevertheless, like all survey techniques, IS quantifies these metrics with varying degrees of error, often a product of the specifications of the ISs, the applications for which they are used, and the circumstances in which they are deployed. The continued description and attempted mediation of several notable limitations, including various sources of

noise and data-processing issues, will further enhance the potential of IS in reef fish monitoring.

This review advises future studies to compare IS estimates of abundance, species richness, and size using alternative methods where possible, particularly to further understand the causes of erroneous IS measurements. When alternative methods cannot be used, abundance and richness estimates from IS must instead be considered as relative. Moreover, the development of a standardised calibration protocol founded on numerical estimates of error from the various causes of inaccurate IS size measurements is critical, not least to inform reef fish biomass estimations for fisheries stock assessments. Supplementing assessments of abundance, species richness, and size with examinations of fish behaviour using IS, particularly in structurally complex habitats where other methods are constrained, will shed further light on fish assemblage dynamics such as predator–prey interactions (Becker et al. 2011a, Price et al. 2013, Rieucou et al. 2016), movements within and between habitats (e.g. McCauley et al. 2014, Capoccioni et al. 2019), reproductive strategies (Tiffan & Rondorf 2005, Crossman et al. 2011, Grabowski et al. 2012, Langkau et al. 2016, Chang et al. 2017), and schooling behaviours (e.g. Handegard et al. 2012, Viehman & Zydlewski 2015). Combined application of IS and optics is also desirable, especially given the potential of each system to mitigate the biases of the other (Accola et al. 2022), and the detail afforded when combining simultaneous IS and optical data (see Terayama et al. 2019).

Improving our capacity to detect reef fish assemblages is critical, especially to monitor the impacts of anthropogenic change on valuable taxa and communities. Non-invasive methods that pose minimal impacts on the target fish assemblages are particularly desirable. Importantly, IS continues to detect taxa that are challenging to monitor with traditional sampling methods (Lankowicz et al. 2020, Jones et al. 2021). The non-intrusiveness and versatility of ISs have motivated their increased use to survey fishes in protected habitats (Griffin et al. 2020, Bennett et al. 2021) and poorly studied biomes (e.g. the deep sea, Giorli & Au 2017, Giorli et al. 2018). Use of IS to characterise the structural complexity of habitats (e.g. Griffin et al. 2020) has markedly improved our knowledge of these systems, providing a fundamental basis for long-term conservation efforts. IS continues to generate important information on the effectiveness of species and habitat management strategies (Kimball et al. 2010, Egg et al. 2017, Accola et al. 2022) that ultimately informs whether conser-

vation targets are being met (Holmes et al. 2005, Bilotta et al. 2011, Rand & Fukushima 2014, Ogburn et al. 2017, Mora et al. 2018, Griffin et al. 2020). This review underlines that IS can contribute to the definition of conservation measures through the surveillance and analysis of reef fish assemblages.

Acknowledgements. We acknowledge Kevin Holden from DeepVision Subsea, Ben Saunders, Iain Parnum, and Damon Driessen for the collection of video and acoustic imagery used in the figures in this review. We thank Tony Scarangella for the provision and skippering of the research vessel in the collection of data from the Rottneest fish towers. We thank Se Songpoy for assistance with imaging sonar deployments in Thailand. This research project was funded by Chevron through a research grant to Curtin University under the Western Australian Energy Research Alliance (AES 17-P2TD-151-A1) and its Anchor Partnership with the UK National Decommissioning Centre. We also acknowledge in-kind support from Net Zero Technology Centre and the University of Aberdeen through their partnership with the UK National Decommissioning Centre.

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*Editorial responsibility: Craig Radford,
Warkworth, New Zealand
Reviewed by: C. T. Pfisterer, F. Martignac*

*Submitted: April 20, 2023
Accepted: July 6, 2023
Proofs received from author(s): August 18, 2023*