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On the behavior of Fish Released Following Fisheries Capture: Methods, Endpoints, and Consequences

Luc LaRochelle[a], Lucas P. Griffin[b], Jacob W. Brownscombe[a,c], Chris K. Elvidge[a], Caleb T. Hasler[d], Jessica A. Robichaud[a], Jamie C. Madden[a], Sean J. Landsman[a], Vincent Raoult[e], Andy J. Danylchuk[f] and Steven J. Cooke[a]

[a]Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Canada; [b]Department of Integrative Biology, University of South Florida, Tampa, Florida, USA; [c]Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, Burlington, Canada; [d]Department of Biology, The University of Winnipeg, Winnipeg, Canada; [e]School of Environment and Science, Griffith University, Southport, Australia; [f]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, Massachusetts, USA

ABSTRACT
Quantifying behavior of fish following fisheries interactions can improve the understanding of sublethal and lethal consequence with implications for ecology, fish welfare, and sustainability of fisheries. Behavior involves the integration of the peripheral or central nervous system in response to stimulus or stimuli (varied challenges experienced by fish during capture in this case) that produces coordinated motor actions from the animal. Methods used to assess behavior of fish captured in recreational or commercial fisheries include behavioral arenas and mazes, human constructed systems such as mesocosms, underwater and above water video recordings or observations (remotely operated vehicles, swimmers), telemetry (radio and acoustic transmitters), and biologgers (often with accelerometer sensors) are synthesized. Endpoints assessed were swimming activity, distance, depth and temperature selection, migration success, refuge seeking or conspecific schools, predator avoidance, and body orientation. Suggestions on new methods, or ways to improve current techniques on assessing the behavior of fish are provided.

KEYWORDS
Catch-and-release; commercial fisheries; discard; fate; recreational fisheries

Introduction

Fishing occurs worldwide in aquatic systems and ranges from individuals partaking in leisure recreational angling (Cowx 2002) to large commercial operations (Misund et al. 2002). Fishing gear, defined here as any tool used to extract fish from the water (consistent with UN FAO terminology), differs across the various fishing sectors and the specific gear to be used is selected based on the purpose of the fishing activity (harvest or release), location and environment, fish size, and target species (Herzog et al. 2005; Millar 1992). Often fishing gear is selected to maximize the catch per unit effort for targeted species; however, the selected gear must also comply with potential species-specific gear restrictions and fishing locations. For example, recreational anglers catch fish using gear including rod-and-reel and tackle with single or multiple hooks, bows and spears, noodling, dip nets, and pot traps, while the gear used in commercial fisheries typically includes gill nets, trawls, longlines, traps or pots, and seine nets. There are also subsistence fisheries that variously embrace gears used by both the recreational and commercial sectors.

Here, the term "fisheries interaction" is considered as a capture and release or discard event of a desired or undesired fish using any fishing gear. The reasons for fish being released can vary within and among sectors. For example, some fish captured by recreational anglers are released to comply with regulations (i.e., season, size, possession limits), conservation ethos, or if the fish is not desired as food (Arlinghaus et al. 2007; Cooke and Schramm 2007; Pitcher and Hollingworth 2002). Commercial fishers release desired fish (i.e., targeted species) or non-desired species (i.e., bycatch) to comply with length requirements, season closures, allocated species quotas, or hold

CONTACT Luc LaRochelle larochelle96@gmail.com Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada.

capacity of fishing vessels (Hall et al. 2000; Heath and Cook 2015; Ryer 2002). Arguably, the primary reason for the release of bycatch is due to the lack of economic benefit that the bycatch species provides, and therefore they are often discarded (Hall 1996). There is a general assumption that fish released from a recreational angling event survive the interaction with negligible fitness consequences (Arlinghaus et al. 2007; Broadhurst et al. 2005; Cooke and Schramm 2007; Wydoski 1977), whereas fish released or discarded from commercial fisheries are assumed to be part of the total landing when stock assessments are made (Robin 2019). Yet, releasing captured fish can be an effective conservation measure for fisheries if fish welfare is considered and the fish are not moribund or dead (Danylchuk et al. 2018). No matter the sector, it is important that the consequences of fisheries interactions on released fish are examined (e.g., Brownscombe et al. 2017; Carruthers et al. 2009).

There is a rich body of literature that focuses on the post-release mortality of released or discarded fish across all fishing sectors, yet mortality may not always be the endpoint of a fisheries interaction. Many of the mortality studies related to fisheries interactions fail to assess how attributes of capture and handling contribute to sub-lethal impacts that can reduce the fitness of individual fish as well as cascading effects at the population level. Moreover, a short-term behavioral impairment may be predictive of long-term fate (e.g., survival) making behavior a useful endpoint (Schreck et al. 1997). Stressors imposed by capture and handling vary in form and intensity; they may be acute or chronic but often are compounded (additive or multiplicative). Generally, capture from fishing gear results in an acute stress event where homeostasis of the fish is disrupted, which may result in the deviation of routine behaviors once released (Barton 2002; Barton and Iwama 1991; Johnson et al. 1992). The severity and duration of the stressor can force fish up to or beyond their physiological limits where maintaining homeostasis is not possible and where death may occur because of physiological exhaustion (Barton 2002; Holder et al. 2022; Schreck 1981; Selye 1936; Wendelaar-Bonga 1997; Wood et al. 1983). Beyond possibly causing mortality, sub-lethal impacts and cascading effects on fitness can also occur and include compromised function, growth, and reproduction (Barton and Iwama 1991; Blas et al. 2007; Schreck 2000). Although physiological biomarkers are often used to quantify the stress experienced by fish, the severity of stress and sub-lethal impacts can also be observed in fish behavior, which can be directly relevant to organismal fitness and ecological processes (e.g., predator-prey interactions).

Monitoring behavior can serve as an important biomarker that can be used to determine the influence sublethal impacts have on the welfare status of individual fish, especially for fish in the wild (Schreck et al. 1997). Behavior is best described as how an organism responds to both external (i.e., environmental) and internal (i.e., physiological) cues or stimuli (Tinbergen 1951), and consists of observable actions resulting from animals' coordination of the endocrine, nervous, and skeletal systems (Tinbergen 1951). Deviation in routine behavior of animals, including fish, is a direct result of the physiological conditions they experience because of a stress event, and behavior is used to cope with stressful stimuli to increase the probability of survival (Johnson et al. 1992). For example, fisheries interactions lead to biochemical and physiological changes within fish (Killen et al. 2022), altering their behavior and ability to perform various functions such as feeding and migration (Schreck 1990; Schreck et al. 1997). Additionally, behavioral responses to cues vary depending on the severity or duration of a stress event (Haller et al. 1998; Wingfield 2003) and are also influenced by differences in intra- and inter-specific traits (reviewed in Øverli et al. 2007). Among individuals or populations, there can be variation related to the duration of time it takes to return to normal or routine behavior post-capture and is a result of individual differences in neuroendocrine regulation, hormonal sensitivity, and metabolic rate (reviewed in Øverli et al. 2007). Further, the motivation of fish to engage in various behaviors is also related to their developmental and life stage (Colgan et al. 1986). For example, reproductively mature fish that are captured during their migration to spawning grounds, or while guarding eggs and fry, will generally demonstrate different behavioral responses post-release than fish that are not reproductive due to differences in available energy, aerobic scope, and motivation (see Brownscombe et al. 2017).

In the context of fisheries interactions, behaviors observed during the post-release period are generally regarded as accurate predictors of the state of the fish and their long-term fate or survival (Beitinger 1990; Iwama et al. 1997). Typically, when a fish is released from a fisheries interaction, they are exhausted (Holder et al. 2022; Kieffer 2000) and their swimming abilities and cognition can be impaired (Arlinghaus et al. 2009; Cooke et al. 2014; Elvidge and Cooke 2020; Raby et al. 2014; Ryer 2002). Deviation in routine movements (frequency and duration of movements), swimming speed, distance traveled, displacement patterns, position in the water column, ability to maintain position, and ability to return to the site of capture are some of the typical indicators associated with altered post-release behavior from a fisheries interaction (Calfee et al. 2016; Schreck 1990). Moreover, swimming impairment (which can also manifest as hyperactivity) associated with fisheries interaction can lead to reduced abilities to avoid or escape predators, including by not being able to seek refuge increasing the risk of post-release predation (Brownscombe et al. 2013; Cooke et al. 2014; Danylchuk et al. 2007). Fish can also learn directly or indirectly from fisheries interactions which can have an impact on their behavior (Lovén Wallerius et al. 2020). Learning is a change in behavior that occurs as a result from lived experiences (i.e., directly; Dill 1983; Kieffer and Colgan 1992) or from social cues conspecifics (Brown and Laland 2002, 2011; Heyes 1994; Kieffer and Colgan 1992). Furthermore, fish that are deeply hooked, fought, handled or air exposed for long periods of time may lack the ability to migrate to spawning grounds (Thorstad et al. 2003). Finally, swimming impairments can result in fish losing their ability to feed due to their lack of ability to seek and capture prey (Schreck 1990).

Changes in individual fish behavior because of a fisheries interaction can have a fitness detriment. This fitness detriment can include the time and energy they must allocate to physiological recovery (Aalbers et al. 2004; Siepker et al. 2006; Stålhammar et al. 2012), the impacts on normal enhancing behaviors (e.g., foraging, spawning, avoiding predators), or worse, immediate, or delayed mortality (Bass et al. 2018; Bouchard et al. 2022; Cooke and Suski 2005; Richard et al. 2013; Ryer 2002; Trippel et al. 2017). These fitness detriments vary substantially depending on fisher behavior (e.g., air exposure time, handling time, gear selection), and ecological context (e.g., predator density, water temperature relative to optima; reviewed in Brownscombe et al. 2017; Cook et al. 2019). It is therefore essential to consider real-world behavior and ecological interactions in assessing the impacts of a fisheries interaction. There are a growing number of approaches to measure the post-release behavior of fish to better understand the fitness detriments of capture and how factors like angler behaviors impact outcomes. Behavior is often complex and challenging to interpret in terms of ecological relevance. For example, is a fish that swims faster for longer during the initial release period less impacted than one that swims slowly to a resting place? In interpreting post-release behavior data, there is a considerable need to contextualize observations with natural baseline conditions (i.e., the "typical" behavioral profile of an uncaptured fish, or the "optimal" post-release behavior profile for a low-stress fish), or additional measures of ecological relevance (e.g., physiological stress measures, depredation rates, habitat use, growth, reproductive output).

It is important to understand behavioral responses to fisheries capture because behavioral traits and responses to natural and anthropogenic disturbances can have cascading effects on selection and thus shape population-level traits, such as demography, life history, and evolution (Candolin and Rahman 2023; Pirotta et al. 2018). Given that behavior acts as a "first line of defense" when it comes to biological processes that contribute to maximizing fitness (Tuomainen and Candolin 2011), and that the capacity to adequately measure fitness can be challenging, measuring behavior responses to disturbance may serve as a good proxy (Candolin and Rahman 2023). In the case of stressors experienced by fish during fisheries interactions (Figure 1), the sensitivity of behavioral response and subsequent recovery from the disturbance may provide important clues as to the extent of such disturbances on fitness (Candolin and Rahman 2023; Schreck et al. 1997). Because the range of behavioral responses in animals is dependent on the scope of genetically determined behavioral reaction norms with these being previously shaped by selection on past generations by environmental factors (Ghalambor et al. 2010; Wong and Candolin 2015), the inability to behaviorally respond to an intense disturbance (e.g., being chased by a predator post-release, Biro et al. 2003) may transform what could have been a sublethal effect into a lethal consequence. Other direct effects on behavior, such as impairment of the search for mates, decreased effectiveness of parental care for the young, and reduced competitiveness for optimum habitats could have effects on individual life history traits that make up the population. Measuring behavior and behavioral plasticity in response to a disturbance may also reveal thresholds that could explain population-level shifts in factors such as size structure and reduced age of maturity that may take longer to manifest (Schreck et al. 1997). As such, individual-level behavioral biomarkers in fish may prove to be the best way to bridge the gap between compounded physiological effects of fisheries interactions, quantify thresholds to different types of stressors, and resulting changes at the population-level including *via* selection (Amiard-Triquet 2009; Pauli and Sih 2017).

The objective of this paper is to is provide an overview of the current methods and endpoints being used to assess the behavior of fish post-fisheries interaction

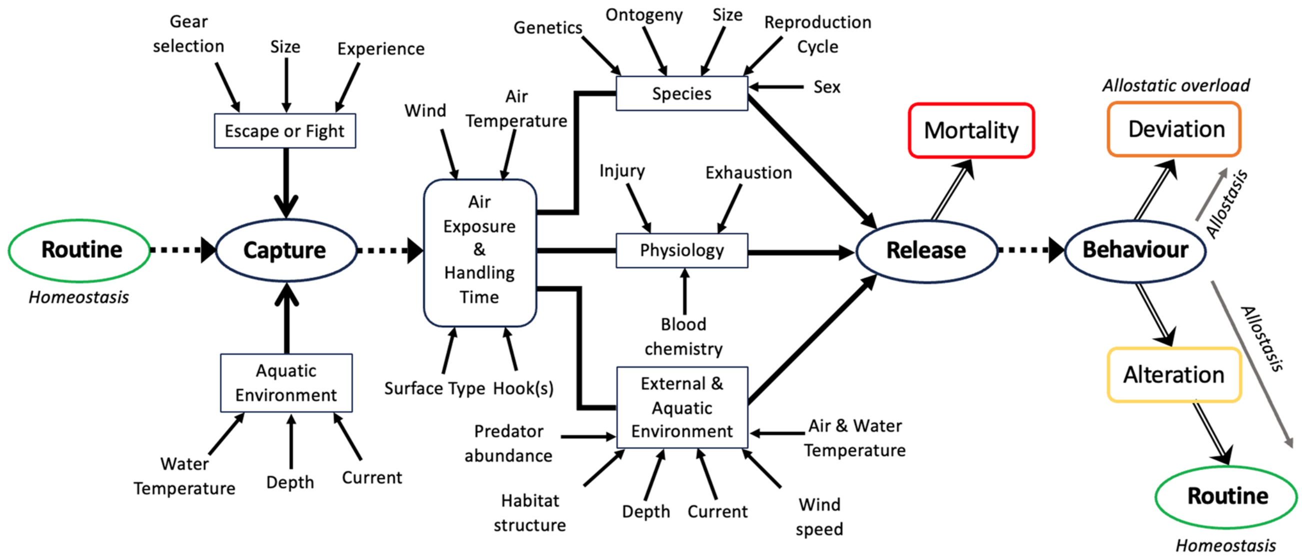

Figure 1. Interactive figure depicting the sequence of events from capture to release that occurs during a fisheries event which can influence the behaviour of fish. The main events that occur (i.e., capture, release) are represented in an oval shape, while the rectangles represent overarching themes that have an influence on those events. Further, arrows pointing at the boxes represent the range of variables that influence those overarching themes. Arrows with the two lines that are pointing away from the main events (ovals) represent the possible outcomes (e.g., mortality, routine).

from commercial, recreational, and subsistence fisheries in marine and freshwater systems. An overview of methods and endpoints is used to assess fish behavior in both lab- and field-settings and detail behavioral consequences that have previously been observed. Further, knowledge gaps in current approaches used to assess fish behavior released from fisheries interactions are highlighted. Donaldson et al. (2008) provided an important overview on how biotelemetry can be used to assess post-release fate and behavior of fish following a capture event, however; it is exclusively focused on biotelemetry. An overview is provided on the many other methods and endpoints used to assess the behavior of fish following fisheries interactions. Finally, anew forward-looking perspective is presented on how to incorporate existing and novel means to monitor the post-release behavior of fish and present a post-release behavior framework, with the goal of developing a structure for key reference points for post-release assessment (Figure 2). Studies that consider or assess behavioral aspects of the selective or evolutionary aspects of fisheries (both mechanisms and consequences, e.g., Cooke et al. 2007; Uusi-Heikkilä et al. 2008; Nannini et al. 2011; Koeck et al. 2019) are excluded because they do not involve direct behavioral impacts from release practices on individual fish.

Methods

The approach used here was not a systematic review or systematic map but rather an overview that is grounded in relevant published literature but supported by the expertise of the authors. The literature review was not exhaustive but did involve using both Google Scholar and Web of Knowledge to locate relevant literature and to determine the different methods used to assesses behavior using a combination of search strings with words including: behav* and (angling or angled or recreational or catch and release or bycatch). Cited reference searches were also conducted for key references and reference lists of papers we located that were germane to the topic were also examined. Searches were conducted in 2024, reviewed in 2025 and only published primary research was included. Individuals also added references from their personal libraries and conducted additional searches using terms more specific to the section they had been tasked with writing using words related to the approach (e.g., telemetry, Remotely Operated Vehicles; ROV) or a specific type of behavior (e.g., feeding, spawning, migration). The approach used here was entirely narrative given the diversity of endpoints/methods making a meta-analysis impossible. Indeed, the evidence base for many of the topics explored here is sufficiently scant that it needed to be complemented with expert knowledge.

Monitoring post-release behavior after a fisheries interaction

Several methods can be used to monitor the behavior of fish post-release. Fish can be monitored in a laboratory where external confounding factors can be

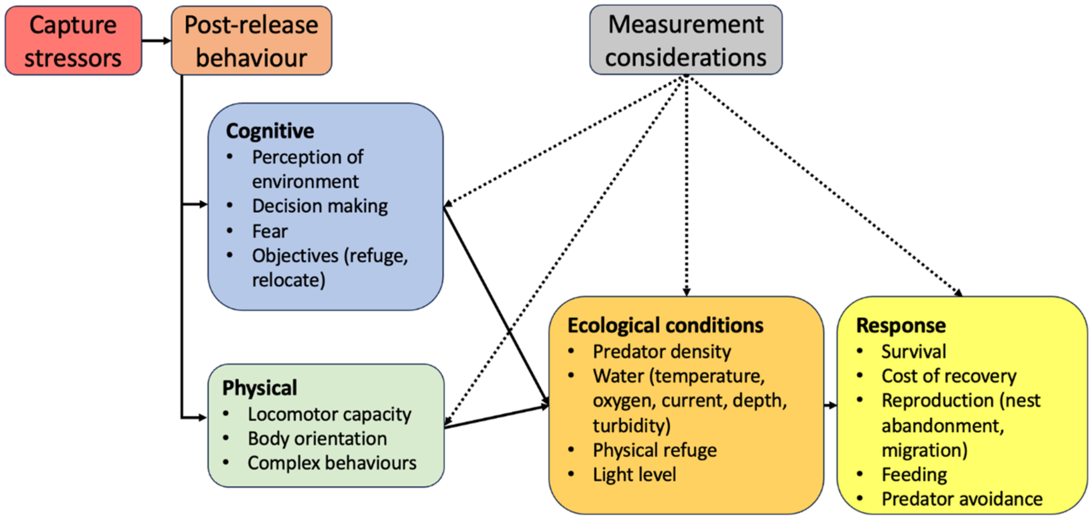

Figure 2. Concept diagram of key reference points that need to be considered when monitoring the post-release behaviour of fish after a fisheries interaction. This framework highlights the importance of including the cognitive and physical capacity of the animal, and the way that the animal then interacts with the surrounding environment given the cognitive and physical constraints.

controlled, or in the field (i.e., wild) where environmental factors are not controllable. Despite best efforts by researchers to design and apply treatments to the study of animal behavior in a precise and rigorous fashion, lab- and field-based studies are literal representations of hypothetico-deductive and inductive logical frameworks, respectively (Mentis 1988). Importantly, these two approaches have often generated conflicting results, particularly in studies of endocrinology and behavior (Calisi and Bentley 2009). Laboratory experiments involving captive animals, whether they are obtained from established breeding lines or wild provenance, have the distinct benefit of allowing selection for similar individuals that have experienced common-garden conditions either for their entire lives or for some predetermined acclimation period following their collection. A fish is often deemed habituated to their new environment when the animal begins feeding again (see Beitinger 1990). This habituation period is important to avoid confounding effects caused by the displacement and confinement of the animal in the new setting. Common-garden conditions facilitate direct manipulation of single variables, often stressors, to evaluate both the magnitude and relative effect of a treatment or treatment level on the experimental animals. By contrast, field studies occur in the wild, where animals are captured and then studied in the location of capture, permitting observation of animals within their natural environment post-release. Studying animals under wild, free-ranging conditions introduces unavoidable uncertainty in the recent experiences and state of a focal individual, such as time since last feeding, number of predators encountered during some preceding interval, or residence time at the sampling site, which may influence the level of stress at time of sampling (Cooke et al. 2016).

Conversely, a criticism of laboratory studies and the hypothetico-deductive approach is that an experimental animal is effectively deprived of the full spectrum of stimuli present under natural conditions, which may lead to artificially enhanced responses to the experimental treatment. In the context of behavioral studies, applying a single treatment in an otherwise static environment may cause an individual to adopt responses of greater magnitudes than may be observed in the field. Individuals that are raised in the laboratory are liberated from the necessary tradeoffs between conflicting time and energy demands such as the need to accrue resources (foraging opportunities, territory defense, courtship, or mating) under risk of predation (Lima and Dill 1990). Attempts to replicate lab-based behavioral studies have largely been equivocal, as unintended differences or bias in experimental settings, including different observers and materials used to construct behavioral trial arenas and house the animals, may be as important in driving variation as the intended manipulated treatment (Lewejohann et al. 2006; Nigri et al. 2022). Despite their putative advantages in reducing environmental uncertainty, laboratory studies alone are insufficient to generate predictions of real-world responses without careful consideration of the context of the study and the ecological relevance of the findings (Table 1, Campbell et al. 2009; Wolff 2003).

Field-based studies involving wild animals have the advantage of inherently capturing real-world tradeoffs between conflicting demands. This advantage comes with greater uncertainty, relying on inductive reasoning to ascribe observed differences to both applied treatments in an experimental context and background variation (e.g., water temperature or chemistry, presence of toxicants) in a mensurative or comparative context between different groups of animals. Whereas lab-based studies may generate artifacts or provide exaggerated estimates of effect sizes, field-based studies may impose lower confidence levels on effect size estimates due to uncontrolled confounding factors (e.g., previous condition of the animal) and wide variation in responses (e.g., intraspecies responses). Therefore, it is crucial that field-based studies have controls that accurately represent the study population of fish. Additionally, real-time studies of emerging topics of ecological concern may be especially prone to observer bias (Clements et al. 2022 but see Munday 2022) and generate irreproducible results. To avoid these outcomes, researchers should carefully consider the context of behavioral studies and stimuli (Campbell et al. 2009) and the benefit of paired lab-field studies (Horn et al. 2022; Mouchet and Dingemanse 2021). The benefit of pairing lab and field studies together, is that researchers can accurately identify sources of behavioral variation and quantify their effects on study species—ideally with reproducible and predictable patterns in both settings (Dingemanse et al. 2010; Dingemanse and Wright 2020; Niemelä and Dingemanse 2018; Wilson and McLaughlin 2007).

Table 1. Table indicates the different methods that can be used to assess the post-release behavior of fish.

Monitoring Method	Strengths	Weaknesses
Behavioral Arena	Good for measuring cognitive abilities Controlled environment	Acclimatization period needed
Biologgers	Fine scale data Multiple deployments Passive tracking	Need to recover tags Limited by battery & memory capacity Tagging effects
Acoustic Telemetry	Long-term Large area coverage Do not need to recover tags Passive tracking	Surgery Tagging effects Receiver download Animal may leave detection array Not very effective in complex (e.g., bottom structure) or noisy environments (e.g., rivers) Single deployment Limited by battery capacity and animal remaining in the array
Radio Telemetry	Good in relatively noisy environments (e.g., rivers)	Active tracking Tagging effects Only good in shallow water Not effective in deep water
Swimmers	Visually see animals Can follow animals at desired distance Do not need to retrieve gear	Limited to swimmer capabilities Not effective in turbid water Can lose sight of animal
Underwater Camera	Visually see animals No tag burden Recorded files (replay) Passive observation	Must retrieve camera Limited by battery & memory capacity Only effective in clear water
Underwater Drone	Visually see animals No tag burden Recorded files (replay) Broader capabilities than humans	Tethered (limited range) Potential behavioral impacts Only effective in clear water Limited speed
Sonar Imaging	Good in deep & turbid water No in water disturbances Recorded files (replay)	Not as effective in shallow water Can lose target animal Lack of imaging resolution
Above Water Camera	Visually see animals No tag burden Recorded files (replay)	Not ideal in the field Acclimatization period needed
Surface Float	Constant visual on animals Can be used in turbid waters Visually see location of animal at longer distances	Not effective in deep water Not effective in complex habitats Drag from the float Tagging effects
Aerial Drone	Effective in shallow & clear water Visual on animal Can follow animals with minimal disturbance No tag burden	Not effective in deep & turbid water Not effective in complex environments with refuge Lack of picture resolution Flight restrictions (spatial and temporal) Potential behavioral impacts

This table also includes the strengths and weaknesses of the methods outlined.

Laboratory

It is possible to assess fish after capture by using common behavioral assays often used in laboratory settings. Examples include: (1) visual observation, which involves placing the fish in a container of water and recording movements (e.g., operculum beats, reflexes, activity, equilibrium loss, e.g., Chopin et al. 1996; Davis 2005; Gingerich et al. 2007); (2) measurement of ecologically relevant behaviors by challenging fish with feeding, predators or other cues (e.g., Olla et al. 1997); (3) placing fish directly into an arena, such as a Z-maze (e.g., Hlina et al. 2021) or custom-built structures (e.g., Cooke et al. 2014), which can offer insights into quantifiable behaviors (e.g., latency to move, time in the maze, furthest distance traveled, total distance traveled) or more complex behaviors if a video recording is made (e.g., activity states); and, (4) swimming tunnels, which can be useful for testing swimming performance following capture (Bieber et al. 2019) and can be used for monitoring physiological parameters, such as metabolic rate (Clark 2022). Additionally, there are other techniques that could be useful for monitoring (or inferring) the behavior of fish *in situ* and may have application to fisheries (Kadar et al. 2022).

There are factors to consider when planning common behavioral assays. For example, behavioral responses tend to vary more than physiological parameters, therefore it may be necessary to increase sample sizes (Arlinghaus et al. 2009). Additionally, the applicability of behaviors may be difficult to ascertain, or the assessment may add bias because there is limited time to habituate fish in containers, fish may use hard surfaces of the containers to remove hooks or as support (Hlina et al. 2021), and it is nearly impossible to eliminate external stimuli while working in the field (e.g., boat noise, vibrations, observer presence). If survival or delayed behavioral changes are important to quantify, transporting fish to a laboratory for long-term monitoring is useful (e.g., Cooke et al. 2014; Olla et al. 1997); however, this can add other stressors (e.g., transportation and holding stress) that limit interpretation of the effects of angling on mortality. Simulating fish capture can also be useful should tightly controlled laboratory conditions be needed to quantify behavioral responses (e.g., Bieber et al. 2019). In these studies, fish are either captured in a scaled down version of a net (e.g., trawl), in a landing net, or by angling in a laboratory environment. By doing so, similar stressors are applied (e.g., injury, fight duration, air exposure, and handling) to increase applicability to what might happen in a real fisheries interaction. Furthermore, in studies that simulated fish capture, experimental variables can be altered to gain further insight into extrinsic factors that might influence the response of fish to capture (e.g., light intensity, Olla et al. 1997; capture depth, Campbell et al. 2009). Ultimately, careful methodological considerations are needed to ensure behavioral outcomes can be applied to "real world" fisheries outcomes and thus be meaningfully used to inform stakeholders and regulations.

Examples of studies that use laboratory-based behavioral assays to assess the impacts of fisheries capture are uncommon, likely due to the unpredictable conditions and issues mentioned above. Additionally, bringing technical gear into the field, and the lack of time needed to handle sensitive equipment and record behaviors can be problematic for the collection of appropriate data. For example, reflex impairment has become a common tool to visually assess the likelihood of survival following release (Lennox et al. 2024). Beyond reflexes, monitoring fish movement in an arena immediately following capture has been shown to be useful. Louison et al. (2023) used an action camera placed over top of a 227 L plastic bin and found that Black Crappie (*Pomoxis nigromaculatus*) exhibited more anxiety-like behavior (i.e., time away from the center of the arena) following ice angling than did Bluegill (*Lepomis macrochirus*).

Most studies that have assessed behavior following capture in fisheries are ones where capture (e.g., fight time, hooking location) and handling are simulated in laboratory settings. The benefit of doing studies in more controllable environments improves the ability to quantify cause-and-effect outcomes. For example, by simulating angling events within hyperbaric chambers, Campbell et al. (2009) demonstrated reflex impairment increased in Red Snapper (*Lutjanus campechanus*) when exposed to deeper depths (i.e., greater pressure) and in higher temperatures (Campbell et al. 2009). This study also highlighted that by doing simulated studies, multiple responses can be evaluated, as both burst swimming speed and predator avoidance were found to be reduced for up to 15 min following the simulated capture at depth. Simulated capture studies are also useful for monitoring behavior prior to and during fisheries capture. For example, through visual observation and calibrated load cells, Chopin et al. (1996) effectively monitored and compared Red Sea Bream (*Pagrus major*) behavior prior to and after capture *via* hook-and-line and in trammel net. Red Sea Bream were found to initially attempt to move away from fishing gear once captured, which was then followed by struggling that would decrease overtime, and active swimming in reverse and finning to maintain position (Chopin et al. 1996). In another simulated study by Pullen et al. (2017), Northern Pike (*Esox lucius*) were caught in the field and subsequently transported to tanks at a nearby lake-side laboratory. Using video cameras, individual Northern Pike were then experimentally hooked in either the esophagus or jaw to assess the effect of hooking location on gill ventilation. Moreover, mazes and other custom-built arenas are used in conjunction with simulated angling events to infer post-release behaviors. For example, placing Bluegill that either retained a hook or did not into a Z-maze suggest that hooking retention influences the time to leave a refuge and were less exploratory (Hlina et al. 2021). In another example, Spanish Flag Snapper (*Lutjanus carponotatus*) that were experimentally exhausted, and air exposed took longer to seek refuge when released into a custom-built arena (Cooke et al. 2014). Finally, laboratory experiments have been great to assess hook avoidance behavior based on direct capture or from indirectly from capture of conspecifics in Common Carp (*Cyprinus carpio;* Klefoth et al. 2013; Lovén Wallerius et al. 2020; Czapla et al. 2023). Hook avoidance after direct capture has also been seen in Crucian Carp (*Carassius auratus*; Chen and Zeng 2022) as well as Red Sea Bream (*Pagrus major*; Takahashi and Masuda 2021). To end, though simulation studies have been useful for discerning cause-and-effect relationships, it is important to note that relating study outcomes to real world fisheries practices and outcomes for fish is difficult and the applicability of the studies can range from being greatly applicable to not at all applicable. Scientists need to be careful when designing experiments and contextualizing results if study findings are to be useful for informing best practices and regulations.

Mesocosms

In the context of this paper mesocosms refer to situations in which fish are held in human constructed systems such as experimental ponds, large raceways, embayment enclosures, enclosed cages or experimental streams (Crossland and La Point 1992; Odum 1984). They differ from fully natural systems in that fish tend to be confined yet contain more ecological realism (and less control of environmental conditions) than a tank. Mesocosms have been used in several studies that involved assessing the behavior of fish after fisheries interactions albeit the majority are in a recreational fisheries context. For example, Cooke et al. (2000) stocked Largemouth Bass that (*Micropterus salmoides*) were implanted with electromyogram radio transmitters (to assess locomotor activity) into experimental ponds in Illinois prior to spawning. After the fish had spawned, some fish were angled from the nest to determine whether locomotor impairment was altered relative to before angling or to non-angled controls. The study revealed that even though nesting male bass did not abandon their nests, they did exhibit locomotor impairments after angling that extended more than 24 h. The experimental ponds enabled them to control sex ratios in ponds and provided an opportunity to implant fish prior to reproduction. Additional experiments in experimental ponds in Illinois involved exposing Largemouth Bass to simulated fishing tournament stressors prior to the reproductive period and then assessing reproduction relative to fish in replicated control ponds (Ostrand et al. 2004). Back-calculation of spawning dates using offspring age data revealed that the fish exposed to tournaments delayed reproduction relative to control fish representing an indirect measure of behavioral alteration. A final example involved Largemouth Bass in a fenced enclosure (a boat slip) in Ontario where fish were implanted with acoustic electrocardiogram transmitters to assess cardiac recovery following angling (Cooke et al. 2004). Although the study had a decidedly physiological focus, the use of the mesocosms (combined with shallow, clear waters) allowed detailed behavioral observations to also be recorded to assist with interpreting the cardiac data. A study in experimental ponds in Denmark involving Northern Pike released fish (following fisheries interactions) either as singletons or with conspecifics (Stålhammar et al. 2012). The authors revealed that angled and released Northern Pike exhibited altered foraging behaviors, but with those impacts somewhat dependent upon the social context at release; fish released with conspecifics resumed feeding behavior more quickly (Stålhammar et al. 2012). Experimental ponds have been valuable in hook avoidance and learning studies for both Common Carp, Largemouth Bass and Rainbow Trout (*Oncorhynchus mykiss*). Like laboratory studies, direct capture has a greater influence on learning behavior and hook avoidance compared to indirect capture or social cues from conspecifics (Beukema 1970; Klefoth et al. 2013; Louison et al. 2019; Lovén Wallerius et al. 2019; Raat 1985).

The only study found with a clear focus on commercial fishing gear that was conducted in mesocosms was done in Norway using Atlantic Mackerel (*Scomber scombrus*) exposed to simulated purse seine fisheries. Schools of mackerel held in massive pens were used to assess behavioral responses crowding and hypoxia (key aspects of purse seine experiences for fish; Anders et al. 2019). Video analysis focused on proximity to conspecifics and tail beats with an increased in tailbeat frequency identified as a possible biomarker for future studies. The other examples using mesocosms all involve assessing refuge seeking behavior following exposure to fishing-related stressors to characterize behavioral impairment. Such studies are inherently difficult in the field, and only one other study tried to do that on a coral reef by using SCUBA to follow fish after release which can only be (i.e., Raby et al. 2018). The first mesocosm example involved a Spanish Flag Snapper captured from the Great Barrier Reef that were placed in a raceway equipped with a natural coral refuge at one end (Cooke et al. 2014). Fish that were exhausted failed to seek out the refuge even if released at the entrance. Conversely, control fish entered the refuge within seconds no matter where they were released. A follow-up study involving Schoolmaster Snapper (*Lutjanus apodus*) captured from mangrove creeks in the Bahamas used mangrove refuges and combined capture-related stressors with chemical alarm cues (Elvidge and Cooke 2020). Fish that were pre-conditioned to the alarm cues sought out refugia no matter the extent of exhaustion they exhibited whereas control fish did not. Brownscombe et al. (2014) attempted to bring more realism by using an isolated mangrove enclosure in the Bahamas where they introduced juvenile Barracuda (*Sphyraena barracuda*) that had been exposed to various levels of exhaustion. Behavioral impairments were observed such that exhausted fish failed to seek out appropriate refuge.

Collectively, these studies provided researchers the opportunity to visually observe fish and therefore obtain detailed behavioral observations yet also provide ecological realism. Several studies have also used the fact that fish could be recaptured or were otherwise confined to make use of various biologging or biotelemetry tools. Given growing interest in such technologies, there is anticipate of more similar work in the future. Mesocosms are often used to assess growth (e.g., Arlinghaus and Hallermann 2007; Skov et al. 2023) and survival (e.g., Booth et al. 2023; Clapp and Clark 1989; Schill 1996; Skov et al. 2023; Tomasso et al. 1996; Weltersbach et al. 2018) given the ability to monitor animals through time (and by collecting all fish at the termination of the study; e.g., by draining a pond or raceway) while also enabling them to engage in "natural" activities but neither growth or mortality represent direct behavioral endpoints despite the fact that behavior can mediate both of them. For example, a reduction in growth observed in a mesocosm may arise due to alterations in feeding behavior although it could also be the result of the physiological costs of recovery or an extended immune response. Given the lack of certainty about behavior that one can draw from growth or mortality alone, those mesocosm studies are not considered here.

Biologgers

Biologgers, also referred to as archival tags and loggers, are a widely used and effective way to track and monitor the behavior of fish (Chung et al. 2021; Cooke et al. 2013; Whitford and Klimley 2019). There are a multitude of types, each offering different advantages in research. Biologgers include sensors that record data at preset time intervals. Depending on the sensors, data readings can include temperature, pressure (depth), salinity, light, magnetic field, and fine scale acceleration in multiple axes (Thorstad et al. 2014). In fish, these tags are typically attached externally, either completely noninvasively (i.e., with a strap), or through dorsal musculature (Raby et al. 2017; Whitney et al. 2017), although they can also be surgically implanted and equipped with heart rate loggers (Neat et al. 2009; Prystay et al. 2019; Wright et al. 2014). Once attached, biologgers will collect a certain number of readings per time interval (set by the user) on the movements of the fish. While the fine scale data that biologgers collect is valuable in studying fish behavior, these tags need to be physically retrieved to be downloaded, a factor which may be limiting for some species or water systems. The retrieval can be addressed in multiple ways: some studies rely on recapture (Neat et al. 2009; Nichol and Chilton 2006; Raby et al. 2017), some snag a float line (Brownscombe et al. 2013), and others use barriers like fish counting fences (Lennox et al. 2019). Conversely, many studies keep the fish on a line for the entire monitoring period (Figure 3A, Bieber et al. 2022; Chhor et al. 2022a; Holder et al. 2020; Griffin et al. 2022; LaRochelle et al. 2021, 2022). Generally, studies use biologgers to measure short-term behavior, and thus most often keep the tags attached for anywhere between 10 mins to one hour. In marine environments, the use of galvanic timed releases has allowed for longer-term studies, as the release mechanism allows the tag to detach from the fish and float to the surface after a certain period (Logan et al. 2022). These floating packages may be equipped with a radio tag for locating the released loggers (Figure 3B; Whitney et al. 2016; LaRochelle et al. 2024). Galvanized releases only work in saltwater, but similar pop-up floating packages have recently been designed for use

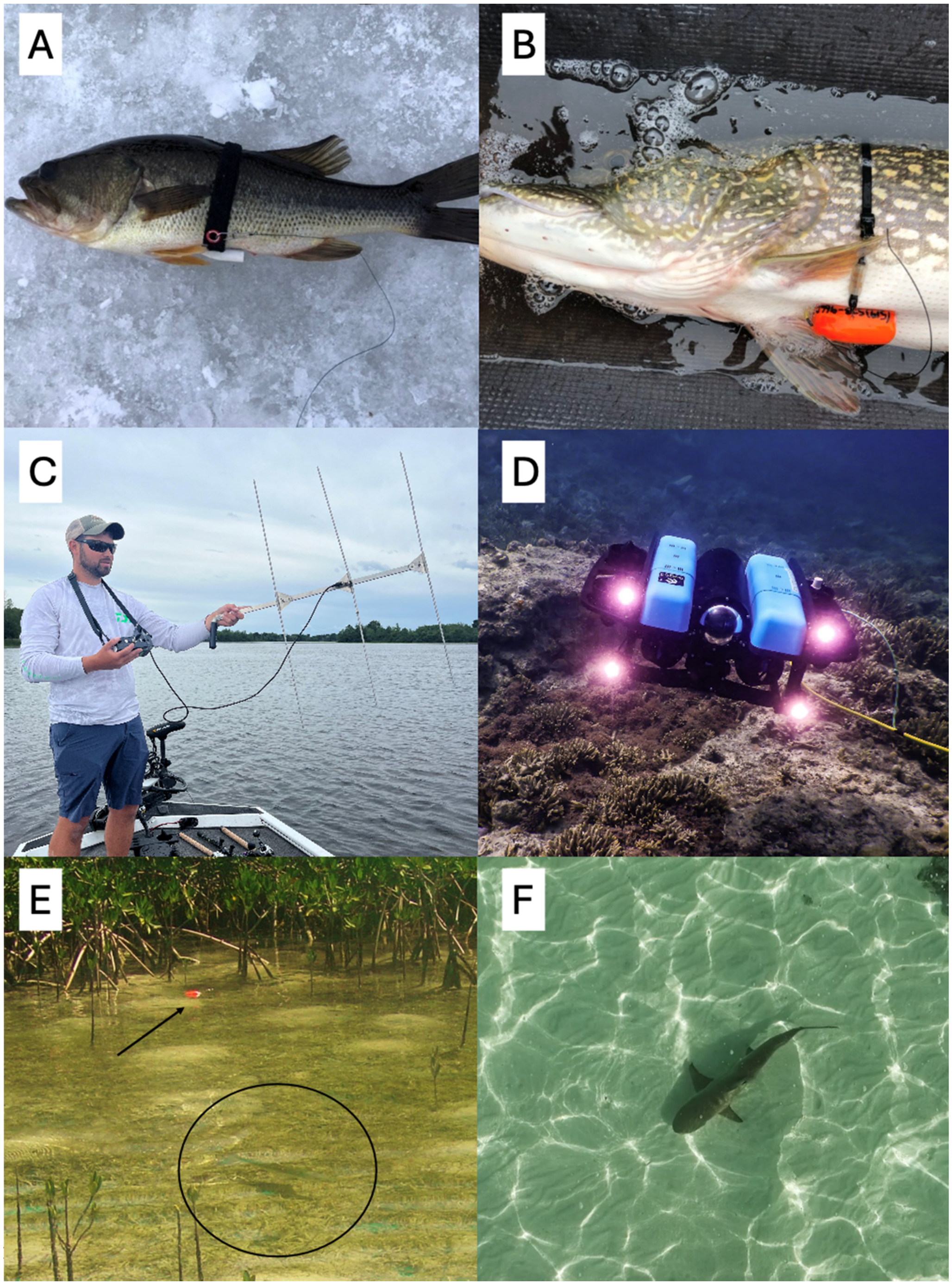

Figure 3. Different methods used to assess the post-release behaviour of fish in the wild. Panel A represents a method used to assess short-term behaviour of fish with a Velcro strap and a biologger. Panel B represents a pop-off biologger package that is used to assess the fine scale post-release behaviour of fish. Panel C is a picture of active radio tracking with an antenna and a receiver. Panel D is an underwater picture of a remotely operated vehicle. Panel E has an arrow pointing at a surface float (above water visual observation) that is attached to a fish (circled). Finally, panel F is an overhead shot of a shark on a flat taken with an arial drone used to assess movements of aquatic animals.

in freshwater, using either a timed-release unit (TRU; Raby et al. 2017) or catgut sutures which lose tensile strength over time (LaRochelle et al. 2023), both allowing longer term monitoring.

Biologgers have been used to monitor the behavior of caught and released fish in recreational fisheries following air exposures (Chhor et al. 2022a), fight times (LaRochelle et al. 2025), recovery tactics (Brownscombe et al. 2013; Chhor et al. 2022b), barotrauma mitigation techniques (Louison et al. 2023; Madden et al. 2024), and different handling behaviors (Griffin et al. 2022; LaRochelle et al. 2021; 2022). In commercial fisheries, biologgers have also been proposed for research, quantifying discard mortality (Neat et al. 2009), behavioral responses to longline capture (Talwar et al. 2020), and effects of barotrauma (Nichol and Chilton 2006; van der Kooij et al. 2007). Often, overall dynamic body acceleration (ODBA) is calculated from acceleration data from biologgers. ODBA can be used in these behavior studies to quantify overall movements and energy expenditure of fish and compare across treatments (as in Bieber et al. 2022; LaRochelle et al. 2022). Valuable insights into angler best practices have been gained using biologgers to monitor the post-release recovery periods and behavior of highly sought after trophy-sized fish, such as Blue Marlin (*Makaira nigricans*), Sailfish (*Istiophorus platypterus*), Atlantic Bluefin Tuna (*Thunnus thynnus*), Arapaima (*Arapaima gigas*), and Northern Pike (Dolton et al. 2022; LaRochelle et al. 2023; Lennox et al. 2018; Logan et al. 2022). Short-term survival (Knotek et al. 2022; Lennox et al. 2018; Whitney et al. 2016, 2017) has also been assessed using biologgers, offering a new understanding of previously unknown mortality rates associated with fisheries interactions.

On the other hand, pop-up satellite archival tags (PSAT) do not need to be physically recovered—a massive advantage that has allowed the study of seldom recaptured or migratory species. These PSAT work by recording light level irradiance from which geolocation can be concluded. The tags are often externally attached through the dorsal musculature and can collect data on pressure (depth) and temperature in addition to light readings and archive the data for long periods of time in its internal storage (Cooke et al. 2013). These PSAT tags are programmed to release from the fish either after a preset amount of time, or when a specified set of conditions (e.g., depth readings that are consistent with a mortality event or full memory capacity) are met. Once the package releases, it floats to the surface where it transmits the stored data to ARGOS satellites, which in turn transfers the information to a base station. The data can then be downloaded and analyzed by the user. The release mechanism on most models, like the galvanic release of some biologgers, relies on saltwater to degrade and release, and thus limits the possible study species to marine, anadromous, or catadromous species (Thorstad et al. 2014). Also, PSAT have been subject to malfunction, premature release, biofouling, and environmental variables which affect the scope of the dataset (Arnold and Dewar 2001; Jepsen et al. 2015). Finally, the tags are limited by their large size, which makes them unsuitable for use on smaller bodied species, although recent lab studies have found success in their use on smaller fish (Naisbett-Jones et al. 2023).

In general, PSAT can provide longer term, yet coarser scale behavioral data compared to biologgers. They have been used in fisheries research to quantify commercial discard mortality in large species such as Blue Sharks (*Prionace glauca*), Shortfin Makos (*Isurus oxyrinchus*), Porbeagles (*Lamma nasus*), Yellowfin Tuna (*Thunnus albacares*), and Thorny Skates (*Amblyraja radiata*) (Campana et al. 2009, 2016; Kneebone et al. 2021; Knotek et al. 2020). Depth data from the tag is used to infer mortality in active pelagic species and characterized as when depth readings are constant for a specific number of days and equal to the total water depth (Campana et al. 2009). For less active species, probable mortality can also be determined by simply increasing the threshold of time showing inactivity and no vertical movements (Ferter et al. 2017). Though most PSAT studies in both recreational and commercial fisheries include mortality estimates (Afonso and Hazin 2014; Campana et al. 2009; Ferter et al. 2017; Knotek et al. 2020; Tracey et al. 2016) these tags also provide valuable behavioral data on large scale movements, ocean migrations, and recovery after fisheries interactions (Bowlby et al. 2021; Patterson et al. 2008).

Acoustic telemetry

Acoustic telemetry is a useful tool for assessing behavioral endpoints in fish, as it allows researchers to track aquatic animals across vast spatial and temporal resolutions without continuous human interference (Ellis et al. 2019). Acoustic telemetry works through the transmission of information from tags to receivers. Acoustic transmitting tags are secured to animals externally or inserted internally *via* the stomach or through surgical implantation. Tags are programmed to transmit unique identifying codes along with dates and times and may also be equipped with pressure (depth), temperature, acceleration sensors or a combination of these, which can provide information on depth, water temperature, and swimming metrics such as speed and activity. This information is transmitted to a receiver, which will receive information from a given tag when an animal passes by closely enough. While receivers are commonly stationary and organized into arrays across areas of interest, they may also be deployed on ocean gliders and large animal carriers (e.g., seals) to create mobile detecting platforms (Hussey et al. 2015). Researchers can then retrieve receivers and obtain a record of animal presence to help evaluate behavioral endpoints such as post-release mortality, migration, spawning, predation, and foraging.

Acoustic telemetry has been used to study post-release mortality in both marine and freshwater environments (e.g., Halttunen et al. 2010; Jackson et al. 2018; McLean et al. 2020; Moxham et al. 2019) by allowing researchers to infer morality from detections or lack thereof. Acoustic telemetry has been used to assess post-release mortality as it relates to issues such as discard mortality (e.g., Bohaboy et al. 2020; Capizzano et al. 2016), hook ingestion (e.g., Butcher et al. 2010; Roberts et al. 2011), and long-line capture (e.g., Afonso and Hazin 2014). High-resolution acoustic telemetry has provided some important information on the recovery time of Northern Pike following angling events (Baktoft et al. 2013). Acoustic telemetry has also been used in assessing the impact of barotrauma on the post-release behavior and impairment of species such as Walleye (*Sander vitreus*; e.g., Gravel and Cooke 2008; Eberts et al. 2018), by allowing researchers to look at how swimming patterns change in response to both the barotrauma and potential mitigation strategies (i.e., fizzing). Acoustic tags containing acceleration or depth sensors, have allowed researchers to quantify swimming metrics and activity at high resolutions. Acoustic transmitters with depth sensors have been used to look at vertical swimming movements post-release (e.g., Ferter et al. 2015; Moser et al. 2018), and acceleration values are often used to determine short-term post release behaviors (e.g., McGarigal and Lowe 2022; McLean et al. 2019). Post-release swimming metrics provides insight into behavioral changes that may result in prolonged impairment or in some instances morality.

One of the largest benefits of using acoustic telemetry as a tool to study behavioral endpoints is that it gives researchers access to environments and animals that would be otherwise difficult to observe. Aquatic ecosystems are vast and difficult for researchers to monitor continuously, especially when considering the depth of some of these habitats. Further, aquatic animals can be highly mobile, making it difficult to track individuals over vast distances with tools like radio telemetry or direct observations. Acoustic telemetry mitigates these challenges and provides unprecedented insights into animal behavior, however for behavioral studies, researchers should consider the impact tagging may have on animals. Tagging procedures can be invasive and may influence the post-release behavior of a tagged fish (Klinard and Matley 2020), therefore it is important to take this into consideration when making inferences of behavioral endpoints.

Radio telemetry

Radio telemetry has been used by fisheries scientists to study fish behavior and ecology since the late 1960s (i.e., Lonsdale and Baxter 1968). This form of telemetry works by transmitters using their on-board batteries to propagate radio waves (typically in the range of 30-300 MHz) to an antenna and finally a receiver (Figure 3C, see Kuechle and Kuechle 2012 for more details). Radio telemetry was developed as a solution to problems associated with early iterations of acoustic transmitters and receivers (mobile and fixed station), which failed to yield acceptable detection efficiency in shallow, turbulent environments or were simply impractical for assessing movement across long distances (see Hockersmith and Beeman 2012). Nevertheless, radio telemetry does not work well in saltwater, deep water (e.g., deeper than 10 m can result in full signal loss), areas with high electrical noise and interference, and areas with large obstructions such as buildings, mountains, and trees. Radio transmitters can be surgically implanted, attached externally to fish, or *via* intragastric insertion (see Bridger and Booth 2003).

Radio telemetry has been widely used in studies assessing the post-release behavioral impacts of recreational catch-and-release angling (see also Donaldson et al. 2008). Active tracking can generally permit more accurate positional estimates for fish, thus making active tracking of radio-tagged fishes an appealing approach to assessing post-release behavior. For example, several studies have used active radio tracking to test the short-term behavioral impacts of fish exposed to air or not exposed to air prior to release (e.g., Largemouth Bass, Thompson et al. 2008; Northern Pike, Arlinghaus et al. 2008; Muskellunge (*E. masquinongy*), Landsman et al. 2011; Common Carp, Rapp et al. 2014; Golden Dorado (*Salminus brasiliensis*), Gagne et al. 2017; Rainbow Trout (Steelhead), Twardek et al. 2018) and the influence of handling methods (Rapp et al. 2012). Other studies have examined the post-release sub-lethal behavioral impact on angled fishes in developing fisheries (Golden Mahseer *Tor khudree*, Bower et al. 2019) or the impacts of high-water temperatures on post-release behavior (Atlantic Salmon *Salmo salar*, Havn et al. 2015). This method has been used to assess the post-release habitat selection of Northern Pike following capture (Klefoth et al. 2008, 2011). Given the popularity of tournament angling for Black Bass, researchers have used active radio-tracking to study the displacement, or lack thereof, of tournament-caught Smallmouth Bass (*M. salmoides*, Bunt et al. 2002; Kaintz and

Bettoli 2010), Largemouth Bass (Maynard et al. 2013), and Spotted Bass (*M. punctulatis*, Hunter and Maceina 2008). Studies have also examined displacement in tournament-caught and released Walleye and Saugers (*S. canadensis*) (Eberts et al. 2018) and Striped Bass (*Morone saxatillis*) (Young and Isely 2006). Although labor intensive, researchers can use active tracking to explore diel (i.e., 24 h) patterns of behavior post-release such as in Northern Pike (Arlinghaus et al. 2008). The use of active radio-tracking has been applied in studies assessing the post-release behavioral impacts of Black Bass experiencing barotrauma (Gravel and Cooke 2008), including the effect of "fizzing" as an intervention (Nguyen et al. 2009). Radio tags have been used to assess behavioral impacts of lure retentions for Northern Pike (Arlinghaus et al. 2009) and nest-guarding Smallmouth Bass (Henry et al. 2009). In both cases, short-term behavioral impairments were noted, but behavior resembled that of control fish by 48 h. In a rather unique study, Pullen et al. (2019) investigated the time it took for Northern Pike released with lures (i.e., crankbaits) still in their jaws or throats to eject them. The authors radio-tagged the lures themselves, not the fish, and found that while deep hooking and lower jaw hooking resulted in reduced movement rates, all but one (50 of 51) fish ejected the lures within 14 days.

Assessments of fishing-induced mortality is another common application of radio telemetry. In catch-and-release Atlantic Salmon fisheries, multiple studies have used radio telemetry to show low overall mortality associated with these types of fisheries (e.g., Lennox et al. 2017 and see Keefe et al. 2022; Whoriskey et al. 2000). Radio telemetry has also helped researchers develop fishery-independent estimates of fishing mortality for Striped Bass (Hightower et al. 2001; Young and Isely 2004) has also occurred in a Striped Bass context. Recently, a series of studies focused on the impacts of high-water temperatures on Muskellunge delayed mortality have demonstrated decreased survival in angled fish when water temperatures exceed 25 °C (Bauerlien et al. 2022). Some radio transmitter designs also allow them to be fitted with mortality sensors, which increase the signal pulse rate if a fish remains stationary for a pre-determined period. This may improve estimates of mortality by reducing ambiguity associated with putative dead fish. For example, Bettoli et al. (2000) applied these kinds of specialized transmitters to estimate relatively low (12%) mortality in Sauger. Lastly, radio telemetry has utility in helping researchers evaluate mortality in endangered species and in developing fisheries, such as the Taimen (*Hucho taimen*) fisheries in Mongolia (Jensen et al. 2009).

Radio telemetry is well-suited for applications in relatively shallow waterbodies when it is necessary to track fish over long distances, especially migratory species, or for waterbodies that are very complex and not suited for fixed station receivers. Questions related to the impacts of catch-and-release angling and commercial fishing on migration success or migratory capabilities of anadromous species like Pacific Salmon and Atlantic Salmon are particularly salient given the value of these species. A stationary radio receiver array established in the Fraser River has helped researchers assess the migration success of Sockeye Salmon (*O. nerka*) captured and released after angling or beach seining (Donaldson et al. 2011) and gill netting (Nguyen et al. 2014). Migratory fate of endangered Fraser River Coho Salmon (*O. kisutch*) was also assessed *via* radio telemetry for fish captured and released as bycatch in a beach seine fishery (Raby et al. 2014) or for fish subjected to simulated angling or gill netting conditions (Chapman et al. 2020). In each study, migratory "success" was achieved when fish were detected at the upstream-most stationary radio receiver. For Atlantic Salmon, researchers used both stationary and active tracking in a series of studies to investigate the impacts of catch-and-release angling on the distance moved during migration (Lennox et al. 2016, 2019) and the ability to ascend natural in-stream barriers (Lennox et al. 2015).

Visual observations

Although tagging fish can be useful for monitoring the post-release behavior of fish in the wild, tagging can be costly for the fish as they are more likely to be stressed because of the tagging procedures and tag burden. For these purposes, and especially for monitoring the short-term (and likely most acute) behavioral responses to capture, visual observations can be used to fill this gap. Within the context of this paper, visual observations will be divided into two sections: visual observations made below the water surface and observations made from above the water surface. This section focuses on studies that observe the post-release behavior of fish in the field (i.e., place of capture). Observations made below the water are either made by snorkelers, or with underwater cameras equipped to underwater robotics (Autonomous Underwater Vehicles; AUV, and ROV), to a swimmer or animal. There is only one study that uses sonar imaging to assess the post-release behavior of schooling fish (Handegard et al. 2017). Cameras are beneficial given their abilities to record, allowing researchers to carefully playback the footage to analyze behavioral data, whereas snorkel surveys are limited to the immediate observation of the fish. Observations made from above the water are typically accomplished by attaching a float to the fish and tracking the float once the fish is released. Surface float studies occur over a short period of time and aim to assess the immediate post-release behavior of fish (<1 h). This method is limited to the amount of time the researcher can spend with each fish during the monitoring period given for the potential of the fish moving away (i.e., losing the visual location of the fish) from the release site.

Below water

Many studies that use snorkel surveys as a method to assess the post-release behavior of fish, use nesting male Black Bass as a model. For example, Kieffer et al. (1995) assessed the influence exhaustion from angling influences the time it takes for male Smallmouth bass to return to their nest. Male Smallmouth Bass that were fought to exhaustion took longer to return to their nest compared to those that were not fought until exhaustion. Similarly, male Largemouth Bass that were air exposed for 2 min and placed in a mock livewell abandoned their nests more than fish that were only air exposed for 2 min. Nest abandonment rate was the lowest for male Largemouth Bass that were not air exposed at all (Diana et al. 2012). Finally, Henry et al. (2009) observed an immediate alteration in the behavior of male Smallmouth Bass that had a lure in their mouth upon release, compared to those that did not have a lure in their mouth. This altered behavior was not present 24 h post-release.

Another method that has been used to observe the post-release behavior of fish involves using a camera to record the behavior of fish underwater. To assess the swimming impairments of Rockfish (*Sebastes spp.*), Hannah and Matteson (2007) equipped a release cage with a camera. They observed that greater capture depths resulted in reduced swimming abilities. Underwater cameras operated by swimmers have been used to assess how the combination of exercise and air exposure influences marine fish (Raby et al. 2018). From the video captured by the swimmer, fish that were exercise and air exposed were in a more vulnerable position post-release, spent more time immobile and took longer to seek refuge. Animal borne imaging (i.e., a camera attached to the animal) was used on Grey Reef Sharks (*Carcharihnus amblyrhynchos*) to determine that hooking trauma led to post-release disorientation and deviation in behavior relative to other Grey Reef Sharks released with cameras (Skomal et al. 2007). On the commercial side of things, the effects of slipping (opening and discharge of fish from purse seine) has been observed with stationary underwater cameras fastened to the commercial vessels to assess the escaping and schooling behavior (Anders et al. 2019). Further, Handegard et al. (2017) used sonar imaging to assess how crowding during the slipping (i.e., releasing unwanted fish from purse seine) process influences the swimming speed and schooling response of Atlantic Mackerel.

Mini Remotely Operated Vehicles (ROV, see Figure 3E), also known as "underwater drones" can be used for these purposes for smaller species (read: slower swimming) to visually monitor post-release behaviors on the short-term (~30 min) and/or over short distances (tether permitting, ~300 m). These mini-ROV are highly maneuverable, usually with 6° of freedom, are typically rated to >100 m depth, often move at sustained speeds up to 3 m s^{-1} and are equipped with high-resolution cameras, which allows them to follow fishes post-release to observe the initial phase of behavioral response to capture. For example, Raoult et al. (2019) used a Bluerobotics BlueROV 2 to examine short-term post-release capture stress for two species of shark (*Cephaloscyllium laticeps* and *Squalus megalops*), by monitoring tail beats as an indicator of condition. In that instance, mini-ROV allowed researchers to determine that different species have differing post-behavior responses to capture in the short-term. Subsequent testing of different mini-ROV configurations have allowed simultaneous monitoring of respiration rates concurrently with tail beats (Raoult, unpublished). Most ROV are also able to be fitted with payloads that can measure various environmental variables of interest (e.g., temperature, depth), while the camera itself can also be used to record habitat and interactions with other species. Where those behavioral or environmental indicators are of interest, mini-ROV can be useful to study post-release behaviors.

Where mini-ROV are tethered to the surface, AUV are not and thus address some of the physical limitations of mini-ROV. These often torpedo-like machines can cover very long distances (>100 km); however, they cannot transmit video to the surface and be "piloted" like ROV. Instead, they can receive intermittent acoustic commands or can be set to track an acoustic signal, such as one from an acoustic tag. This means that if researchers want to study post-release behavior with an AUV, the target animal needs to be tagged with an acoustic tag for the AUV to target (Skomal et al. 2015; Hawkes et al. 2020). These approaches allow AUV to track animals and their behaviors over longer time periods (<3 h) relative to ROV (Gabriel 2018). Most AUV used for these purposes are fairly large and as a result carry payloads including acoustic doppler current profilers, USBL (acoustic GPS) and conductivity-meters: while these have not been explicitly used to understand post-release behaviors to date, they offer the potential to better understand how released animals respond to small-scale environmental variation. Yet, the complexity of AUV does make them expensive relative to mini-ROVs, which may make them difficult to use more broadly. Like ROV, numerous consumer-focused models are currently in development that should make them more accessible for researchers in the near future.

Above water

Studies where fish are observed from above the water without cameras tend to occur in shallow water habitats and all use floats attached to the fish as a visual indication of where the fish are. The only study that occurred in freshwater assessed the impacts that air exposure had on the post-release behavior of Northern Pike during a 1-h monitoring period. Northern Pike released after being air exposed for 300 s spent more time resting and took longer to engage in their first movement compared to Northern Pike that were not air exposed following capture (Arlinghaus et al. 2009). Floats have been fasted to marine fish angled on near-shore flats to assess how angling and fish handling practices influences the post-release predation rate and swimming activity of Bonefish (Figure 3E, Brownscombe et al. 2013; Danylchuk et al. 2007; *Alubla spp.*, Cooke and Philipp 2004; Lennox et al. 2017). Danylchuk et al. (2007) observed that 15% of the Bonefish captured by anglers were predated during the first 20 mins post-release. Results from Lennox et al. (2017) suggest that greater post-release predation occurs when Bonefish are air exposed. Further, Danylchuk et al. (2014) attached floats to juvenile Lemon Sharks (*Negaprion brevirostris*) and monitored their swimming behavior for a 15-minute monitoring period following an angling event.

Aerial drones also known as UAVs (Unoccupied Aerial Vehicles) can also be useful for tracking post-release behaviors in shallow environments, though no studies have explicitly done so. These tools are now commonplace and affordable, and due to their speed can capture rapid movements that may occur post-release, cover broad distances (~km range, aerial restrictions permitting) and track movement for ~30 min. While limited to studies occurring in shallow (<5 m) and clear waters, they have already transformed research of aquatic animals (Figure 3F, Butcher et al. 2021; Raoult et al. 2020) as well as recreational fishing practices (Winkler et al. 2022). Aerial drones can collect high-resolution video of animals (and thus post-release behaviors) and can also collect high-resolution movement data of animals that could also be used to characterize post-release behaviors (sinuosity, mean speed, resting periods, see Raoult et al. 2018) and kinematics (Porter et al. 2020). Since imagery is collected from known altitudes and camera parameters, they can also be used to capture physical measurements and link behaviors to morphological characteristics that may be difficult to assess during the capture of larger animals (e.g., condition, size). Aerial drones could also be used to assess how conspecifics (e.g., Rieucau et al. 2018), other species (e.g., Doan and Kajiura 2020) and humans (Pirotta et al. 2022) interact with released animals.

Challenges of controls and baselines

Throughout these studies, there is generally a lack of true controls, or the baseline behavior, of animals being studies. It is extremely challenging to obtain such data on fish in the wild (Pollock and Pine 2007). Different techniques are used to overcome such challenges and involve tagging or using technology to observe behavior below the surface of the water that can cause unintended consequences to the baseline behavior of individuals.

Many studies report the use of controls, but these controls are generally fish that were captured and presented with a less stressful situation (e.g., no air exposure and minimal handling). Although this can provide important information on how different aspects of the fisheries interaction can influence the post-release behavior of fish, it fails to control for the actual capture and tagging period. Further, there are typically tagging effects associated with studies that use radio and acoustic telemetry or biologging studies. Similarly, there could be some confounding influences on the behavior of fish when being monitored with swimmers, ROV creating alien noise or from AUV casting shadows on the water. Most study lack the fundamental understanding of how the observation technique influences the behavior of the animals without the influence of a fisheries interaction. This is a major shortcoming when assessing the post-release behavior following a fisheries interaction.

An ideal study design for assessing fish following a capture event in the wild should include real baselines or controls that would provide some pre and post capture behavioral data. This could be achieved by capturing fish, tagging them with acoustic transmitters (ideally high-resolution transmitters, e.g., Baktoft et al. 2013) and releasing them to be recaptured (Ferter et al. 2015. It would also be important to allow these fish to recover from the initial capture event and the tagging event prior to being recaptured to avoid for confounding tagging effects. A sub-population of the tagged fish should then be recaptured, subjected to different treatments, including a control treatment, and then released. The other fish should not be captured and used as a proxy for baseline behavior as an indication of normal behavior without being captured (Pollock and Pine 2007). Together, this study design would provide some important pre-capture behavioral data, some baseline behavior (fish that were not caught), controls that were captured and finally those that were manipulated in a desired way (e.g., air exposed). Similarly, this process could occur with internal heart-rate loggers or tri-axial accelerometers. Realistically, this would be more challenging given that these fish would need to be caught three times to recover the biologger.

Research gaps

The study of fish behavior following their capture has evolved, driven by technological advancements and increased recognition and connection between behavioral assessments and capture outcomes (Cooke et al. 2016; Davis 2005). The importance of continuing to develop baselines and reference points for comparing observed behaviors with controls is highlighted by the effectiveness of these methods in research with larger species, where tagging effects are minimized and biologger retention times are greatest. For example, the deployment of PSATs and tri-axial accelerometers on larger elasmobranchs for extended periods has been instrumental in understanding the effects of capture against established baseline behaviors (Binstock et al. 2023). To increase retention times for bony fish, and thus develop baseline behavior estimates, recent developments for pop-off tri-axial accelerometers have been developed for smaller bony fish (see LaRochelle et al. 2023), yet tagging effects still need to be evaluated and reduced (Macaulay et al. 2021). Ultimately, overcoming these challenges to establish comprehensive, optimal behavioral baselines over extended periods requires ongoing technological advancements and the integration of multiple methods (Lennox et al. 2019; Lowerre-Barbieri et al. 2019), such as noninvasive observational techniques.

An additional research gap is framing post-release responses within ecological or fitness-relevant contexts. Although ODBA (see Chhor et al. 2022a for use in post-release studies; LaRochelle et al. 2021) from biologgers serves as useful indicators of likely sublethal effects, pinpointing the precise consequences on organismal fitness remains challenging. Tools such as respirometry and swim tunnels have provided additional insights on the metabolic detriment associated with fisheries interactions (Clark et al. 2012; Pringle et al. 2025; Raby et al. 2015). Yet, the direct relationship between these physiological responses to energetic demands are often not explored. Integrating behavior and physiological responses within a bioenergetic framework (Brownscombe et al. 2022), which examines how fish allocate energy through the equation Energy Consumed = Metabolism + Waste + Growth (Brett and Groves 1979), offers a more complete approach. This framework assumes elevated cardiac function or ODBA as proxies for increased energy expenditure. Therefore, calibrating biologging data to measure energy expenditure in fish using methods like respirometry and swim tunnels may provide a promising avenue for understanding the energetic tradeoffs fish face when subjected to capture and release (Cooke et al. 2016). For example, Watson et al. (2020) estimated the initial energetic costs associated with fight time and fish size during capture, highlighting the energetic cost of fisheries interactions and its impact on growth and reproduction. Although this energetics approach is relatively new and an interesting avenue within the context of post-release behavior research, limitations and assumptions need to be clearly outlined. As this field continues to advance, bridging these knowledge gaps will be important to provide contextual findings for improved conservation strategies and fish handling practices.

Considerations and methods to improve monitoring the behavior of fish

In fisheries with depredation issues, there is a clear connection between behavior and an obvious fitness-related endpoint (short-term mortality). With bonefish, Brownscombe et al. (2013) found less-stressed individuals swam at higher speeds immediately post-release, followed by resting in nearshore tidal creeks, and had lower depredation rates relative to stressed individuals that swam more consistently at moderate speeds into open nearshore areas where predators were present. Juvenile great barracuda also exhibited reduced refuge seeking capacity post-release, due to both physical and cognitive impairment in higher stressed fish (Brownscombe et al. 2014). For fish that are angled from depths and/or colder waters, a quick return to depth/temperature, followed by a period of rest is considered optimal (Ferter et al. 2015). The duration of this rest period, or any abnormal behavior, may also be a relevant endpoint. For example, the time to return to normal activity rhythms, or time to resume foraging can be used as endpoints (Le Pichon et al. 2015). This is presumably related to the magnitude of stress and total costs of recovery. Further, the interaction between multiple environmental stressors can have a compounding effect on post-release behavior. This suggests that when making observations of post-release behavior in the field, researchers should consider how environmental variables like water and air temperatures might be cumulative rather than an independent effect on fish behavior (Figure 2). These examples highlight the need to consider more complex behaviors and ecological interactions to fully understand the cost and benefits of post-release behavior.

There are many technical challenges with measuring post-release behavior, with various technological solutions with benefits and caveats (Table 2). Visual observations are generally limited in temporal and spatial scope and only feasible in certain systems (Raby et al. 2018). Video biologging is insightful but limited to large species (Logan et al. 2022) and poses attachment and recovery challenges. With advances in technology, cameras no longer need to be equipped to animals and therefore do not need to be limited to large animals. Underwater and aerial unoccupied vehicles (i.e., drones) could be useful for obtaining video data on the post-release behavior (Raoult et al. 2019). Although drones are limited to use in relatively clear waters, advances in live imaging sonars allow visual data such as fish movement and size to be assessed in completely turbid environments (Bennett et al. 2021; McSpadden et al. 2024). Miniaturization of imaging sonars also enables them to be mounted to mini-ROVs and used instead of cameras, meaning mini-ROV could be used in turbid environments to visually assess behavior similarly to other work (Raoult et al. 2019). Moreover, remote field-based monitoring methods outlined above are relatively novel in aquatic sciences, and a key knowledge gap is how these approaches might affect the behaviors of the organisms they are trying to observe. For example, some data suggests aerial drones have little impact on fishes (e.g. Bourke et al. 2023) but any impacts are likely to be species and location dependent. All these vehicles use electric motors to propel them, which produce electrical fields as well as noise, and have various visual footprints (i.e., shadows) that may be perceived as threatening by target species. Consistent technological advancements in this area mean that new capabilities continue to become available to researchers and the quality of data will only improve into the future.

Attachment and retrieval challenges are inherent to all biologging, including tri-axial accelerometers, which provide detailed insights into post-release behavior, but most applications to date use a tether for retrieval and monitor fish for less than 1 h (e.g., Holder et al. 2020; LaRochelle et al. 2021). More recently, pop-off biologging packages equipped with a biologger (tri-axial acceleration, temperature, pressure, and magnetometer sensors) and a radio transmitter have been used to monitor the short-term post-release behavior for up to 12 h (LaRochelle et al. 2023). Longer-term monitoring is most often achieved with acoustic telemetry, which often requires the complications of surgical implantation to reduce tag burden and injury (with exceptions Jepsen et al. 2015). This approach is one of the few that can examine longer term recovery to normal behavioral rhythms (e.g., Le Pichon et al. 2015; Wilson et al. 2017). Yet, the resolution of telemetry accelerometers currently limits the capacity to measure more detailed elements of behavior such as feeding. Integration of algorithms

Table 2. This table shows the different monitoring methods that can be used to assess different behavioral endpoints.

Endpoint	Monitoring method	Example
Swimming activity		
	Biologgers	LaRochelle et al. (2023)
	Acoustic telemetry	McLean et al. (2019)
	Underwater camera	Raby et al. (2018)
	Aerial drone	Raoult et al. (2018)
	Underwater drone	Raoult et al. (2019)
	Surface floats	Danylchuk et al. (2007)
	Swim tunnel	Bieber et al. (2022)
Distance		
	Ultrasonic tags	Cooke and Philipp (2004)
	Radio tags	Bunt et al. (2002)
Body orientation		
	Biologgers	Madden et al. (2024)
	Underwater camera	Hannah and Matteson (2007)
Water temperature selection	Biologgers	LaRochelle et al. (2021)
Depth selection		
	Biologgers	Madden et al. (2024)
	Acoustic telemetry	Eberts et al. (2018)
Maze completion		
	Above water observation	Hlina et al. (2021)
Nest abandonment		
	Snorkel survey	Diana et al. (2012)
Migration		
	Radio telemetry	Donaldson et al. (2011)
Predation		
	Surface floats	Lennox et al. (2017)
Seeking refuge		
	Above water visual observation	Brownscombe et al. (2014)
Seeking schools		
	Underwater camera	Anders et al. (2019)
	Sonar imaging	Handegard et al. (2017)

There is also an example provided for previous studies that have used a given monitoring method to assess a certain endpoint.

from higher resolution accelerometry into transmitter technology is an important avenue for longer term post-release behavior tracking, along with other sensors such as heart rate and predation sensors. Beyond the use of transmitter tags, pop-off biologging packages that record fine-scale behavior (acceleration, temperature, pressure) for a longer period could prove to be beneficial for filling the void in knowledge between the observed behavior and the ecological relevance.

Conclusion

There are several different endpoints (see Table 2) that can be assessed when observing the post-release behavior of fish after a fisheries interaction and majority of these endpoints can be observed with multiple different techniques (Table 1). There is no single method that is better than another and they all have their time in place. Scientists that want to assess the post-release behavior of fish should select a monitoring method strategically based on the target species, the environment, and the desired monitoring duration (Tables 1 and 2).

Advances in technology has significantly improved the abilities scientist to track and observe animals in the wild, yet there are still limitations to each method. One important thing to note about observing the post-release behavior of fish, is the need to use multiple different observing methods to truly understand the natural behavior of the fish without confounding disturbances of the observing method (e.g., a combination of acoustic tagging and ROV). It is becoming apparent there is a need for a better understanding of the baseline behaviors of fish across different monitoring methods (e.g., pop-off tag, ROV, radio tag). Having the baseline behavior of fish across the different monitoring methods would allow us to accurately decipher the deviations in behavior that occur due to the capture event and the deviations in behavior that occur because of the monitoring method. Further, studies that monitor the post-release behavior of fish after a fisheries capture must contextualize their findings within the ecological aspects of the system (Figure 2). Fish behavior can vary significantly based on factors that humans induce on them (Figure 1); however, it is important to recognize the ecological context when conducting post-release behavioral monitoring.

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ORCID

Luc LaRochelle http://orcid.org/0000-0002-7058-4852

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